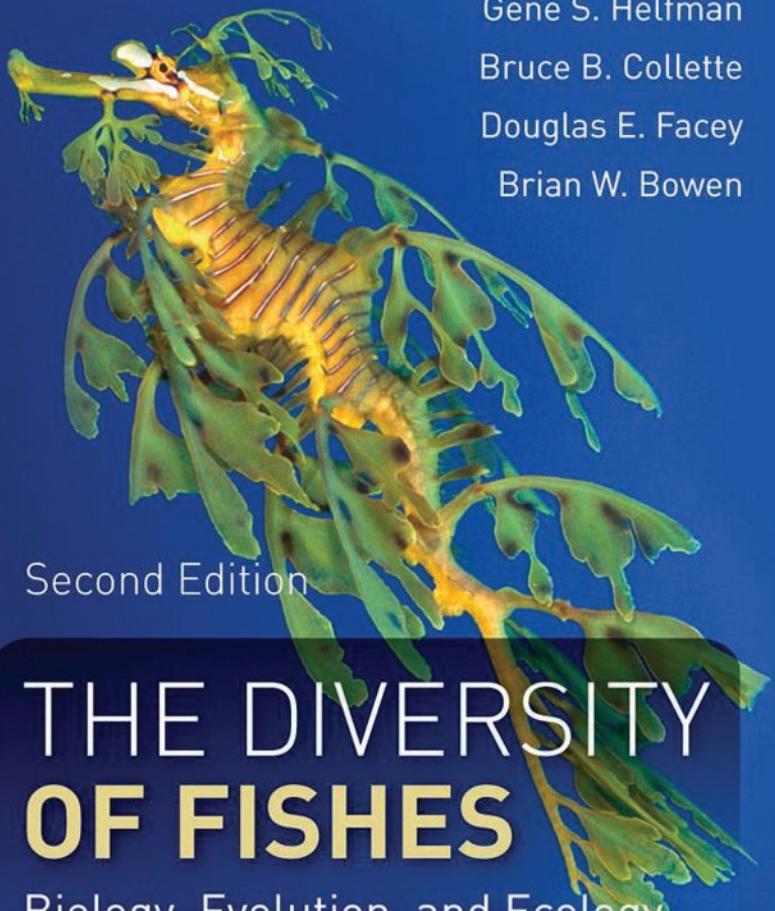
Gene S. Helfman
Bruce B. Collette
Douglas E. Facey
Brian W. Bowen



Second Edition

THE DIVERSITY OF FISHES

Biology, Evolution, and Ecology

WILEY-BLACKWELL

THE DIVERSITY OF FISHES

Dedications:

To our parents, for their encouragement of our nascent interest in things biological;

To our wives – Judy, Sara, Janice, and RuthEllen – for their patience and understanding during the production of this volume;

And to students and lovers of fishes for their efforts toward preserving biodiversity for future generations.

Front cover photo:

A Leafy Sea Dragon, *Phycodurus eques*, South Australia. Well camouflaged in their natural, heavily vegetated habitat, Leafy Sea Dragons are closely related to seahorses (Gasterosteiformes: Syngnathidae). "Leafies" are protected by Australian and international law because of their limited distribution, rarity, and popularity in the aquarium trade. Legal collection is highly regulated, limited to one "pregnant" male per year. See Chapters 15, 21, and 26. Photo by D. Hall, www.seaphotos.com.

Back cover photos (from top to bottom):

A school of Blackfin Barracuda, *Sphyraena qenie* (Perciformes, Sphyraenidae). Most of the 21 species of barracuda occur in schools, highlighting the observation that predatory as well as prey fishes form aggregations (Chapters 19, 20, 22). Blackfins grow to about 1 m length, display the silvery coloration typical of water column dwellers, and are frequently encountered by divers around Indo-Pacific reefs. Barracudas are fast-start predators (Chapter 8), and the pan-tropical Great Barracuda, *Sphyraena barracuda*, frequently causes ciguatera fish poisoning among humans (Chapter 25).

Longhorn Cowfish, *Lactoria cornuta* (Tetraodontiformes: Ostraciidae), Papua New Guinea. Slow moving and seemingly awkwardly shaped, the pattern of flattened, curved, and angular trunk areas made possible by the rigid dermal covering provides remarkable lift and stability (Chapter 8).

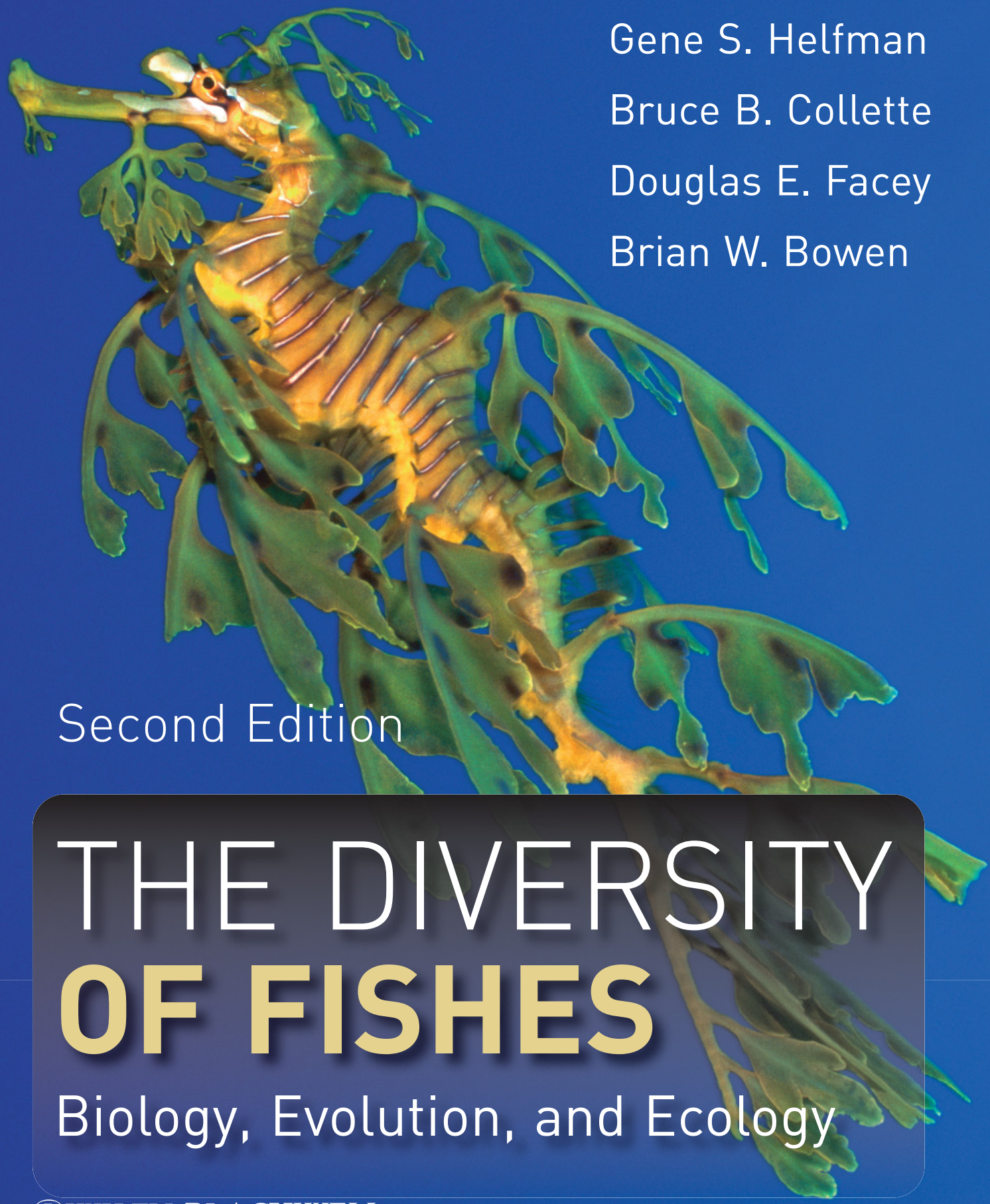
A Silvertip Shark, *Carcharhinus albimarginatus* (Carcharhiniformes: Carcharhinidae), with a Sharksucker (*Echeneis naucrates*, Perciformes: Echeneidae) attached. This symbiotic relationship between an elasmobranch (Chapter 12) and an advanced acanthopterygian teleost (Chapter 15) probably benefits both, the Sharksucker scavenging scraps from the shark's meals and in turn picking parasitic copepods off the shark. Remoras also attach to whales, turtles, billfishes, rays, and an occasional diver. Remoras generate sufficient suction to hang on even at high speeds via a highly modified first dorsal fin.

A recently discovered 10 cm long Indonesian antennariid, nicknamed the Psychedelic Frogfish (Lophiiformes: Antennariidae) (Chapters 14, 18). Among its atypical traits are its shallow water habitat, a lack of an illicial lure, jet propulsion, and a bouncing method of movement, and its practice of hiding in holes, not to mention the spectacular head and body coloration.

A mating pair of Mandarinfish, *Synchiropus splendidus* (Perciformes: Callionymidae), Indonesia. These small (6 cm), secretive dragonets live among coral branches or rubble, and usually emerge just after sunset to mate. Recently extruded eggs can be seen just below the pair.

Lionfish, *Pterois volitans* (Scorpaeniformes: Pteroidae), are native to the Indo-Pacific region. They have been introduced along the southeastern coast of the USA and the Bahamas, apparently due to aquarium releases. In their native habitats they seldom reach high densities but have undergone a population explosion on Bahamian reefs. Atlantic reef fishes are naive to lionfish predatory tactics, and predation rates by lionfish are high.

Photos by D. Hall, www.seaphotos.com.



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Brief contents

BRIEF CONTENTS

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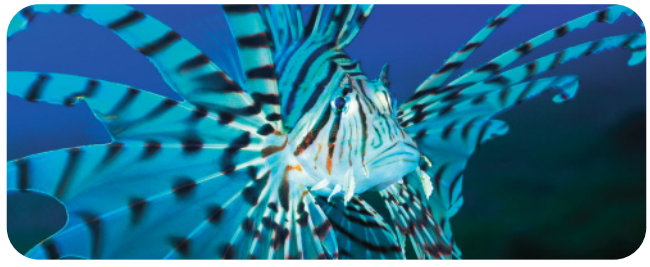


Preface to the second edition

PREFACE TO THE SECOND

The first edition of *The diversity of fishes* was successful beyond our wildest dreams. We have received constant and mostly positive feedback from readers, including much constructive criticism, all of which convinces us that the approach we have taken is satisfactory to ichthyological students, teachers, and researchers. Wiley-Blackwell has validated that impression: by their calculations, *The diversity of fishes* is the most widely adopted ichthyology textbook in the world.

However, ichthyology is an active science, and a great deal of growth has occurred since this book was first published in 1997. Updates and improvements are justified by active and exciting research in all relevant areas, including a wealth of new discoveries (e.g., a second coelacanth species, 33 more megamouth specimens, several new record tiniest fishes, and exciting fossil discoveries including some that push back the origin of fishes many million years and another involving a missing link between fishes and amphibians), application of new technologies (molecular genetics, transgenic fish), and increased emphasis on conservation issues (e.g., Helfman 2007). Websites on fishes were essentially nonexistent when the first edition was being produced; websites now dominate as an instant source of information. Many of the volumes we used as primary references have themselves been revised. Reflective of these changes, and of shortcomings in the first edition, is the addition of a new chapter and author. Genetics received insufficient coverage, a gross omission that has been corrected by Brian Bowen's contribution of a chapter devoted to that subject and by his suggested improvements to many other chapters. Brian's contributions were aided by extensive and constructive comments from Matthew Craig, Daryl Parkyn, Luiz Rocha, and Robert Toonen. He is especially grateful to John Avise, Robert Chapman, and John Musick for their guidance and mentorship during his professional career, and most of all to his wife, RuthEllen, for her forbearance and support.

Among the advances made in the decade following our initial publication, a great deal has been discovered about the phylogeny of major groups, especially among jawless fishes, sarcopterygians, early actinopterygians, and holocephalans. In almost all taxa, the fossil record has expanded, prompting reanalysis and sometimes culminating in conflicting interpretations of new findings. A basic textbook is not the appropriate place to attempt to summarize or critique the arguments, opinions, and interpretations. We have decided to accept one general compilation and synthesis. As in the 1997 edition, where we adopted with little adjustment the conclusions and terminology of Nelson (1996), we here follow Nelson (2006), who reviews the recent discoveries and clearly presents and assesses the many alternative hypotheses about most groups. Instructors who used our first edition will have to join us in learning and disseminating many changed names as well as rearrangements among taxa within and among phylogenies, especially Chapters 11–13. Science is continually self-correcting. We should applaud the advances and resist the temptation to comfortably retain familiar names and concepts that have been modified in light of improved knowledge.

Also, we have now adopted the accepted practice of capitalizing common names.

Acknowledgments

Thanks especially to the many students and professionals who corrected errors in the first edition (J. Andrew, A. Clarke, D. Hall, G.D. Johnson, H. Mattingly, P. Motta, L.R. Parenti, C. Reynolds, C. Scharpf, E. Schultz, M.L.J. Stiassny, and S. Vives proved particularly alert editors). Their suggestions alone led to many changes, to which we have added literally hundreds of new examples, facts, and updates. Wiley-Blackwell has provided a website for this second edition, www.wiley.com/go/helfman, through which we hope to again correct and update the information provided here. We encourage any and all to inform us wherever they encounter real or apparent errors of any kind in this text. Please write directly to us. Chief responsibilities fell on GSH for Chapters 1, 8–15, and 18–26 (genehelfman@gmail.com); on BBC for Chapters 2–4 and 16 (collettb@si.edu); on DEF for Chapters 5–7 (dfacey@smcvt.edu), and on BWB for Chapter 17 (bbowen@hawaii.edu). Once again and more than anything, we want to get it right.

Preface to the first edition

PREFACE TO THE FIRST E

Two types of people are likely to pick up this book, those with an interest in fishes and those with a fascination for fishes. This book is written by the latter, directed at the former, with the intent of turning interest into fascination.

Our two major themes are adaptation and diversity. These themes recur throughout the chapters. Wherever possible, we have attempted to understand the adaptive significance of an anatomical, physiological, ecological, or behavioral trait, pointing out how the trait affects an individual's probability of surviving and reproducing. Our focus on diversity has prompted us to provide numerous lists of species that display particular traits, emphasizing the parallel evolution that has occurred repeatedly in the history of fishes, as different lineages exposed to similar selection pressures have converged on similar adaptations.

The intended audience of this book is the senior undergraduate or graduate student taking an introductory course in ichthyology, although we also hope that the more seasoned professional will find it a useful review and reference for many topics. We have written this book assuming that the student has had an introductory course in comparative anatomy of the vertebrates, with at least background knowledge in the workings of evolution. To understand ichthyology, or any natural science, a person should have a solid foundation in evolutionary theory. This book is not the place to review much more than some basic ideas about how evolutionary processes operate and their application to fishes, and we strongly encourage all students to take a course in evolution. Although a good comparative anatomy or evolution course will have treated fish anatomy and systematics at some length, we go into considerable detail in our introductory chapters on the anatomy and systematics of fishes. The nomenclature introduced in these early chapters is critical to understanding much of the information presented later in the book; extra care spent reading those chapters will reduce confusion about terminology used in most other chapters.

More than 27,000 species of fishes are alive at present. Students at the introductory level are likely to be overwhelmed by the diversity of taxa and of unfamiliar names. To facilitate this introduction, we have been selectively inconsistent in our use of scientific versus common names. Some common names are likely to be familiar to most readers, such as salmons, minnows, tunas, and freshwater sunfishes; for these and many others, we have used the common family designation freely. For other, less familiar groups (e.g., Sundaland noodlefishes, trahiras, morwongs), we are as likely to use scientific as common names. Many fish families have no common English name and for these we use the Anglicized scientific designation (e.g., cichlids, galaxiids, labrisomids). In all cases, the first time a family is encountered in a chapter we give the scientific family name in parentheses after the common name. Both scientific and common designations for families are also listed in the index. As per an accepted convention, where lists of families occur, taxa are listed in phylogenetic order. We follow Nelson et al. (1994, now updated) on names of North American fishes and Robins et al. (1991, also now updated) on classification and names of families and of higher taxa. In the few instances where we disagree with these sources, we have tried to explain our rationale.

Any textbook is a compilation of facts. Every statement of fact results from the research efforts of usually several people, often over several years. Students often lose sight of the origins of this information, namely the effort that has gone into verifying an observation, repeating an experiment, or making the countless measurements necessary to establish the validity of a fact. An entire dissertation, representing 3–5 or more years of intensive work, may be distilled down to a single sentence in a textbook. It is our hope that as you read through the chapters in this book, you will not only appreciate the diversity of adaptation in fishes, but also consider the many ichthyologists who have put their fascination to practical use to obtain the facts and ideas we have compiled here. To acknowledge these efforts, and because it is just good scientific practice, we have gone to considerable lengths to cite the sources of our information in the text, which correspond to the entries in the lengthy bibliography at the end of the book. This will make it possible for the reader to go to a cited work and learn the details of a study that we can only treat superficially. Additionally, the end of each chapter contains a list of supplemental readings, including books or longer review articles that can provide an interested reader with a much greater understanding of the subjects covered in the chapter.

This book is not designed as a text for a course in fisheries science. It contains relatively little material directly relevant to such applied aspects of ichthyology as commercial or sport fisheries or aquaculture; several good text and reference books deal specifically with those topics (for starters, see the edited volumes by Lackey & Nielsen 1980, Nielsen & Johnson 1983, Schreck & Moyle 1990, and Kohler & Hubert 1993). We recognize however that many students in a college-level ichthyology class are training to become professionals in those or related disciplines. Our objectives here are to provide such readers with enough information on the general aspects of ichthyology to make informed, biologically sound judgments and decisions, and to gain a larger appreciation of the diversity of fishes beyond the relatively small number of species with which fisheries professionals often deal.

Adaptations versus adaptationists

Our emphasis throughout this text on evolved traits and the selection pressures responsible for them does not mean that we view every characteristic of a fish as an adaptation. It is important to realize that a living animal is the result of past evolutionary events, and that animals will be adapted to current environmental forces only if those forces are similar to what has happened to the individual's ancestors in the past. Such phylogenetic constraints arise from the long-term history of a species. Tunas are masters of the open sea as a result of a streamlined morphology, large locomotory muscle mass connected via efficient tendons to fused tail bones, and highly efficient respiratory and circulatory systems. But they rely on water flowing passively into their mouths and over their gills to breathe and have reduced the branchiostegal bones in the throat region that help pump water over their gills. Tunas are, therefore, constrained phylogenetically from using habitats or foraging modes that require them to stop and hover, because by ceasing swimming they would also cease breathing.

Animals are also imperfect because characteristics that have evolved in response to one set of selective pressures often create problems with respect to other pressures. Everything in life involves a trade-off, another recurring theme in this text. The elongate pectoral fins ("wings") of a flyingfish allow the animal to glide over the water's surface faster than it can swim through the much denser water medium. However, the added surface area of the enlarged fins creates drag when the fish is swimming. This drag increases costs in terms of a need for larger muscles to push the body through the water, requiring greater food intake, time spent feeding, etc. The final mix of traits evolved in a species represents a compromise involving often-conflicting demands placed on an organism. Because of phylogenetic constraints, trade-offs, and other factors, some fishes and some characteristics of fishes appear to be and are poorly adapted. Our emphasis in this book is on traits for which function has been adequately demonstrated or appears obvious. Skepticism about apparent adaptations can only lead to greater understanding of the complexities of the evolutionary process. We encourage and try to practice such skepticism.

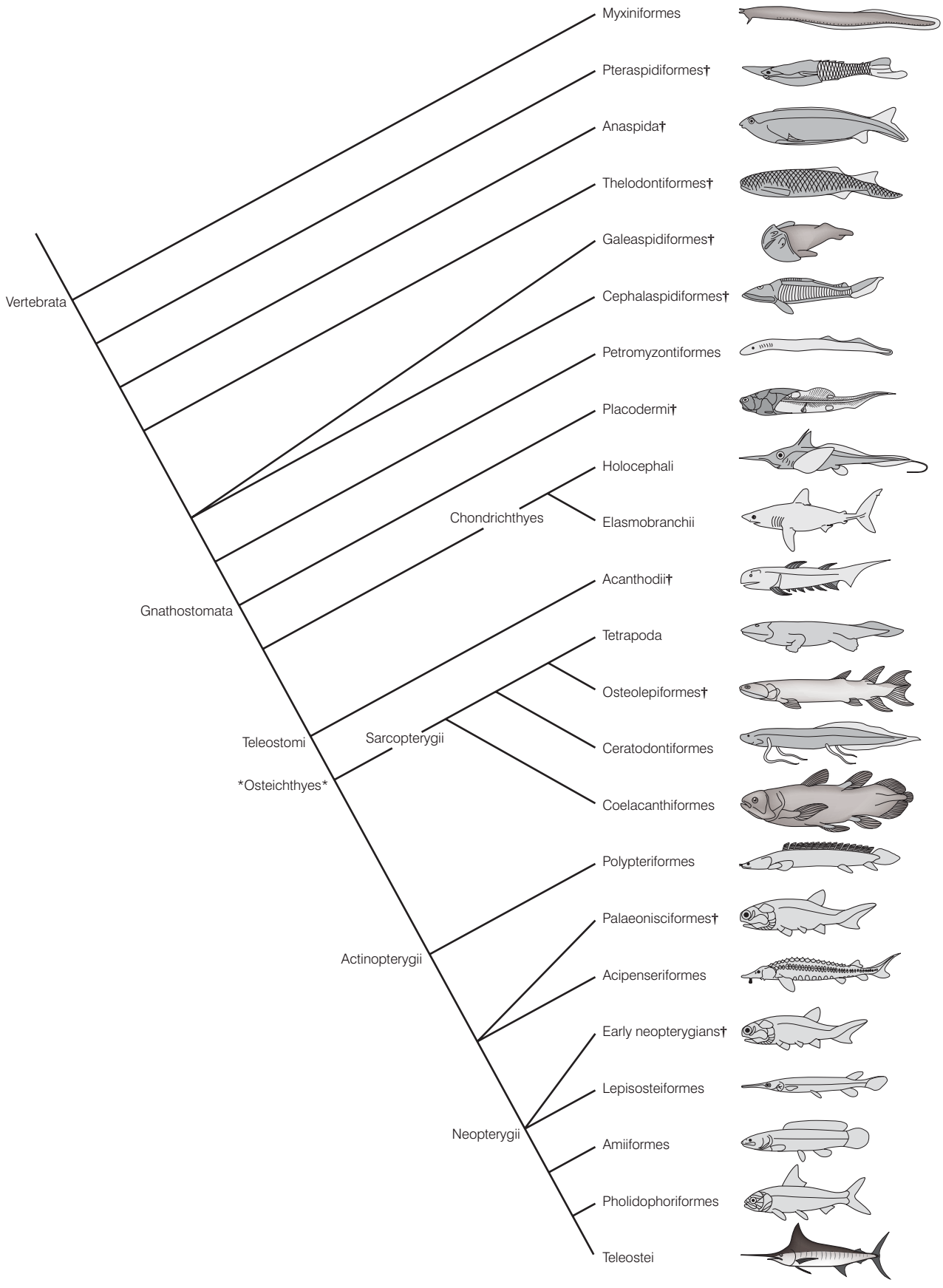
Acknowledgments

This book results from effort expended and information acquired over most of our professional lives. Each of us has been tutored, coaxed, aided, and instructed by many fellow scientists. A few people have been particularly instrumental in facilitating our careers as ichthyologists and deserve special thanks: George Barlow, John Heiser, Bill McFarland, and Jack Randall for GSH; Ed Raney, Bob Gibbs, Ernie Lachner, and Dan Cohen for BBC; Gary Grossman and George LaBar for DEF. The help of many others is acknowledged and deeply appreciated, although they go unmentioned here.

Specific aid in the production of this book has come from an additional host of colleagues. Students in our ichthyology classes have written term papers that served as literature surveys for many of the topics treated here; they have also critiqued drafts of chapters. Many colleagues have answered questions, commented on chapters and chapter sections, loaned photographs, and sent us reprints, requested and volunteered. Singling out a few who have been particularly helpful, we thank C. Barbour, J. Beets, W. Bemis, T. Berra, J. Briggs, E. Brothers, S. Concelman, J. Crim, D. Evans, S. Hales, B. Hall, C. Jeffrey, D. Johnson, G. Lauder, C. Lowe, D. Mann, D. Martin, A. McCune, J. Meyer, J. Miller, J. Moore, L. Parenti, L. Privitera, T. Targett, B. Thompson, P. Wainwright, J. Webb, S. Weitzman, D. Winkelman, J. Willis, and G. Wippelhauser. Joe Nelson provided us logistic aid and an early draft of the classification incorporated into the 3rd edition of his indispensable *Fishes of the world*. Often animated and frequently heated discussions with ichthyological colleagues at annual meetings of the American Society of Ichthyologists and Herpetologists have been invaluable for separating fact from conventional wisdom. Gretchen Hummelman and Natasha Rajack labored long and hard over copyright permissions and many other details. Academic departmental administrators gave us encouragement and made funds and personnel available at several crucial junctures during production. At the University of Georgia we thank J. Willis (Zoology), R. Damian (Cell biology), and G. Barrett, R. Carroll, and R. Pulliam (Ecology) for their support. At St. Michael's College, we thank D. Bean (Biology). The personnel of Blackwell Science, especially Heather Garrison, Jane

Humphreys, Debra Lance, Simon Rallison, Jennifer Rosenblum, and Gail Segal, exhibited patience and professionalism at all stages of production.

Finally, a note on the accuracy of the information contained in this text. As Nelson Hairston Sr. has so aptly pointed out, "Statements in textbooks develop a life independent of their validity." We have gone to considerable lengths to get our facts straight, or to admit where uncertainties lie. We accept full responsibility for the inevitable errors that do appear, and we welcome hearing about them. Please write directly to us with any corrections or comments. Chief responsibilities fell on GSH for Chapters 1, 8–15, and 17–25; on BBC for Chapters 2–4 and 16; and on DEF for Chapters 5–7.



Hypothesized phylogenetic relationships among living and extinct (†) fish groups. Mostly after Nelson (2006). (See Chapters 11, 13.)

Figure I *(opposite)*

A school of Blackfin Barracuda, *Sphyraena qenie* (Perciformes, Sphyraenidae). Most of the 21 species of barracuda occur in schools, highlighting the observation that predatory as well as prey fishes form aggregations (Chapters 19, 20, 22). Blackfins grow to about 1 m length, display the silvery coloration typical of water column dwellers, and are frequently encountered by divers around Indo-Pacific reefs. Barracudas are fast-start predators (Chapter 8), and the pantropical Great Barracuda, *S. barracuda*, frequently causes ciguatera fish poisoning among humans (Chapter 25). Photo by D. Hall, www.seaphotos.com.

PART I
Introduction

Chapter 1

The science of ichthyology

Chapter contents

CHAPTER CONTENTS

Fishes make up more than half of the 55,000 species of living vertebrates. Along with this remarkable taxonomic diversity comes an equally impressive habitat diversity. Today, and in the past, fishes have occupied nearly all major aquatic habitats, from lakes and polar oceans that are ice-covered through much of the year, to tropical swamps, temporary ponds, intertidal pools, ocean depths, and all the more benign environments that lie within these various extremes. Fishes have been ecological dominants in aquatic habitats through much of the history of complex life. To colonize and thrive in such a variety of environments, fishes have evolved obvious and striking anatomical, physiological, behavioral, and ecological adaptations. Students of evolution in general and of fish evolution in particular are aided by an extensive fossil record dating back more than 500 million years. All told, fishes are excellent showcases of the evolutionary process, exemplifying the intimate relationship between form and function, between habitat and adaptation. Adaptation and diversity are interwoven throughout the evolutionary history of fishes and are a recurring theme throughout this book.

What is a fish?

It may in fact be unrealistic to attempt to define a "fish", given the diversity of adaptation that characterizes the thousands of species alive today, each with a unique evolutionary history going back millions of years and including many more species. Recognizing this diversity, one can define a fish as "a poikilothermic, aquatic chordate with appendages (when present) developed as fins, whose chief respiratory organs are gills and whose body is usually covered with scales" (Berra 2001, p. xx), or more simply, a fish is an aquatic vertebrate with gills and with limbs in the shape of fins (Nelson 2006). To most biologists, the term "fish" is not so much a taxonomic ranking as a convenient description for aquatic organisms as diverse as hagfishes, lampreys, sharks, rays, lungfishes, sturgeons, gars, and advanced ray-finned fishes.

Definitions are dangerous, since exceptions are often viewed as falsifications of the statement (see, again, Berra 2001). Exceptions to the definitions above do not negate them but instead give clues to adaptations arising from particularly powerful selection pressures. Hence loss of scales and fins in many eel-shaped fishes tell us something about the normal function of these structures and their inappropriateness in benthic fishes with an elongate body. Similarly, homeothermy in tunas and lamnid sharks instructs us about the metabolic requirements of fast-moving predators in open sea environments, and lungs or other accessory breathing structures in lungfishes, gars, African catfishes, and gouramis indicate periodic environmental conditions where gills are inefficient for transferring water-dissolved oxygen to the blood. Deviation from "normal" in these and other exceptions are part of the lesson that fishes have to teach us about evolutionary processes.

The diversity of fishes

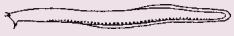
Numerically, valid scientific descriptions exist for approximately 27,977 living species of fishes in 515 families and 62 orders (Nelson 2006; W. Eschmeyer pers. comm.; Table 1.1) (note: "**fish**" is singular and plural for a single species, "**fishes**" is singular and plural for more than one species; see Fig. 1.1). Of these, 108 are jawless fishes (70 hagfishes and 38 lampreys); 970 are cartilaginous sharks (403), skates

Table 1.1

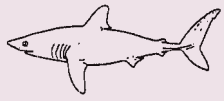
The diversity of living fishes. Below is a brief listing of higher taxonomic categories of living fishes, in phylogenetic order. This list is meant as an introduction to major groups of living fishes as they will be discussed in the initial two sections of this book. Many intermediate taxonomic levels, such as infraclasses, subdivisions, and series, are not presented here; they will be detailed when the actual groups are discussed in Part III. Only a few representatives of interesting or diverse groups are listed. Taxa and illustrations from Nelson (2006).

Subphylum Cephalochordata – lancelets

Subphylum Craniata
- Superclass Myxinomorphi
  - Class Myxini – hagfishes



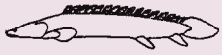
- Superclass Petromyzontomorphi
  - Class Petromyzontida – lampreys
- Superclass Gnathostomata – jawed fishes
  - Class Chondrichthyes – cartilaginous fishes
    - Subclass Elasmobranchii – sharklike fishes
    - Subclass Holocephali – chimaeras



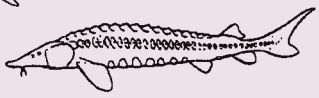
- Grade Teleostomi – bony fishes
  - Class Sarcopterygii – lobe-finned fishes
    - Subclass Coelacanthimorpha – coelacanths

    - Subclass Dipnoi – lungfishes

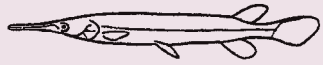
  - Class Actinopterygii – ray-finned fishes
    - Subclass Cladistia – bichirs



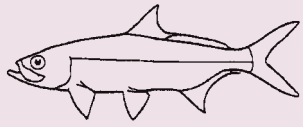
    - Subclass Chondrostei – paddlefishes, sturgeons



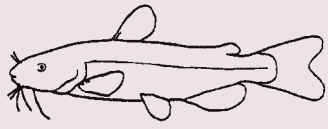
    - Subclass Neopterygii – modern bony fishes, including gars and bowfin[a]



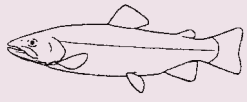
      - Division Teleostei
        - Subdivision Osteoglossomorpha – bonytongues



        - Subdivision Elopomorpha – tarpons, bonefishes, eels
        - Subdivision Otocephala
          - Superorder Clupeomorpha – herrings
          - Superorder Ostariophysi – minnows, suckers, characins, loaches, catfishes

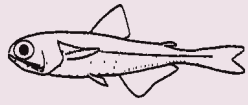


        - Subdivision Euteleostei – advanced bony fishes
          - Superorder Protacanthopterygii – pickerels, smelts, salmons
            [Order Esociformes – pikes, mudminnows][b]



          - Superorder Stenopterygii – bristlemouths, marine hatchetfishes, dragonfishes

          - Superorder Ateleopodomorpha – jellynose fishes
          - Superorder Cyclosquamata – greeneyes, lizardfishes
          - Superorder Scopelomorpha – lanternfishes
          - Superorder Lampriomorpha – opahs, oarfishes
          - Superorder Polymixiomorpha – beardfishes



          - Superorder Paracanthopterygii – troutperches, cods, toadfishes, anglerfishes

          - Superorder Acanthopterygii – spiny rayed fishes: mullets, silversides, killifishes, squirrelfishes, sticklebacks, scorpionfishes, basses, perches, tunas, flatfishes, pufferfishes, and many others

[a] Gars and Bowfin are sometimes separated out as holosteans, a sister group to the teleosts (see Chapter 13).
[b] The esociform pikes and mudminnows are not as yet assigned to a superorder (see Chapter 14).

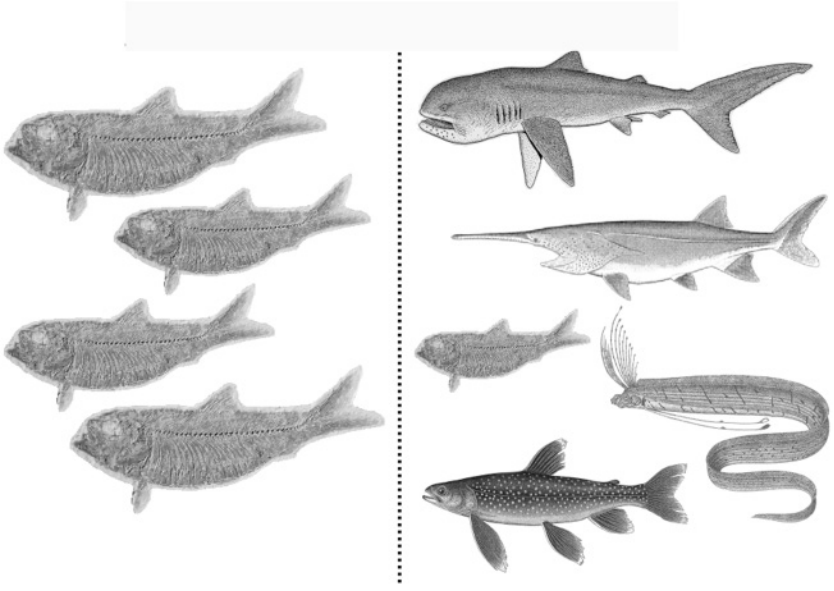


Figure 1.1
Fish versus fishes. By convention, "fish" refers to one or more individuals of a single species. "Fishes" is used when discussing more than one species, regardless of the number of individuals involved. Megamouth, paddlefish, and char drawings courtesy of P. Vecsei; oarfish drawing courtesy of T. Roberts.

and rays (534), and chimaeras (33); and the remaining 26,000+ species are bony fishes; many others remain to be formally described. When broken down by major habitats, 41% of species live in fresh water, 58% in sea water, and 1% move between fresh water and the sea during their life cycles (Cohen 1970). Geographically, the highest diversities are found in the tropics. The Indo-West Pacific area that includes the western Pacific and Indian oceans and the Red Sea has the highest diversity for a marine area, whereas South America, Africa, and Southeast Asia, in that order, contain the most freshwater fishes (Berra 2001; Lévêque et al. 2008). Fishes occupy essentially all aquatic habitats that have liquid water throughout the year, including thermal and alkaline springs, hypersaline lakes, sunless caves, anoxic swamps, temporary ponds, torrential rivers, wave-swept coasts, and high-altitude and high-latitude environments. The altitudinal record is set by some nemacheiline river loaches that inhabit Tibetan hot springs at elevations of 5200 m. The record for unheated waters is Lake Titicaca in northern South America, where pupfishes live at an altitude of 3812 m. The deepest living fishes are cusk-eels, which occur 8000 m down in the deep sea.

Variation in body length ranges more than 1000-fold. The world's smallest fishes – and vertebrates – mature at around 7–8 mm and include an Indonesian minnow, *Paedocypris progenetica*, and two gobioids, *Trimmatom nanus* from the Indian Ocean and *Schindleria brevipinguis* from Australia's Great Barrier Reef (parasitic males of a deepsea anglerfish *Photocorynus spiniceps* mature at 6.2 mm, although females are 10 times that length). The world's longest cartilaginous fish is the 12 m long (or longer) Whale Shark *Rhincodon typus*, whereas the longest bony fish is the 8 m long (or longer) Oarfish *Regalecus glesne*. Body masses top out at 34,000 kg for whale sharks and 2300 kg for the Ocean Sunfish *Mola mola*. Diversity in form includes relatively fishlike shapes such as minnows, trouts, perches, basses, and tunas, but also such unexpected shapes as boxlike trunkfishes, elongate eels and catfishes, globose lumpsuckers and frogfishes, rectangular ocean sunfishes, question-mark-shaped seahorses, and flattened and circular flatfishes and batfishes, ignoring the exceptionally bizarre fishes of the deep sea.

Superlative fishes

A large part of ichthyology's fascination is the spectacular and unusual nature of the subject matter (see Lundberg et al. 2000). As a few examples:

- Coelacanths, an offshoot of the lineage that gave rise to the amphibians, were thought to have died out with the dinosaurs at the end of the Cretaceous, 65 million years ago. However, in 1938, fishermen in South Africa trawled up a very live Coelacanth. This fortuitous capture of a living fossil not only rekindled debates about the evolution of higher vertebrates, but underscored the international and political nature of conservation efforts (see Chapter 13).
- Lungfishes can live in a state of dry "suspended animation" for up to 4 years, becoming dormant when their ponds dry up and reviving quickly when immersed in water (see Chapters 5, 13).
- Antarctic fishes live in water that is colder than the freezing point of their blood. The fishes keep from freezing by avoiding free ice and because their blood contains antifreeze proteins that depress their blood's

freezing point to –2°C. Some Antarctic fishes have no hemoglobin (see Chapter 18).

- Deepsea fishes include many forms that can swallow prey larger than themselves. Some deepsea anglerfishes are characterized by females that are 10 times larger than males, the males existing as small parasites permanently fused to the side of the female, living off her blood stream (see Chapter 18).
- Fishes grow throughout their lives, changing their ecological role several times. In some fishes, differences between larvae and adults are so pronounced that many larvae were originally described as entirely different taxa (see Chapter 9).
- Fishes have maximum life spans of as little as 10 weeks (African killifishes and Great Barrier Reef pygmy gobies) and as long as 150 years (sturgeons and scorpaenid rockfishes). Some short-lived species are annuals, surviving drought as eggs which hatch with the advent of rains. Longer lived species may not begin reproducing until they are 20 years old, and then only at 5+ year intervals (see Chapter 10).
- Gender change is common among fishes. Some species are simultaneously male and female, whereas others change from male to female, or from female to male (see Chapters 10, 21).
- Fishes engage in parental care that ranges from simple nest guarding to mouth brooding to the production of external or internal body substances upon which young feed. Many sharks have a placental structure as complex as any found in mammals. Egg-laying fishes may construct nests by themselves, whereas some species deposit eggs in the siphon of living clams, on the undersides of leaves of terrestrial plants, or in the nests of other fishes (see Chapters 12, 21).
- Fishes are unique among organisms with respect to the use of bioelectricity. Many fishes can detect biologically meaningful, minute quantities of electricity, which they use to find prey, competitors, or predators and for navigation. Some groups have converged on the ability to produce an electrical field and obtain information about their surroundings from disturbances to the field, whereas others produce large amounts of high-voltage electricity to deter predators or stun prey (see Chapters 6, 19, 20).
- Fishes are unique among vertebrates in their ability to produce light; this ability has evolved independently in different lineages and can be either autogenic (produced by the fish itself) or symbiotic (produced by bacteria living on or in the fish) (see Chapter 18).
- Although classically thought of as cold-blooded, some pelagic sharks and tunas maintain body temperatures warmer than their surroundings and have circulatory systems specifically designed for such temperature maintenance (see Chapter 7).
- Predatory tactics include attracting prey with modified body parts disguised as lures, or by feigning death. Fishes include specialists that feed on ectoparasites, feces, blood, fins, scales, young, and eyes of other fishes (see Chapters 19, 20).
- Fishes can significantly change the depth of their bodies by erecting their fins or by filling themselves with water, an effective technique for deterring many predators. In turn, the ligamentous and levering arrangement of mouth bones in some fishes allows them to increase mouth volume when open by as much as 40-fold (see Chapters 8, 20).
- Some of the most dramatic field and laboratory demonstrations of evolution as an ongoing process result from studies of fishes. Both natural and sexual selection have been experimentally manipulated in Guppies, swordtails, and sticklebacks, among others. These investigations show how competition, predation, and mate choice lead to adaptive alterations in body shape and armor, body color and color vision, and feeding habits and locales (see Chapters 17, 19, 20, 24). Fishing has also proven to be a powerful evolutionary force, affecting population structure and size, ages and sizes at which fish reproduce, body shape, and behavior (see Chapter 26).

Additionally, and although not covered in detail in this text, fishes have become increasingly important as laboratory and assay organisms. Because of small size, ease of care, rapid growth and short generation times, and larval anatomical features, such species as Medaka, *Oryzias latipes*, and Zebrafish, *Danio rerio*, are used increasingly in studies of toxicology, pharmacology, neurobiology, developmental biology, cancer and other medical research, aging, genomics, and recombinant DNA methodology (e.g., Geisler et al. 1999; Bolis et al. 2001; Tropepe & Sive 2003; Zbikowska 2003).

A brief history of ichthyology

Fishes would be just as diverse and successful without ichthyologists studying them, but what we know about their diversity is the product of the efforts of workers worldwide over several centuries. Students in an introductory course often have difficulty appreciating historical treatments of the subject; the names are strange, the people are dead (sometimes as a result of their scientific efforts), and the relevance is elusive. However, science is a human endeavor and knowing something about early ichthyologists, their activities, and their contributions to the storehouse of knowledge that we possess today should help give a sense

of the dynamics and continuity of this long-established science.

Although natural historians in most cultures have studied fishes for millenia, modern science generally places its roots in the works of Carl Linne (Linnaeus). Linnaeus produced the first real attempt at an organized system of classification. Zoologists have agreed to use the 10th edition of his *Systema naturae* (1758) as the starting point for our formal nomenclature. The genius of Linnaeus' system is what we refer to as **binomial nomenclature**, naming every organism with a two-part name based on **genus** (plural **genera**) and **species** (singular and plural, abbreviated **sp.** or **spp.**, respectively). Linnaeus did not care much for fishes so his ichthyological classification, which put the diversity of fishes at less than 500 species, is actually based largely on the efforts of Peter Artedi, the acknowledged "father of ichthyology". Artedi reportedly drowned one night after falling into a canal in Amsterdam while drunk, albeit under suspicious circumstances implicating a jealous mentor.

In the mid-1800s, the great French anatomist Georges Cuvier joined forces with Achille Valenciennes to produce the first complete list of the fishes of the world. During those times, French explorers were active throughout much of the world and many of their expeditions included naturalists who collected and saved material. Thus, the *Histoire naturelle de poissons* (1829–1849) includes descriptions of many previously undescribed species of fishes in its 24 volumes. This major reference is still of great importance to systematic ichthyologists today, as are the specimens upon which it is based, many of which are housed in the Museum National d'Histoire Naturelle in Paris.

A few years later, Albert Günther produced a multivolume *Catalogue of fishes in the British Museum* (1859–1870). Although initially designed to simply list all the specimens in the British collections, Günther included all the species of which he was aware, making this catalog the second attempt at listing the known fishes of the world.

The efforts of Linnaeus, Artedi, Cuvier and Valenciennes, and Günther all placed species in genera and genera in families based on overall resemblance. A modern philosophical background to classification was first developed by Charles Darwin with the publication of his *On the origin of species* in 1859. His theory of evolution meant that species placed together in a genus were assumed to have had a common origin, a concept that underlies all important subsequent classifications of fishes and other organisms.

The major force in American ichthyology was David Starr Jordan. Jordan moved from Cornell University to the University of Indiana and then to the presidency of Stanford University. He and his students and colleagues were involved in describing the fishes collected during explorations of the United States and elsewhere in the late 1800s and early 1900s. In addition to a long list of papers, Jordan and his co-workers, including B. W. Evermann, produced several publications which form the basis of our present knowledge of North American fishes. This includes the four-volume *The fishes of North and Middle America* (1896–1990) which described all the freshwater and marine fishes known from the Americas north of the Isthmus of Panama. Jordan and Evermann in 1923 published a list of all the genera of fishes that had ever been described, which served as the standard reference until recently, when it was updated and replaced by Eschmeyer (1990).

Overlapping with Jordan was the distinguished British ichthyologist, C. Tate Regan, based at the British Museum of Natural History. Regan revised many groups and his work formed the basis of most recent classifications. Unfortunately, this classification was never published in one place and the best summary of it is in the individual sections on fishes in the 14th edition of the *Encyclopedia Britannica* (1929).

A Russian ichthyologist, Leo S. Berg, first integrated paleoichthylogy into the study of living fishes in his 1947 monograph *Classification of fishes, both recent and fossil*, published originally in Russian and English. He was also the first ichthyologist to apply the **-iformes** uniform endings to orders of fishes, replacing the classic and often confusing group names.

In 1966, three young ichthyologists, P. Humphry Greenwood at the British Museum, Donn Eric Rosen at the American Museum of Natural History, and Stanley H. Weitzman at the US National Museum of Natural History, joined with an old-school ichthyologist, George S. Myers of Stanford University, to produce the first modern classification of the majority of present-day fishes, the Teleostei. This classification was updated in Greenwood's 3rd edition of J. R. Norman's classic *A history of fishes* (Norman & Greenwood 1975), and is the framework, with modifications based on more recent findings, of the classification used by Nelson and followed in this book.

Details of the early history of ichthyology are available in D. S. Jordan's classic *A guide to the study of fishes*, Vol. I (1905). For a more thorough treatment of the history of North American ichthyology, we recommend Myers (1964) and Hubbs (1964). An excellent historical synopsis of European and North American ichthyologists can also be found in the introduction of Pietsch and Grobecker (1987); a compilation focusing on the contributions of women ichthyologists appears in Balon et al. (1994). Some recent and important discoveries are reviewed in Lundberg et al. (2000).

Additional sources of information

This book is one view of ichthyology, with an emphasis on diversity and adaptation (please read the preface). It is by

no means the final word nor the only perspective available. As undergraduates, we learned about fishes from other textbooks, some of which are in updated editions from which we have taught our own classes. All of these books are valuable. We have read or reread them during the production of this book to check on topics deserving coverage, and we frequently turn to them for alternative approaches and additional information. Among the most useful are Lagler et al. (1977), Bone et al. (1995), Hart and Reynolds (2002a, 2002b), Moyle and Cech (2004), and Barton (2006). The 1997 edition of the present text was summarized by Helfman (2001). For laboratory purposes, Cailliet et al. (1986) is very helpful. From a historical perspective, books by Jordan (1905, 1922), Nikolsky (1961), and Norman and Greenwood (1975) are informative and enjoyable.

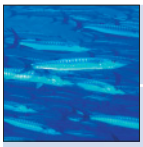
Three references have proven indispensable during the production of this book, and their ready access is recommended to anyone desiring additional information and particularly for anyone contemplating a career in ichthyology or fisheries science. Most valuable is Nelson's *Fishes of the world* (4th edn, 2006). For North American workers, the current edition of Nelson et al. *Common and scientific names of fishes from the United States, Canada, and Mexico* (6th edn, 2004) is especially useful. Finally, of a specialized but no less valuable nature, is Eschmeyer's *Catalog of the genera of recent fishes* (1990, updated in 2005 and available at www.calacademy.org). The first two books, although primarily taxonomic lists, are organized in such a way that they provide information on currently accepted phylogenies, characters, and nomenclature; Nelson (2006) is remarkably helpful with anatomical, ecological, evolutionary, and zoogeographic information on most families. Eschmeyer's volumes are invaluable when reading older or international literature because they give other names that have been used for a fish (**synonymies**) and indicate the family to which a genus belongs.

Of a less technical but useful nature are fish encyclopedias, such as Wheeler's (1975) *Fishes of the world*, also published as *The world encyclopedia of fishes* (1985), *McClane's new standard fishing encyclopedia* (McClane 1974), or Paxton and Eschmeyer's (1998) *Encyclopedia of fishes* (the latter is fact-filled and lavishly illustrated). Species guides exist for most states and provinces in North America, most countries in Europe (including current and former British Commonwealth nations), and some tropical nations and regions. These are too numerous and too variable in quality for listing here; a good source for titles is Berra (2001). Two of our favorite geographic treatments of fishes are as much anthropological as they are ichthyological, namely Johannes' (1981) *Words of the lagoon* and Goulding's (1980) *The fishes and the forest*. A stroll through the shelves of any decent public or academic library is potentially fascinating, with their collections of ichthyology texts dating back a century, geographic and taxonomic guides to fishes, specialty texts and edited volumes, and works in or translated from many languages. Among the better known, established journals that specialize in or often focus on fish research are *Copeia*, *Transactions of the American Fisheries Society*, *Environmental Biology of Fishes*, *North American Journal of Fisheries Management*, *US Fishery Bulletin*, *Canadian Journal of Fisheries and Aquatic Sciences*, *Canadian Journal of Zoology*, *Journal of Fish Biology*, *Journal of Ichthyology* (the translation of the Russian journal *Voprosy Ikhtiologii*), *Australian and New Zealand Journals of Marine and Freshwater Research*, *Bulletin of Marine Science*, and *Japanese Journal of Ichthyology*.

The world wide web has developed into an indispensable source for technical information, spectacular photographs, and updated conservation information concerning fishes. Although websites come and go – and although web information often suffers from a lack of critical peer review – many sites have proven themselves to be both dependable and reliable. For general, international taxonomic information, the Integrated Taxonomic Information System (ITIS, www.itis.usda.gov/index.html) and Global Biodiversity Information Facility (GBIF, www.gbif.org) are starting points. For user-friendliness and general information, FishBase (www.FishBase.org) is the unquestioned leader. Photographs and drawings are most easily accessed via Google and A9, which are cross-linked (http://images.google.com, www.A9.com). For conservation status and background details, www.redlist.org is the accepted authority on international issues, and NatureServe (www.natureserve.org) is the most useful clearinghouse for North American taxa. Several museums maintain updated information on fishes; our favorites are the Australian Museum (www.amonline.net.au/fishes), University of Michigan Museum of Zoology (http://animaldiversity.ummz.umich.edu), Florida Museum of Natural History (www.flmnh.ufl.edu/fish, which is especially good for sharks), and the California Academy of Sciences (www.calacademy.org/research/ichthyology); for North American freshwater fishes, see the Texas Memorial Museum (www.utexas.edu/tmm/tnhc/fish/na/naindex) and the North American Native Fishes Association website (http://nanfa.org/checklist.shtml). The best sites provide links to many additional sites that offer more localized or specific information.

Although **diving** does not in itself constitute a biological science any more than does casual bird watching, snorkeling and scuba diving are essential methods for acquiring detailed information on fish biology. Two of us (Helfman, Collette) credit the thousands of hours we have spent underwater as formative and essential to our understanding of fishes. A full appreciation for the wonders of adaptation in fishes requires that they be viewed in their natural habitat, as they would be seen by their conspecifics, competitors, predators, and neighbors (it is fun to try to think like a fish). We strongly urge anyone seriously interested in any aspect of

fish biology to acquire basic diving skills, including the patience necessary to watch fishes going about their daily lives. **Public and commercial aquaria** are almost as valuable, particularly because they expose an interested person to a wide zoogeographic range of species, or to an intense selection of local fishes that are otherwise only seen dying in a bait bucket or at the end of a fishing line. Our complaint about such facilities is that, perhaps because of space constraints or an anticipated short attention span on the part of viewers, large aquaria seldom provide details about the fascinating lives of the animals they hold in captivity. Home aquaria are an additional source for inspiration and fascination, although we are deeply ambivalent about their value because so many tropical fishes are killed or habitats destroyed in the process of providing animals for the commercial aquarium trade, particularly for marine tropicals.



Summary

SUMMARY

1. Fishes account for more than half of all living vertebrates and are the most successful vertebrates in aquatic habitats worldwide. There are about 28,000 living species of fishes, of which approximately 1000 are cartilaginous (sharks, skates, ray), 108 are jawless (hagfishes, lampreys), and the remaining 26,000 are bony fishes.
2. A fish can be defined as an aquatic vertebrate with gills and with limbs in the shape of fins. Included in this definition is a tremendous diversity of sizes (from 8 mm gobies and minnows to 12+ m whale sharks), shapes, ecological functions, life history scenarios, anatomical specializations, and evolutionary histories.
3. Most (about 60%) of living fishes are primarily marine and the remainder live in fresh water; about 1% move between salt and fresh water as a normal part of their life cycle. The greatest diversity of fishes is found in the tropics, particularly the Indo-West Pacific region for marine fishes, and tropical South America, Africa, and Southeast Asia for freshwater species.
4. Unusual adaptations among fishes include African lungfishes that can live in dry mud for up to 4 years, supercooled Antarctic fishes that live in water colder than the freezing point of their blood, deepsea fishes that can swallow prey larger than themselves (some deepsea fishes exist as small males fused to and entirely parasitic on larger females), annual species that live less than a year and other species that may live 150 years, fishes that change sex from female to male or vice versa, sharks that provide nutrition for developing young via a complex placenta, fishes that create an electric field around themselves and detect biologically significant disturbances of the field, light-emitting fishes, warm-blooded fishes, and at least one taxon, the coelacanth, that was thought to have gone extinct with the dinosaurs.
5. Historically important contributions to ichthyology were made by Linnaeus, Peter Artedi, Georges Cuvier, Achille Valenciennes, Albert Günther, David Starr Jordan, B. W. Evermann, C. Tate Regan, and Leo S. Berg, among many others.
6. The literature on fishes is voluminous, including a diversity of college-level textbooks, popular and technical books, and websites that contain information on particular geographic regions, taxonomic groups, or species sought by anglers or best suited for aquarium keeping or aquaculture. Scientific journals with local, national, or international focus are produced in many countries. Another valuable source of knowledge is public aquaria. Observing fishes by snorkel or scuba diving will provide anyone interested in fishes with indispensable, first-hand knowledge and appreciation.

Chapter 2

Systematic procedures

Chapter contents

CHAPTER CONTENTS

The basis of a taxonomically oriented discipline such as ichthyology is an organized, hierarchical system of names of fishes and evolutionary hypotheses associated with those names. This underlying structure provides a basis for identifying and discriminating among fish species and for understanding relationships among species and higher taxa. It also provides the common language that allows communication and discussion among ichthyologists. This enterprise is generally known as **systematics**. In this chapter, we discuss the need for and value, functions, and goals of systematic procedures, different philosophies for classifying organisms, and how systematic procedures may lead to an increase in our understanding of fishes.

Why do we need a system of classification? Things must be named and divided into categories before we can talk about and compare them. This includes cars, athletes, books, plants, and animals. We cannot deal with all the members of a class (such as the 28,000 species of fishes) individually, so we must put them into some sort of classification. Different types of classifications are designed for different functions. For example, one can classify automobiles by function (sedan, van, pickup, etc.) or by manufacturer (Ford, General Motors, Toyota, etc.). Baseball players can be classified by position (catcher, pitcher, first baseman, etc.) or by team (Cubs, Orioles, etc.). Books may be shelved in a library by subject or by author. Similarly, animals can be classified ecologically as grazers, detritivores, carnivores, and so forth, or phylogenetically, on the basis of their evolutionary relationships.

Good reasons exist for ecologists to classify organisms ecologically, but this is a special classification for special purposes. The most general classification is considered to be the most **natural classification**, defined as the classification that best represents the phylogenetic (= evolutionary) history of an organism and its relatives. A phylogenetic classification of taxonomic groups (**taxa**) holds extra information because the categories are predictive. Just as experience with one bad Ford automobile may lead an owner to generalize about other Fords, phylogenetic classification can also be predictive. If one species of fish in a genus builds a nest, it is likely that other species in that genus also do so.

Species

Species are the fundamental unit of classification schemes. What is a species, and how should species be arranged in a phylogenetic classification? The early 20th century British ichthyologist C. Tate Regan (1926) defined a species as "A community, or a number of related communities whose distinctive morphological characters are, in the opinion of a competent systematist, sufficiently definite to entitle it, or them to a specific name". This practical, but somewhat circular, definition of a species, now termed a **morphospecies**, does not depend on evolutionary concepts.

In the late 1930s and early 1940s, the first major attempts were made to integrate classification with evolution. Julian

Huxley integrated genetics into evolution in his book *The new systematics* in 1940. In *Systematics and the origin of species*, Ernst Mayr (1942, p. 120) introduced the **biological species concept**. To Mayr, species were "groups of actually or potentially interbreeding populations which are reproductively isolated from other such groups". This was an important effort to move away from defining species strictly on the basis of morphological characters. This definition has been modified to better fit current concepts of evolution: an **evolutionary species** "is a single lineage of ancestor–descendant populations which maintains its identity from other such lineages and which has its own evolutionary tendencies and historical fate" (Wiley 1981, p. 25). An entire issue of *Reviews in Fish Biology and Fisheries* was devoted to "The species concept in fish biology" (Nelson 1999).

Taxonomy versus systematics

These two words are not exact synonyms but rather describe somewhat overlapping fields. **Taxonomy** deals with the theory and practice of describing biodiversity (including naming undescribed species), arranging this diversity into a system of classification, and devising identification keys. It includes the rules of nomenclature that govern use of taxonomic names. **Systematics** emphasizes the study of relationships postulated to exist among species or higher taxa, such as families and orders. Lundberg and McDade (1990) have presented a good summary of systematics oriented toward those interested in fishes. The two primary journals dealing with systematics of animals are *Systematic Biology* (formerly *Systematic Zoology*), published by the Society of Systematic Biologists, and *Cladistics*, published by the Willi Hennig Society. For journals dealing with systematics of fishes see Chapter 1, Additional sources of information.

Approaches to classification

Three general philosophies of classification have dominated scientific thought in the area of systematics: cladistics, phenetics, and evolutionary systematics.

A revolution in systematic methodology was begun by a German entomologist, Willi Hennig. He introduced what has become known as **cladistics**, or **phylogenetic systematics**, following publication of the 1966 English translation of an extensively revised version of his 1950 German monograph. His fundamental principle was to divide characters into two groups: **apomorphies** (more recently evolved, derived, or advanced characters) and **plesiomorphies** (more ancestral, primitive, or generalized characters). The goal is to find **synapomorphies** (shared derived characters) that diagnose **monophyletic** groups, or **clades** (groups containing an ancestor and all its descendant taxa). **Symplesiomorphies** (shared primitive characters) do not provide data useful for constructing phylogenetic classifications because primitive characters may be retained in a wide variety of distantly related taxa; advanced as well as primitive taxa may possess symplesiomorphies. **Autapomorphies**, specialized characters that are present in only a single taxon, are important in defining that taxon but are also not useful in constructing a phylogenetic tree.

All three major systematic approaches produce some sort of graphic illustration that depicts the different taxa, arranged in a manner that reflects their hypothesized relationships. In cladistics, taxa are arranged on a branching diagram called a **cladogram** (Box 2.1, Fig. 2.1).

Box 2.1

BOX 2.1

Cladistic success: the Louvar

An ideal example of how cladistics should work concerns the oceanic fish known as the Louvar (*Luvarus imperialis*). Most ichthyologists have classified the Louvar as a strange sort of scombroid fish (Scombroidei), the perciform suborder that contains the tunas, billfishes, and snake mackerels. However, a comprehensive morphological and osteological study (Tyler et al. 1989) showed clearly that the Louvar is actually an aberrant pelagic relative of the surgeonfishes (Acanthuroidei). This example is instructive because the study utilized 60 characters from adults and 30 more from juveniles (Fig. 2.1). Homoplasies – characters postulated to be reversals (return to original condition) or independent acquisitions (independently evolved) – were minimal. With the cladistic approach, synapomorphies show that the relationships of the Louvar are with the acanthuroids, whereas noncladistic analysis overemphasized caudal skeletal characters, leading to placement among the scombroids.

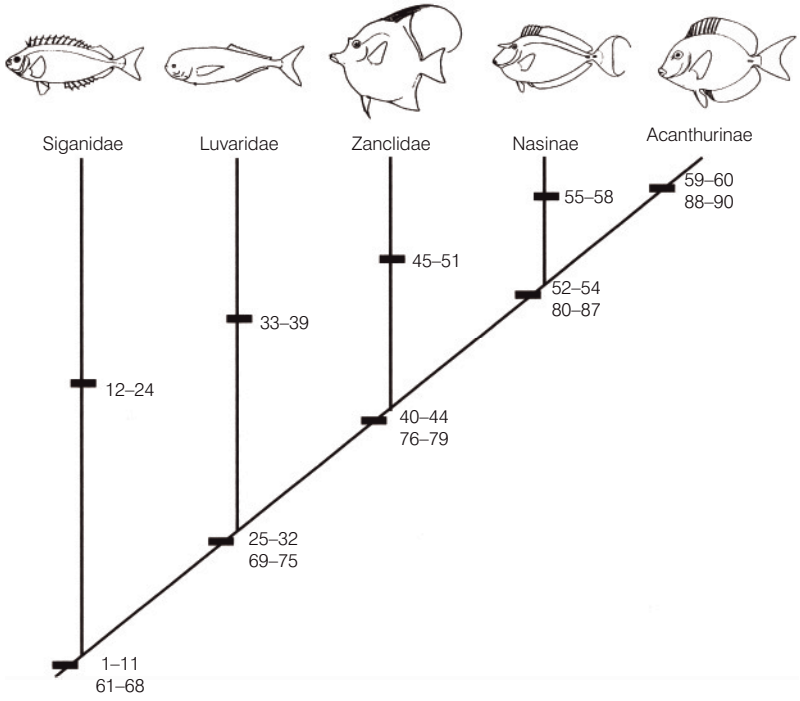


Figure 2.1

Cladogram of hypothesized relationships of the Louvar (*Luvarus*, Luvaridae) and other Acanthuroidei. Arabic numerals show synapomorphies: numbers 1 through 60 represent characters from adults, 61 through 90 characters from juveniles. Some sample synapomorphies include: 2, branchiostegal rays reduced to four or five; 6, premaxillae and maxillae (upper jawbones) bound together; 25, vertebrae reduced to nine precaudal plus 13 caudal; 32, single postcleithrum behind the pectoral girdle; 54, spine or plate on caudal peduncle; 59, teeth spatulate. From Tyler et al. (1989).

Monophyletic groups are defined by at least one synapomorphy at a node, or branching point, on the cladogram. Deciding whether a character is plesiomorphic or apomorphic is based largely on outgroup analysis, that is, finding out what characters are present in **outgroups**, closely related groups outside the taxon under study, which is designated the ingroup. More than one outgroup should be used to protect against the problem of interpreting an apomorphy in an outgroup as a symplesiomorphy. The **polarity** of a character or the inferred direction of its evolution (e.g., from soft-rayed to spiny-rayed fins) is determined using outgroup comparison or ontogeny. **Sister groups** are the most closely related clades in the nodes of a cladogram. Problems arise when there are **homoplasies**, which are shared, independently derived similarities such as parellelisms, convergences, or secondary losses. These do not reflect the evolutionary history of a taxon.

A primary goal of phylogenetic systematics is the definition of monophyletic groups. Current researchers agree on the necessity of avoiding **polyphyletic groups** – groups containing the descendants of different ancestors. Most researchers are equally adamant that monophyletic should be equal to holophyletic, groups containing all the descendants of a single ancestor, and avoiding **paraphyletic groups**, groups that do not contain all the descendants of a single ancestor. **Grades** are groups that are defined by their morphological or ecological distinctness and not necessarily by synapomorphies.

Ideally, when constructing a classification, a taxon can be defined by a number of synapomorphies. However, conflicting evidence frequently exists. Some characters show the relationships of group A to group B, but other characters may show relationships of group A to group C. The principle used to sort out the confusion is that of **parsimony**: select the hypothesis that explains the most data in the simplest or most economical manner (Box 2.1).

With large numbers of characters and large numbers of taxa, it frequently becomes necessary to utilize computer programs to identify the most parsimonious hypotheses, which may be defined as the hypotheses requiring the fewest number of steps to progress from the outgroup to the terminal taxa on a cladogram. Phylogenetic programs based on parsimony algorithms include Hennig86 (Farris 1988), PAUP (phylogenetic analysis using parsimony; Swofford 2003), and NONA (Goloboff 1999). Maximum likelihood models to infer phylogenies have been programmed (e.g., MrBayes; Ronquist & Huelsenbeck 2003) to handle the enormous amount of data generated from molecular sequences. A thorough explanation of cladistic methodology is presented by Wiley (1981), and cogent, brief summaries can be found in Lundberg and McDade (1990) and Funk (1995).

Cladistic techniques and good classifications based on these techniques have proved particularly useful in analyzing the geographic distribution of plants and animals in a process called vicariance biogeography (see Box 16.2).

Phenetics, or **numerical taxonomy**, is a second approach to systematics. Phenetics starts with species or other taxa as **operational taxonomic units** (OTUs) and then clusters the OTUs on the basis of overall similarity, using an array of numerical techniques. Advocates of this school believe that the more characters used the better and more natural

the classification should be (Sneath & Sokal 1973). Some of the numerical techniques devised by this school are useful in dealing with masses of data and have been incorporated into cladistics. However, few modern systematists subscribe to the view that using a host of characters, without distinguishing between plesiomorphies and apomorphies, will provide a natural classification. Some molecular systematists still use phenetic methods to treat their data. Graphic representations in phenetics, known as **phenograms**, look like tennis ladders, with OTUs in place of the competitors. Relatedness is determined by comparing measured linear distances between OTUs; the closer two units are, the more closely related they are.

Evolutionary systematics, as summarized by Mayr (1974), holds that **anagenesis**, the amount of time and differentiation that have taken place since groups divided, must also be taken into consideration along with **cladogenesis**, the process of branch or lineage splitting between sister groups. Evolutionary relationships are expressed on a tree called a **phylogram**. The contrast between cladistic and evolutionary schools can be demonstrated by considering how to classify birds. Cladists emphasize the fact that crocodiles and birds belong to the same evolutionary line by insisting they must be included within a named monophyletic group, Archosauria, in a phylogenetic classification. Evolutionary systematists emphasize the long time gap between fossil crocodilians and modern birds and believe that birds and crocodiles must be treated as separate evolutionary units.

Most leading ichthyological theorists favor the cladistic school and tend to consider any problems resulting from strictly following cladistic theory as minor. On the other hand, many practical ichthyologists, working at the species level, ignore the controversy so they can get on with the business of describing and cataloging ichthyological diversity before humans exterminate large segments of it.

Taxonomic characters

Whichever system of classification is employed, characters are needed to differentiate taxa and assess their interrelationships. Characters, as Stanford ichthyologist George Myers once said, are like gold – they are where you find them. Characters are variations of a homologous structure and, to be useful, they must show some variation in the taxon under study. Useful definitions of a wide variety of characters were presented by Strauss and Bond (1990). Characters can be divided, somewhat arbitrarily, into different categories.

Meristic characters originally referred to characters that correspond to body segments (myomeres), such as numbers of vertebrae and fin rays. Now, meristic is used for almost any countable structure, including numbers of scales, gill rakers, cephalic pores, and so on. These characters are useful because they are clearly definable, and usually other investigators will produce the same counts. In most cases, they are stable over a wide range of body size. Also, meristic characters are easier to treat statistically, so comparisons can be made between populations or species with a minimum of computational effort.

Morphometric characters refer to measurable structures such as fin lengths, head length, eye diameter, or ratios between such measurements. Some morphometric characters are harder to define exactly, and being continuous variables, they can be measured to different levels of precision and so are less easily repeated. Furthermore, there is the problem of **allometry**, whereby lengths of different body parts change at different rates with growth (see Chapter 10). Thus analysis of differences is more complex than with meristic characters. Size factors have to be compensated for through use of such techniques as regression analysis, analysis of variance (ANOVA), and analysis of covariance (ANCOVA) so that comparisons can be made between actual differences in characters and not differences due to body size. Principal components analysis (PCA) also adjusts for size, particularly if size components are removed by shear coefficients, as recommended by Humphries et al. (1981).

Widely used definitions of most meristic and morphometric characters were presented by Hubbs and Lagler (1964); some of these are illustrated in Fig. 2.2.

Anatomical characters include characters of the skeleton (osteology) and characters of the soft anatomy, such as position of the viscera, divisions of muscles, and branches of blood vessels. Some investigators favor osteological characters because such characters have been thought to vary less than other characters. In some cases, this supposition has been due to the use of much smaller sample sizes than with the analysis of meristic or morphometric characters.

Other characters can include almost any fixed, describable differences among taxa. For example, color can include such characters as the presence of stripes, bars, spots, or specific colors. Photophores are light-producing structures that vary in number and position among different taxa. Sexually dimorphic ("two forms") structures can be of functional value, including copulatory organs used by males to inseminate females, like the gonopodium of a guppy (modified anal fin) or the claspers of chondrichthyans (modified pelvic fins). Cytological (including karyological), electrophoretic, serological, behavioral, and physiological characters are useful in some groups.

Molecular characters, especially nuclear DNA and mitochondrial DNA (mtDNA) have become increasingly useful at all levels of classification (Hillis & Moritz 1996; Page & Holmes 1998; Avise 2004; see Chapter 17). All organisms contain DNA, RNA, and proteins. Closely related organisms show a high degree of similarity in molecular structures. Molecular systematics uses such data to build trees

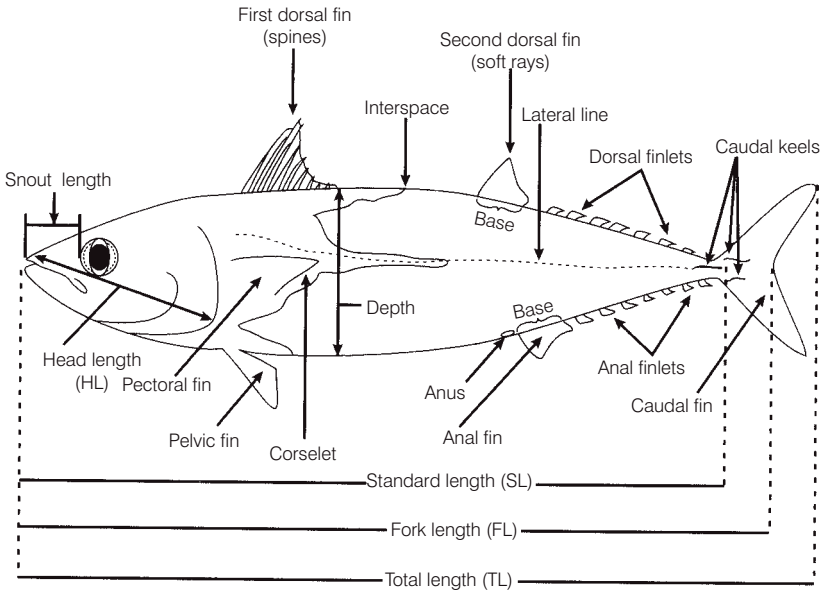


Figure 2.2
Some meristic and morphometric characters shown on a hypothetical scombrid fish.

showing relationships. It is becoming easier and cheaper to sequence longer sequences of nucleotides.

Molecular data can be used to test hypotheses of relationships based on morphological data. An example are the analyses of similar morphological data sets for the Scombroidei by Collette et al. (1984) and by Johnson (1986) that produced different cladograms resulting in very different classifications. In a computer-generated cladogram (WAGNER 78; Farris 1970), Collette et al. (1984) postulated a sister-group relationship of the Wahoo (*Acanthocybium*) and Spanish mackerels (*Scomberomorus*) within the family Scombridae. In contrast, Johnson (1986) placed the Wahoo as sister to the billfishes within a greatly expanded Scombridae that includes billfishes as a tribe, instead of being in the separate families Xiphiidae and Istiophoridae. In part, the different authors reached different conclusions because they analyzed the data sets differently. Another part of the differences in classification centers on the large amount of homoplasy present. No matter which classification is employed, a large number of characters must be postulated to show reversal or independent acquisition. Either more data or a different method of analysis was needed to resolve the conflict. Molecular data, both nuclear and mitochondrial DNA (Orrell et al. 2006), supports the view that the Wahoo is a scombrid and strongly refutes a close relationship between billfishes and scombroids.

Another use of molecular data is in what has been termed **barcoding**. This relies on differences between species in a relatively short segment of mtDNA, an approximately 655 base pair region of cytochrome oxidase subunit I gene (COI) which Hebert et al. (2003) have proposed as a global bioidentification system for animals. It has been likened to the barcodes that we see on items in grocery stores. For barcoding to be successful, within-species DNA sequences need to be more similar to each other than to sequences of different species. Successful barcoding will facilitate identification of fishes, linking larvae with adults, forensic identification of fish fillets and other items in commerce, and identification of stomach contents. One potential problem is that using only a mitochondrial marker may fail to discriminate between species due to introgression of some maternally inherited characters, as has apparently happened between two species of western Atlantic Spanish mackerels, *Scomberomorus maculatus* and *S. regalis* (Banford et al. 1999; Paine et al. 2007).

To test its utility in fishes, Ward et al. (2005) barcoded 207 species of fishes, mostly Australian marine fishes. With no exceptions, all 207 sequenced species were discriminated. Similarly, except for one case of introgression, all 17 species of western Atlantic Scombridae were successfully discriminated with COI (Paine et al. 2007). Successes like these led to ambitious plans at a 2005 workshop held at the University of Guelph in Canada to sequence all species of fishes for the Fish Barcode of Life or FISH-BOL, fostered by the Consortium for the Barcode of Life and the Census of Marine Life. This is planned to be part of a grand scheme to produce a DNA global database for all species on planet Ocean.

Vertebrate classes

Many textbooks list five classes of vertebrates: Pisces (28,000 species), Amphibia (4300), Reptilia (6000), Aves (9000), and Mammalia (4800). But as Nelson (1969) clearly demonstrated, this five-class system is anthropomorphic, with bird and mammal groups overemphasized

by the mammal doing the classification – that is, us. The morphological and evolutionary gap between the Agnatha, the jawless vertebrates (lampreys and hagfishes), and other groups of fishes is much greater than between the classes of jawed fishes on the one hand and the tetrapods on the other hand. Thus fishes (or Pisces) is not a monophyletic group but a grade used for convenience for the Agnatha, Chondrichthyes, bony fishes, the fossil Acanthodii and several primitive, extinct jawless superclasses (see Chapter 11).

Units of classification

Systematists use a large number of units to show relationships at different levels. Most of these units are not necessary except to the specialist in a particular group. For example, ray-finned fishes fall into the following units: kingdom: Animalia; phylum: Chordata (chordates); subphylum: Vertebrata (vertebrates); superclass: Gnathostomata (jawed vertebrates); grade: Teleostomi or Osteichthyes (bony fishes); and class: Actinopterygii (ray-finned fishes). Classification of three representative fishes is shown in Table 2.1.

Note the uniform endings for order (*-iformes*), suborder (*-oidei*), family (*-idae*), subfamily (*-inae*), and tribe (*-ini*). Also, note that the group name is formed from a stem plus the ending. This means that if you learn that the Yellow Perch is *Perca flavescens*, you can construct much of the rest of classification by adding the proper endings. Percidae is the family including the perches, Percoidei is the suborder of perchlike fishes, and Perciformes is the order containing the perchlike fishes and their relatives.

It is conventional to italicize the generic and specific names of animals and plants to indicate their origin from Latin (or latinized Greek or other language). Generic names are always capitalized, but species names are always in lowercase (unlike for some plant species names). The names of higher taxonomic units such as families and orders are never italicized but are always capitalized because they are proper nouns. Sometimes it is convenient to convert the name of a family or order into English (e.g., Percidae into percid, Scombridae into scombrid), in which case the name is no longer capitalized. Common names of fishes have not usually been capitalized in the past but this has recently changed, recognizing that the names are really proper nouns (Nelson et al. 2002). Capitalizing common names avoids the problem of understanding a phrase like "green sunfish". Does this mean a sunfish that is green or does it refer to the Green Sunfish, *Lepomis cyanellus*?

It is also conventional to list higher taxa down to orders in phylogenetic sequence, beginning with the most primitive and ending with the most advanced, reflecting the course of evolution. This procedure has the additional advantage that closely related species are listed near each other, facilitating comparisons. As knowledge about the relationships of organisms increases, changes need to be made in their classification. An instructive example of justification for changing the order in classification was presented by Smith (1988) in a paper entitled "Minnows first, then trout". Smith explained that he placed the minnows and relatives (Cypriniformes) before the trouts and salmons (Salmoniformes) in his book on the fishes of New York State to reflect the more primitive or plesiomorphic phylogenetic position of the Cypriniformes.

Table 2.1

Classification of Atlantic Herring, Yellow Perch, and Atlantic Mackerel.

Taxonomic unit	Herring	Perch	Mackerel
Division	Teleostei	→	→
Subdivision	Clupeomorpha	Euteleostei	→
Order	Clupeiformes	Perciformes	→
Suborder	Clupeoidei	Percoidei	Scombroidei
Family	Clupeidae	Percidae	Scombridae
Subfamily	Clupeinae	Percinae	Scombrinae
Tribe	Clupeini	Percini	Scombrini
Genus species subspecies	*Clupea* *harengus* *harengus*	*Perca* *flavescens*	*Scomber* *scombrus*
Author	Linnaeus	Mitchill	Linnaeus

International Code of Zoological Nomenclature

The **International Code of Zoological Nomenclature** is a system of rules designed to foster stability of scientific names for animals. Rules deal with such topics as the definition of publication, authorship of new scientific names, and types of taxa. Much of the code is based on the **Principle of Priority**, which states that the first validly described name for a taxon is the name to be used. Most of the rules deal with groups at the family level and below. Interpretations of the code and exceptions to it are controlled by the International Commission of Zoological Nomenclature, members of which are distinguished systematists who specialize in different taxonomic groups.

Species and subspecies are based on type specimens, the specimens used by an author in describing new taxa at this

level. Type specimens should be placed in permanent archival collections (see below) where they can be examined by future researchers. **Primary types** include: (i) the **holotype**, the single specimen upon which the description of a new species is based; (ii) the **lectotype**, a specimen subsequently selected to be the primary type from a number of **syntypes** (a series of specimens upon which the description of a new species was based before the code was changed to disallow this practice); (iii) the **neotype**, a replacement primary type specimen that is permitted only when there is strong evidence that the original primary type specimen was lost or destroyed and when a complex nomenclatorial problem exists that can only be solved by the selection of a neotype.

Secondary types include **paratypes**, additional specimens used in the description of a new species, and **paralectotypes**, the remainder of a series of syntypes when a lectotype has been selected from the syntypes. Among the many other kinds of types, mention should also be made of the **topotype**, a specimen taken from the same locality as the primary type and, therefore, useful in understanding variation of the population that included the specimen upon which the description was based, and the **allotype**, a paratype of opposite sex to the holotype and useful in cases of sexual dimorphism.

Taxa above the species level are based on type taxa. For example, the **type species** of a genus is not a specimen but a particular species. Similarly, a family is based on a particular genus.

PhyloCode

Recently, a group of systematists has proposed replacing the Linnean system with the PhyloCode based explicitly on phylogeny (Cantino & de Queiroz 2004). They claim that the PhyloCode is simple and will properly reflect evolutionary connections between species, thus promoting stability and clarity in nomenclature. However, critics say that the Linnean system does effectively organize and convey information about taxonomic categories, and that replacing this system does not justify redefining millions of species and higher taxonomic levels (Harris 2005).

Name changes

Why do the scientific names of fishes sometimes change? There are four primary reasons that systematists change names of organisms: (i) "**splitting**" what was considered to be a single species into two (or more); (ii) "**lumping**" two species that were considered distinct into one; (iii) changes in classification (e.g., a species is hypothesized to belong in a different genus); and (iv) an earlier name is discovered and becomes the valid name by the Principle of Priority. Frequently, name changes involve more than one of these reasons, as shown in the following examples.

An example of "splitting" concerns the Spanish Mackerel of the western Atlantic (*Scomberomorus maculatus*), which was considered to extend from Cape Cod, Massachusetts, south to Brazil. However, populations referred to this species from Central and South America have 47–49 vertebrae, whereas *S. maculatus* from the Atlantic and Gulf of Mexico coasts of North America have 50–53 vertebrae. This difference, along with other morphometric and anatomical characters, formed the basis for recognizing the southern populations as a separate species, *S. brasiliensis* (Collette et al. 1978).

An example of "lumping" concerns tunas of the genus *Thunnus*. Many researchers believed that the species of tunas occurring off their coasts must be different from species in other parts of the world. Throughout the years, 10 generic and 37 specific names were applied to the seven species of *Thunnus* recognized by Gibbs and Collette (1967). Fishery workers in Japan and Hawaii recorded information on their Yellowfin Tuna as *Neothunnus macropterus*, those in the western Atlantic as *Thunnus albacares*, and those in the eastern Atlantic as *Neothunnus albacora*. Large, long-finned individuals, the so-called Allison Tuna, were known as *Thunnus* or *Neothunnus allisoni*. Based on a lack of morphological differences among the nominal species, Gibbs and Collette postulated that the Yellowfin Tuna is a single worldwide species. Gene exchange among the Yellowfin Tuna populations was subsequently confirmed using molecular techniques (Scoles & Graves 1993), further justifying lumping the different nominal species. Following the Principle of Priority, the correct name is the **senior synonym**, the earliest species name for a Yellowfin Tuna, which is *albacares* Bonnaterre 1788. Other, later names are **junior synonyms**.

Tunas also illustrate the other two kinds of name changes. Some researchers placed the bluefin tunas in the genus *Thunnus*, the Albacore in *Germo*, the Bigeye in *Parathunnus*, the Yellowfin Tuna in *Neothunnus*, and the Longtail in *Kishinoella*, almost a genus for each species. Gibbs and Collette (1967) showed that the differences are really among species rather than among genera, so all seven species should be grouped together in one genus. But which genus? Under the Principle of Priority, *Thunnus* South 1845 is the senior synonym, and the other, later names are junior synonyms – *Germo* Jordan 1888, *Parathunnus* Kishinouye 1923, *Neothunnus* Kishinouye 1923, and *Kishinoella* Jordan and Hubbs 1925.

The name of the Rainbow Trout was changed from *Salmo gairdnerii* to *Oncorhynchus mykiss* in 1988 (Smith & Stearley 1989), affecting many fishery biologists and experimental biologists as well as ichthyologists (see Box 14.1). As with the tunas, this change involved a new generic classification as well as the lumping of species previously considered distinct.

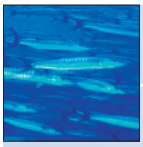
Collections

Important scientific specimens are generally stored in **collections** where they serve as **vouchers** to document identification in published scientific research. Collections are similar to libraries in many respects. Specimens are filed in an orderly and retrievable fashion. Curators care for their collections and conduct research on certain segments of them, much as librarians care for their collections. Historically most collections of fishes have been preserved in formalin and then transferred to alcohol for permanent storage. Now there is increasing attention to adding skeletons and cleared and stained specimens to collections to allow researchers to study osteology. Many major fish collections, such as that at the University of Kansas, also house tissue collections, some in ethyl alcohol, some frozen at –2°C. Qualified investigators can borrow material from collections or libraries for their scholarly study.

Collections may be housed in national museums, state or city museums, university museums, or private collections. The eight major fish collections in the United States (and their acronyms) include the National Museum of Natural History (USNM), Washington, DC; University of Michigan Museum of Zoology (UMMZ), Ann Arbor; California Academy of Sciences (CAS), San Francisco; American Museum of Natural History (AMNH), New York; Academy of Natural Sciences (ANSP), Philadelphia; Museum of Comparative Zoology (MCZ), Harvard University, Cambridge, Massachusetts; Field Museum of Natural History (FMNH), Chicago; and Natural History Museum of Los Angeles County (LACM). These eight collections contain more than 24.2 million fishes (Poss & Collette 1995). An additional 118 fish collections in the United States and Canada hold 63.7 million more specimens; at such locales, emphasis is often on regional rather than national or international fish faunas. These regional collections include the Florida State Museum at the University of Florida (UF), which has grown by the incorporation of fish collections from the University of Miami and Florida State University, and the University of Kansas (KU), which also houses a very important collection of fish tissues, vital for research in molecular systematics.

The most significant fish collections outside the United States are located in major cities of nations that played important roles in the exploration of the world in earlier times (Berra & Berra 1977; Pietsch & Anderson 1997) or have developed more recently. These include the Natural History Museum (formerly British Museum (Natural History); BMNH), London; Museum National d'Histoire Naturelle (MNHN), Paris; Naturhistorisches Museum (NHMV), Vienna; Royal Ontario Museum (ROM), Toronto; Rijksmuseum van Natuurlijke Historie (RMNH), Leiden; Zoological Museum, University of Copenhagen (ZMUC); and the Australian Museum (AMS), Sydney. Leviton et al. (1985) list most of the major fish collections of the world and their acronyms.

The use of museum specimens has been primarily by systematists in the past. This will continue to be an important role of collections in the future, but other uses are becoming increasingly important. Examples include surveys of parasites (Cressey & Collette 1970) and breeding tubercles (Wiley & Collette 1970); comparison of heavy metal levels in fish flesh today with material up to 100 years old (Gibbs et al. 1974); long-term changes in biodiversity at specific sites (Gunning & Suttkus 1991); and pre- and post-impoundment surveys that could show the effects of dam construction. Many major collections are now computerized (Poss & Collette 1995) and more and more data are becoming accessible as computerized databases, some linked together and available on the internet. An example is FISHNET (http://www.fishnet2.net/index.html), a distributed information system that links together fish specimen data from more than two dozen institutions worldwide.



Summary

SUMMARY

1. The best classification is the most natural one, that which best represents the phylogenetic (= evolutionary) history of an organism and its relatives.
2. Species are the fundamental unit of classification and can be defined as a single lineage of ancestor–descendent populations that maintains its identity from other such lineages. Species are usually reproductively isolated from other species.
3. Taxonomy deals with describing biodiversity (including naming undescribed species), arranging biodiversity into a system of classification, and devising identification keys. Rules of nomenclature govern the use of taxonomic names. Systematics focuses on relationships among species or higher taxa.
4. Cladistics, or phylogenetic systematics, is a widely used system of classification in which characters are divided into apomorphies (derived or advanced traits) and plesiomorphies (primitive or generalized traits). The goal is to find synapomorphies (shared derived characters) that define monophyletic groups, or clades (groups containing an ancestor and all its descendant taxa).
5. Taxonomic characters can be meristic (countable), morphometric (measurable), morphological (including color), cytological, behavioral, electrophoretic, or molecular (nuclear or mitochondrial).
6. Ray-finned fishes are generally classified as: kingdom: Animalia; phylum: Chordata (chordates); subphylum: Vertebrata (vertebrates); superclass: Gnathostomata (jawed vertebrates); grade: Teleostomi or Osteichthyes (bony fishes); and class: Actinopterygii (ray-finned fishes).
7. The International Code of Zoological Nomenclature promotes stability of scientific names for animals. These rules deal with such matters as the definition of publication, authorship of new scientific names, and types of taxa.
8. Species and subspecies are based on type specimens, and higher taxa on type taxa. Primary types include the holotype, the single specimen upon which the description of a new species is based. Secondary types include paratypes, which are additional specimens used in the description of a new species.

Supplementary reading

SUPPLEMENTARY READING

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Nelson JS, Starnes WC, Warren ML. 2002. A capital case for common names of species of fishes – a white crappie or a White Crappie? *Fisheries* 27(7):31–33.

Journals

Cladistics, Willi Hennig Society.

Systematic Biology, Society of Systematic Biologists.

Websites

Catalog of Fishes, http://www.calacademy.org/research/ichthyology/catalog/fishcatsearch.html for names, spellings, authorships, dates, and other matters.

FishBase, http://fishbase.org/ for photos and information on fishes.

ITIS (Integrated Taxonomic Information System), http://www.itis.gov/index.html for authoritative taxonomic information on fishes (and other animals and plants).

Figure II *(opposite)*

Longhorn Cowfish, *Lactoria cornuta* (Tetraodontiformes: Ostraciidae), Papua New Guinea. Slow moving and seemingly awkwardly shaped, the pattern of flattened, curved, and angular trunk areas made possible by the rigid dermal covering provides remarkable lift and stability (Chapter 8). Photo by D. Hall, www.seaphotos.com.

PART II

Form, function, and ontogeny

Chapter 3

Skeleton, skin, and scales

Chapter contents

CHAPTER CONTENTS

Fundamental to appreciating the biology of any group of organisms is knowledge of basic anatomy. We present here a brief outline of fish anatomy in four sections: osteology and the integumentary skeleton (skin and scales) in this chapter, soft anatomy and the nervous system in the next chapter. For a comprehensive treatment of fish anatomy, see Harder (1975); for brief updates on each of the organ systems, see the relevant chapters in Ostrander (2000). The skeleton provides much of the framework and support for the remainder of the body, and the skin and scales form a transitional boundary that protects the organism from the surrounding environment. The general osteological description given here and many of the figures are based on members of a family of advanced perciform fishes, the tunas (Scombridae). A drawing of the skeleton of a whole Little Tuna (*Euthynnus alletteratus*) from Mansueti and Mansueti (1962) is included for orientation (Fig. 3.1). Comparative notes on other actinopterygian fishes are added where needed. For a brief summary of the skeletal system see Stiassny (2000), and for a dictionary of names used for fish bones, see Rojo (1991).

Skeleton

The **osteology** (study of bones) of fishes is more complicated than in other vertebrates because fish skeletons are made up of many more bones. For example, humans (sarcopterygian) have 28 skull bones, a primitive reptile (sarcopterygian) has 72, and a fossil chondrostean (actinopterygian) fish more than 150 skull bones (Harder 1975). The general evolutionary trend from primitive actinopterygians to more advanced teleosts and from aquatic sarcopterygians to tetrapods has been toward fusion and reduction in number of bony elements (see Chapter 11, Trends during teleostean phylogeny).

Why do we need to know about the osteology of fishes? First of all, we cannot really understand such processes as feeding, respiration, and swimming without knowing which jaw bones, branchial bones, and fin supports are involved. Knowledge of the skeleton is necessary to understand the relationships of fishes and much of classification is based on osteology. Identification of bones is also important in paleontology, in identifying food of predatory fishes, and in zooarcheology for learning about human food habits from kitchen midden material.

If learning about fish bones is important, how does one go about studying them? Large fishes can be fleshed out and then either cleaned by repeated dipping in hot water or by putting the fleshed out skeleton in a colony of dermestid beetles that eat the flesh and leave the bones (Rojo 1991). Bemis et al. (2004) have recently described a method that requires fairly complete dissection of the specimen and alcohol dehydration to dry it out. Study of the osteology of small fishes and juveniles of large species was difficult until the development of techniques of clearing and staining. This technique, using the enzyme trypsin, makes the flesh transparent. Then the bones are stained with alizarin red S and the cartilages with Alcian blue (Potthoff 1984; Taylor & van Dyke 1985).

The **skull**, or cranium (Fig. 3.2), is the part of the axial endoskeleton that encloses and protects the brain and most of the sense organs. It is a complex structure derived from several sources. Homologies of some fish skull bones are still debated (e.g., the origin and composition of the vomer in the roof of the mouth). The skull has two major components: the neurocranium and the branchiocranium. The **neurocranium** is composed of the chondrocranium and the

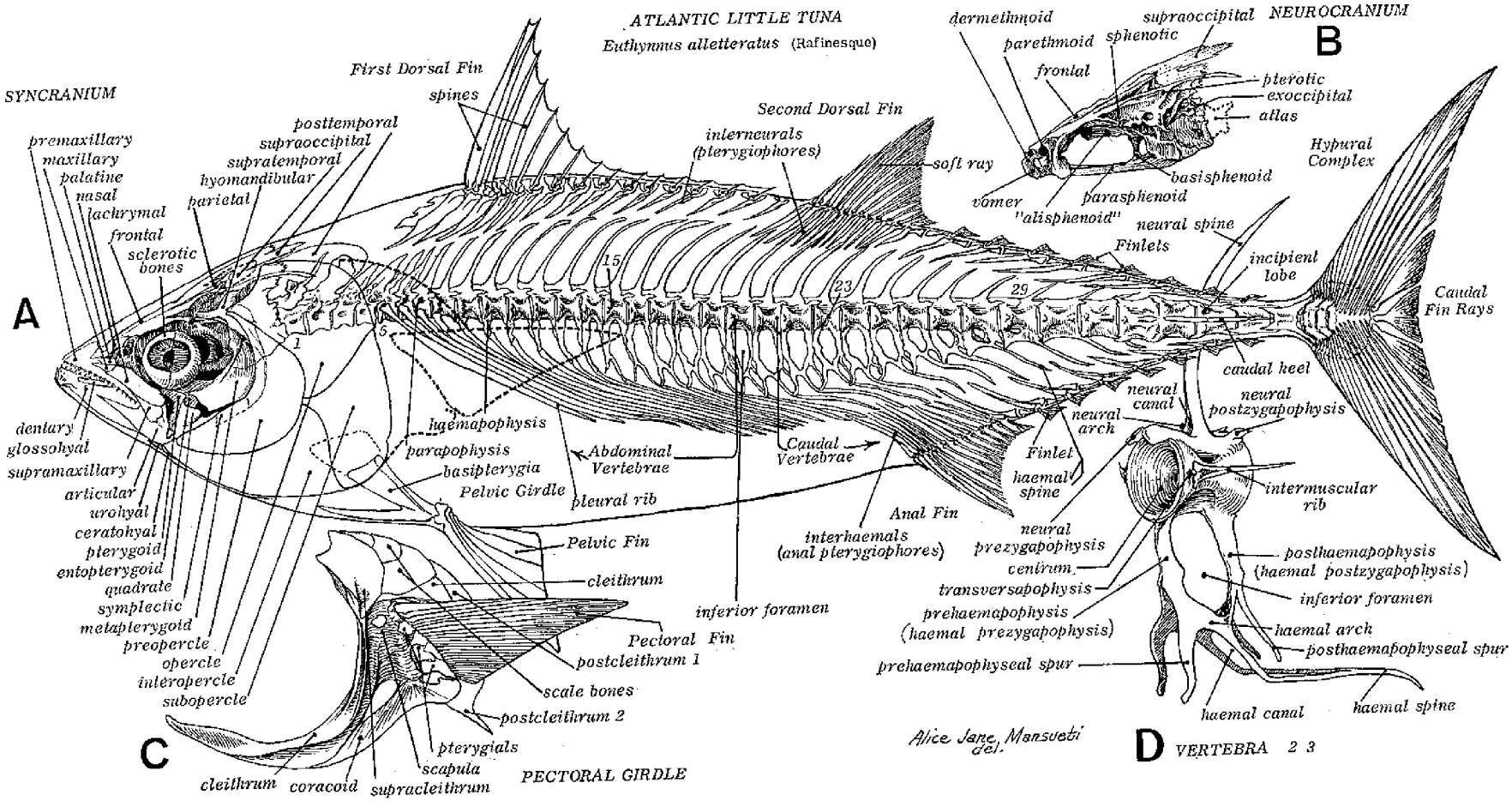


Figure 3.1

Osteology of the Little Tuna (*Euthynnus alletteratus*). From Mansueti and Mansueti (1962).

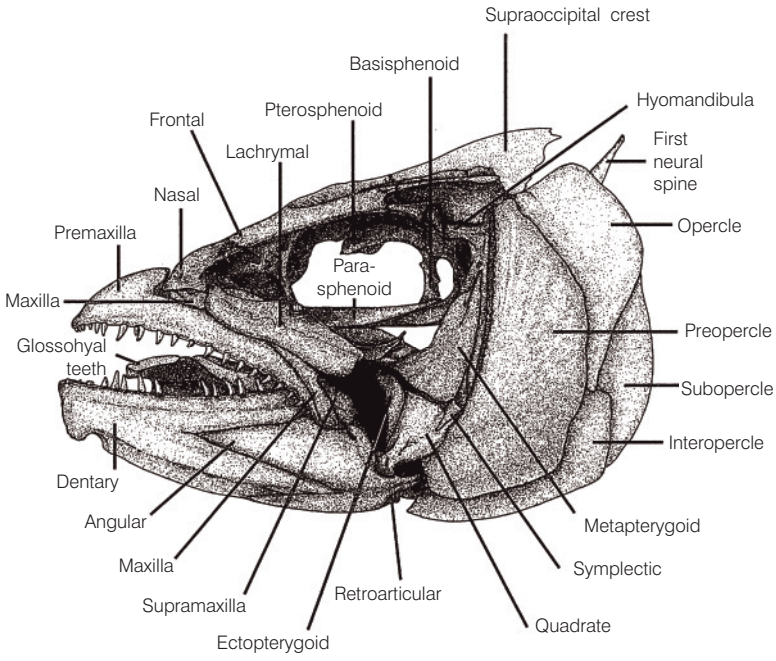


Figure 3.2
Lateral view of the skull of the Dogtooth Tuna (*Gymnosarda unicolor*). From Collette and Chao (1975).

dermatocranium. The **chondrocranium** derives from the embryonic cartilaginous braincase. Its bones ossify (harden) during ontogeny as cartilage is replaced by bone. **Cartilage replacement** (or **endochondral**) **bones** and **dermal bones** have similar histological structure but differ in that cartilage bones are preformed in cartilage before they ossify. Some bones, however, are of complex origin coming from both sources. The **dermatocranium** consists of dermal bones. It is believed that the bones of the dermatocranium evolved from scales that became attached to the chondrocranium.

The **branchiocranium**, or visceral cranium, consists of a series of endoskeletal arches that formed as gill arch supports. The branchiocranium is also known as the splanchnocranium because it is derived from splanchnic mesoderm. The circumorbital, opercular, and branchiostegal bones overlie the branchiocranium, which abuts the neurocranium and pectoral girdle.

Skulls differ among the basic groups of fishes. Hagfishes and lampreys ("agnathans") lack true biting jaws. Toothlike structures are present, but these are horny rasps, not true teeth (see Chapter 13, Jawless fishes). The round mouth has some internal cartilaginous support, hence the alternative name Cyclostomata. It was once thought that lamprey jaws had been lost in association with parasitism. However, the probable fossil ancestors of the lampreys, the primitive cephalaspidomorphs (see Chapter 11), also lacked jaws, so lack of jaws is now thought to be a primitive character. The neurocranium of chondrichthyan sharks and rays is a single cartilaginous structure, the jaws and branchial arches consisting of a series of cartilages.

Neurocranium

The chondrocranium of bony fishes is derived from cartilaginous capsules that formed around the sense organs. To clarify spatial relationships among the large number of bones in the skull, it helps to divide the skull into four regions associated with major centers of ossification. From anterior to posterior, these regions are the **ethmoid**, **orbital**, **otic**, and **basicranial**. For each region, the cartilage bones will be discussed first, followed by the dermal bones, which tend to roof over, and often fuse with the underlying cartilage bones. Consult Harder (1975, pl. 1A-C) for a three-part plate of overlays that greatly helps visualize how the teleost skull bones fit together.

Ethmoid region

The ethmoid region remains variably cartilaginous even in adults of most teleosts (see Table 1.1) but there are also dermal elements fused to some of these bones. Two main sets of cartilage bones form the ethmoid region. Paired **lateral ethmoids** (or parethmoids) form the posterolateral wall of the ethmoid region and the anterior wall of the orbit (Figs 3.3–3.5). The median chondral **ethmoid** (or **supraethmoid**) is the most anterodorsal skull bone. It often has a dermal element fused to it, in which case it is usually termed the mesethmoid. There are also two sets of dermal bones in this region. The median often dentigerous (tooth-bearing) **vomer**, which may be absent in a few teleosts, lies ventral to the mesethmoid, whereas the paired dermal **nasals** are lateral to the ethmoid region, associated with the

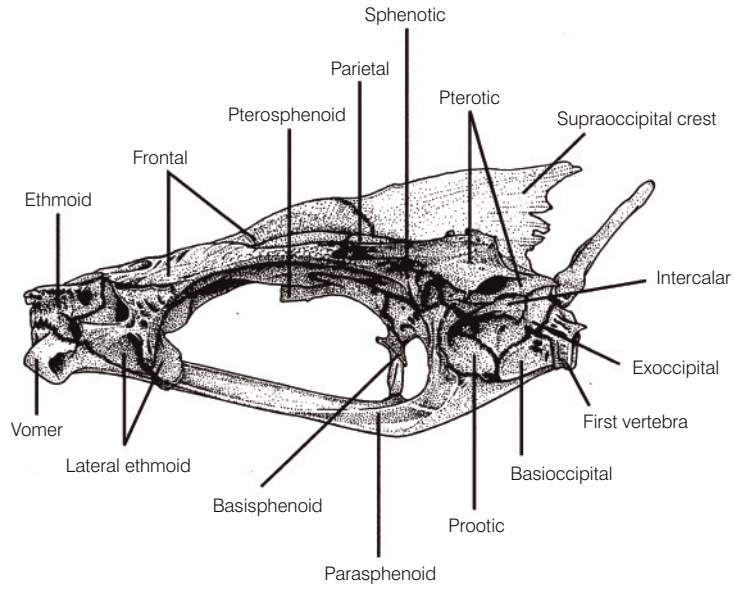


Figure 3.3
Lateral view of the neurocranium of the Dogtooth Tuna (*Gymnosarda unicolor*). From Collete and Chao (1975).

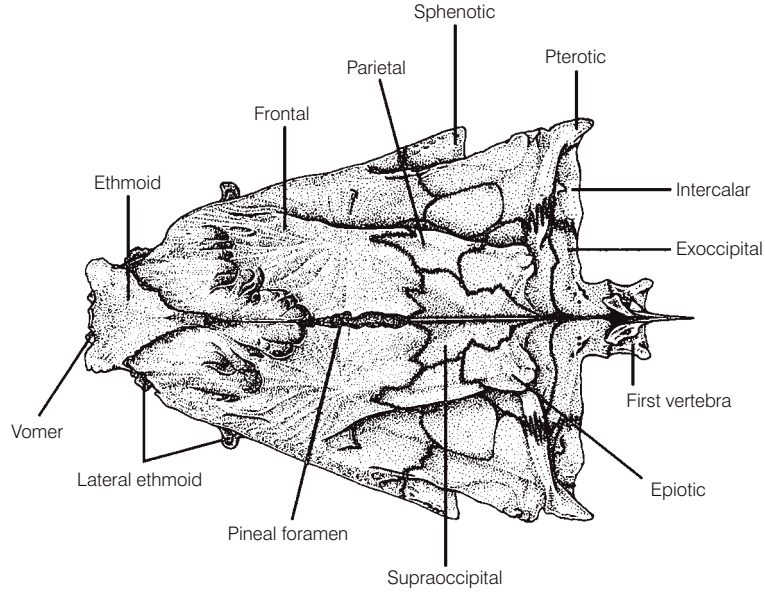


Figure 3.4
Dorsal view of the neurocranium of the Dogtooth Tuna (*Gymnosarda unicolor*). From Collete and Chao (1975).

olfactory nasal capsule. The vomer is usually considered, phylogenetically, to be compound (chondral median ventral ethmoid + dermal vomer).

Orbital region

The region that surrounds the orbit is composed of three sets of cartilage bones and two sets of dermal bones. Cartilage bone components include paired **pterosphenoids** (alisphenoids in earlier literature), which meet along the ventral median line of the skull. The median **basisphenoid** extends from the pterosphenoids down to the parasphenoid and may divide the orbit into left and right halves. **Sclerotic** cartilages or bones protect and support the eyeball itself. Two sets of dermal bones are the paired **frontals**, which cover most of the dorsal surface of the cranium, and the **circumorbitals**. The circumorbitals form a ring around the eye in primitive bony fishes. However, this ring is reduced to a chain of small infraorbital bones under and behind the eye in advanced bony fishes. Advanced teleosts usually have **infraorbital 1**; the **lachrymal**, or preorbital; IO_2, or jugal; IO_3, or true suborbital, which may bear a suborbital shelf that supports the eye; and the **dermosphenotic bones**, or postorbitals, which bear the infraorbital or suborbital lateral line canal (Fig. 3.6). Many primitive teleosts also have an antorbital and a supraorbital.

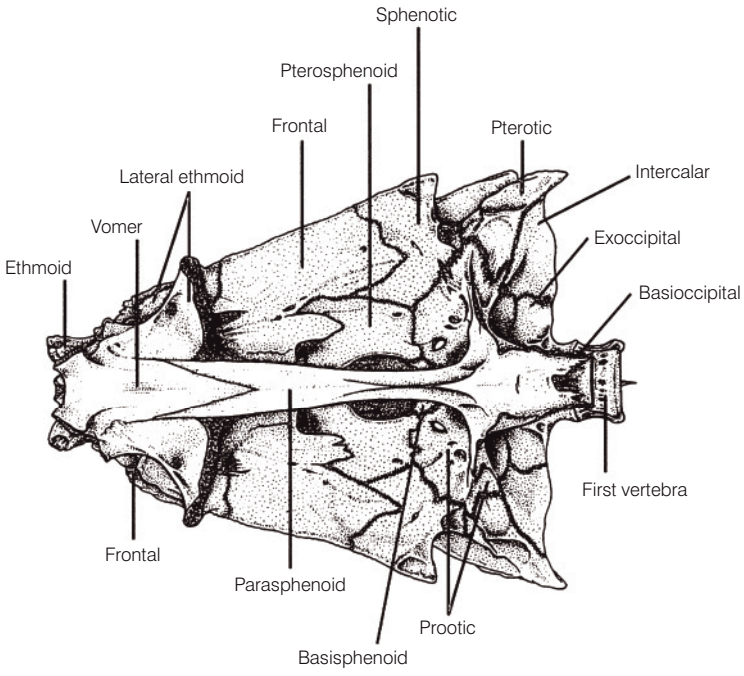


Figure 3.5
Ventral view of the neurocranium of the Dogtooth Tuna (*Gymnosarda unicolor*). From Collete and Chao (1975).

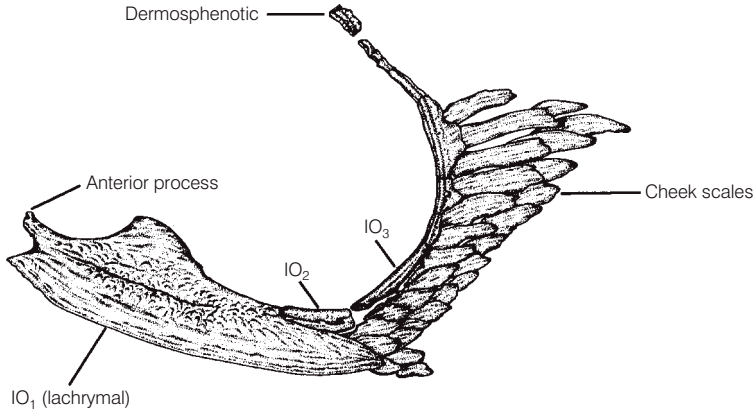


Figure 3.6
Left infraorbital bones in lateral view of the Spanish Mackerel (*Scomberomorus maculatus*). From Collete and Russo (1985b).

Otic region

Five cartilage bones enclose each bilateral otic (ear) chamber inside the skull (see Figs 3.3–3.5). Paired **sphenotics** form the most posterior dorsolateral part of the orbit roof. Paired **pterotics** form the posterior outer corners of the neurocranium and enclose the horizontal semicircular canal. Paired **prootics** form the floor of the neurocranium and enclose the utriculus of the inner ear. Paired **epiotics**, more recently called **epioccipitals**, lie posterior to the parietals and lateral to the supraoccipital and contain the posterior vertical semicircular canal. The median process of the posttemporal, by which the pectoral girdle is attached to the posterior region of the skull, attaches to the epiotics. The epiotics enclose part of the posterior semicircular canal. Paired **intercalars** (or opisthotics) fit between the pterotics and exoccipitals and articulate with the lateral process of the posttemporal. There is only one pair of entirely dermal bones in the otic region, the paired **parietals**, which roof part of the otic region and articulate with the frontals anteriorly, the supraoccipital medially, and the epiotics posteriorly.

Basicranial region

Three sets of cartilage bones, one pair plus two median bones, form the cranial base. Paired lateral **exoccipitals** form the sides of the foramen magnum (Fig. 3.7), which is the passageway for the spinal cord. The median **basioccipital** is the most posteroventral neurocranium bone and articulates with the first vertebra. The dorsal median **supraoccipital** bone usually bears a posteriorly directed

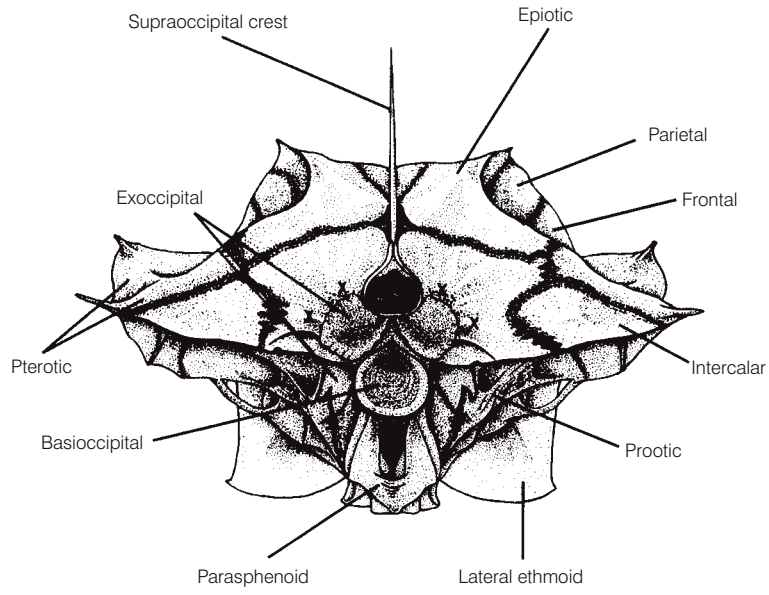


Figure 3.7
Rear view of the skull of a bonito (*Sarda chiliensis*). The crosses indicate points of attachment of epineural bones. From Collete and Chao (1975).

supraoccipital crest that varies among teleosts from a slight ridge to a prominent crest. The only dermal bone in the basicranial region is the median **parasphenoid**, a long cross-shaped bone that articulates with the vomer anteriorly and forms the posteroventral base of the skull.

Branchiocranium

The branchiocranium is divisible into five parts: the mandibular, palatine, hyoid, opercular, and branchial.

Mandibular arch

The **mandibular arch** forms the upper jaw and is known as the palatoquadrate cartilage in Chondrichthyes. It is composed entirely of dermal bones in bony fishes. The mandibular arch may have three sets of bones. The dentigerous (tooth-bearing) **premaxillae** are the anteriormost elements. The **maxillae** are dentigerous in some soft-rayed fishes, but the maxilla is excluded from the gape in more advanced spiny-rayed fishes. The third bone that may be present is the **supramaxilla**. It is a small bone on the posterodorsal margin of the maxilla. Some teleosts, like the herringlike fishes (Clupeoidei), have multiple supramaxillae.

The lower jaw consists of Meckel's cartilage in Chondrichthyes. In bony fishes, the dermal, dentigerous **dentary** bone (Fig. 3.8) covers Meckel's cartilage, which is reduced to a thin rod extending posteriorly along the inner face of the dentary to the angular. A dorsoposterior ossification of Meckel's cartilage forms an **articular**. The **angular** (sometimes called articular) is a large, posterior dermal bone that fits into the V of the dentary. A ventroposterior dermal ossification forms the **retroarticular** (sometimes called angular), a small bone attached to the posteroventral corner of the angular. In most teleosts the angular fuses with one or both articulars. Two additional ossifications associated with Meckel's cartilage are usually also present, a small nublike sesamoid ossification (the **coronomeckelian**) and a **mentomeckelian** at the distal tip which becomes incorporated (often early in ontogeny) with the dentary. The lower jaw forms a single functional unit in most bony fishes, but in the Kissing Gourami (*Helostoma temmincki*), African characins of the genus *Distochodus*, and some parrotfishes of the genus *Scarus* there is a mobile joint between the dentary and the angular (Liem 1967; Vari 1979; Bellwood 1994).

Teeth

The oral jaws and many pharyngeal bones may bear teeth. Many different terms have been applied to the different sizes and shapes of teeth (see also Chapter 8, Dentition). Although the different kinds form a continuum, they can be divided into several types:

1. **Canine**: large conical teeth frequently located at the corners of the mouth; for example, snappers (*Lutjanus*).
2. **Villiform**: small, fine teeth.
3. **Molariform**: pavementlike crushing teeth, as in cownose rays (Rhinopterinae) in which they form plates, or as individual molars in fishes such as the wolffishes (Anarhichadidae).
4. **Cardiform**: fine, pointed teeth arranged as in a wool card; for example, the pharyngeal teeth in pickerels (*Esox*).
5. **Incisor**: large teeth with flattened cutting surfaces adapted for feeding on mollusks and crustaceans; for example, chimaeras (Holocephali).

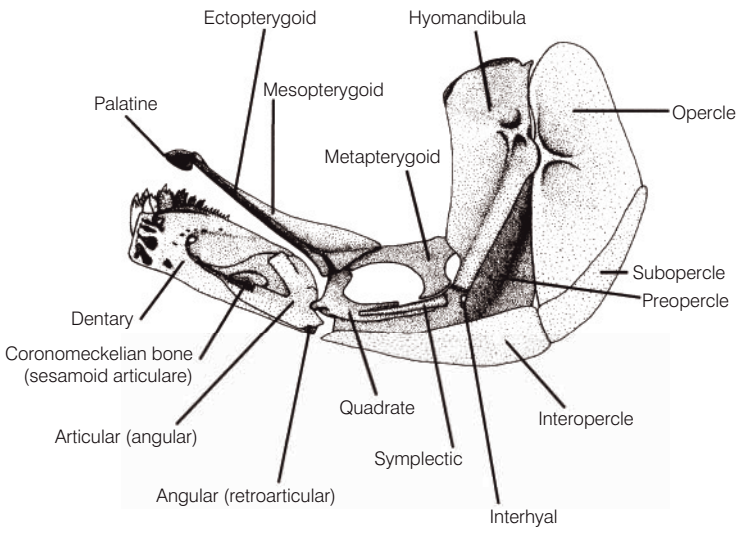


Figure 3.8
Lateral bones of face and lower jaw suspension of a generalized characin (*Brycon meeki*). From Weitzman (1962).

6 Teeth fused into beaks for scraping algae off corals, as in parrotfishes (Scaridae) and Pacific knifejaws (Oplegnathidae), or for biting crustaceans or echinoderms, as in blowfishes (Tetraodontiformes).
7 Flattened triangular cutting teeth, as in sharks and piranhas. Sharp, cutting teeth are uncommon in bony fishes with the exception of some characins (Characoidei) such as *Myleus* that feed on plants and *Serrasalmus*, a genus of the infamous carnivorous piranhas.
8 Pharyngeal teeth: many teleosts have well-developed pharyngeal teeth including fishes like cichlids and parrotfishes, which also have well-developed teeth in their jaws, and minnows and suckers (Cypriniformes), which lack teeth in their jaws.

Palatine and hyoid arches

The **palatine arch** consists of four pairs of bones in the roof of the mouth (see Fig. 3.8). The **palatines** are cartilage bones that are frequently dentigerous. They have been called "plowshare" bones because of their characteristic shape. The dermal **ectopterygoids** are narrow bones, sometimes T-shaped, sometimes dentigerous. The dermal **entopterygoids** (or mesopterygoids) are thin bones that roof the mouth. The **metapterygoids** are cartilage bones, quadrangular-shaped and articulating with the quadrate and hyomandibula.

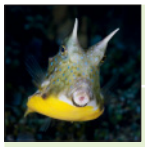
The **suspensorium** consists of a chain of primarily cartilage bones that attach the lower jaw and opercular apparatus to the skull (see Fig. 3.8). The **hyomandibula** is an inverted L-shaped bone that connects the lower jaw and opercular bones to the neurocranium. The **symplectic** is a small bone that fits into the groove of the quadrate. The **quadrate** is a triangular bone with a groove for the symplectic; it has an articulating facet to which the lower jaw is attached (Box 3.1).

The **hyoid complex** is a series of five pairs of bones (Fig. 3.10) that lie medial to the lower jaw and opercular bones and lateral to the branchiostegal rays that attach to them. The anteriormost bones are the dorsal and ventral **hypohyals** (or basihyals). They are followed by the anterior **ceratohyal**, a long flat bone that interdigitates with the posterior ceratohyal posteriorly and to which some of the branchiostegal rays attach. The posterior ceratohyal (or epihyal) is a triangular bone to which some of the branchiostegal rays attach. The **interhyal** is a small, rod-shaped bone that attaches the hyoid complex to the suspensorium. The **glossohyal** is an unpaired flattened bone that lies over the anterior basibranchial and supports the tongue.

The dermal bones of the hyoid arch are the **branchiostegal rays**, elongate, flattened, riblike structures (Fig. 3.10) that attach to the ceratohyal and epihyal. They are important in respiration, particularly in bottom-dwelling species. Their number and arrangement are useful in tracing phylogenies (see McAllister 1968). The median **urohyal** is a flattened, elongate, unpaired bone that lies inside the rami (branches) of the lower jaw. The urohyal is an ossification of a median tendon in the sternohyoideus muscle, and is a sesamoid ossification (not a dermal bone) and synapomorphy of teleosts.

Opercular and branchial series

The **opercular apparatus** consists of four pairs of wide, flat dermal bones that form the gill covers, protect the



Box 3.1

Jaw suspension

Much interest and controversy has arisen over which of the gill arches of the agnathan ancestors gave rise to the gnathostome jaws. Zoologists are not certain whether the jaw-forming arch was the first in the series, or whether it was posterior to a premandibular arch that has been lost (Walker & Liem 1994). Classically, four principal types of jaw attachment have been recognized (Fig. 3.9).

1. **Amphistylic** suspension is found in primitive sharks. The upper jaw is attached to the cranium by ligaments at the orbital and otic processes of the palatoquadrate. The hyoid arch is attached to the chondrocranium and lower jaw and is involved in suspension of both jaws.
2. **Hyostylic** suspension is found in most chondrichthyans and all actinopterygians (but Maisey (1980) found no dividing line between amphistyly and hyostyly in living sharks). The otic contact of the palatoquadrate has been lost, so that both jaws are suspended from the chondrocranium by way of ligamentous attachments to the hyomandibula, which is attached to the otic region of the neurocranium. **Methyostylic** suspension is a variety of hyostyly present in Actinopterygii. Remnants of the second gill arch (palatine and pterygoid bones) connect in the roof of the mouth. Dermal bones, the premaxilla and maxilla, form a new upper jaw. A new dermal anterior lower jaw element, the dentary, is connected with the angular, which is suspended from the otic capsule by hyoid derivatives.
3. **Autostylic** suspension is present in lungfishes and tetrapods. The processes of the palatoquadrate articulate with or fuse to the chondrocranium. The hyoid arch is no longer involved with jaw suspension. The hyomandibula becomes the columella of the inner ear in tetrapods.
4. **Holostylic** suspension is a variety of autostyly found only in the Holocephali, (chimaeras). The palatoquadrate is fused to the chondrocranium and supports the lower jaw in the quadrate region. The name Holocephali means "whole head", in reference to the upper jaw being a part of the cranium.

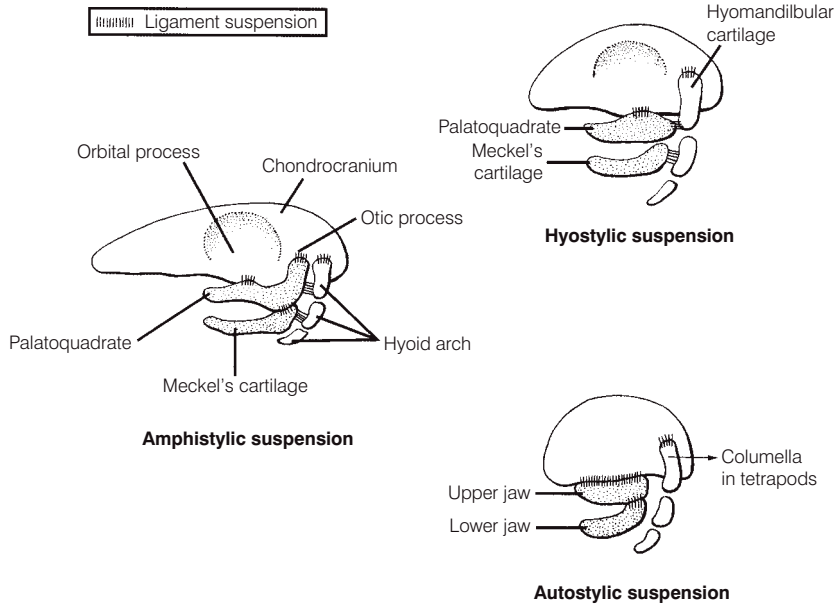


Figure 3.9
Major types of jaw suspension in fishes. From Walker and Liem (1994).

underlying gill arches, and are involved in respiration and feeding. The **opercle** is usually more or less rectangular and is usually the largest and heaviest of the opercular bones (see Figs 3.2, 3.8). It has an anterior articulation facet connecting with the hyomandibula. The **subopercle** is the innermost and most posterior element. The preopercle is the anteriormost element. It overlies parts of the other three opercular bones. The **interopercle** is the most ventral bone.

The **branchial complex** consists of four pairs of gill arches, gill rakers, pharyngeal tooth patches, and supporting bones (Fig. 3.11). All elements of the gill arch are cartilage bones but may have toothed dermal elements incorporated. Three **basibranchials** form a chain from anterior to posterior. The first basibranchial is partially covered by the median **glossohyal**; the second and third serve as attachments for the hypobranchials and ceratobranchials. Three pairs of **hypobranchials** connect the basibranchials with the first three ceratobranchials, the fourth is cartilaginous. **Ceratobranchials** are the longest bones in the branchial arch and support most of the gill filaments and gill rakers. The fourth ceratobranchial is more irregular than the first three. The fifth is usually expanded, bears a tooth plate, and is sometimes called the **lower pharyngeal bone**. Four pairs of **epibranchials** attach basally to the ceratobranchials. They vary from being long and slender (like a short ceratobranchial) to short and stubby. Four pairs of **pharyngobranchials** attach to the epibranchials. The first is suspensory and attaches to the braincase. The other three may have dermal tooth patches attached to them and are then termed **upper pharyngeal bones**. For a detailed account of the gill arches and their use in tracing fish phylogeny, see Nelson (1969).

For a general reference to the osteology of the skull of many species, consult Gregory (1933); for a more complete treatment of ostariophysan fishes, Harrington (1955) and Weitzman (1962) are excellent sources. A complete review of the braincase of actinopterygian fishes and their fossil ancestors, pholidophorids and leptolepids, was presented by Patterson (1975).

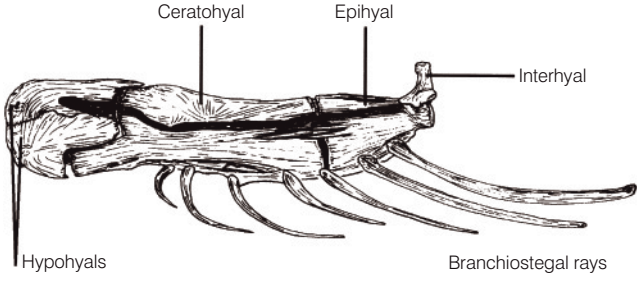


Figure 3.10
Left hyoid complex in lateral view of a Spanish mackerel (*Scomberomorus commerson*). From Collete and Russo (1985b).

Postcranial skeleton

The **notochord** is primitively a supporting structure in chordates. It is a simple, longitudinal rod composed of a group of cells that, when viewed in cross-section, appear to be arranged as concentric circles. The most primitive chordate to possess a notochord is the "tadpole" larva of tunicates. The notochord provides support for an elongate body while swimming. Notochordal cells inside the notochord are few in number and contain large vacuoles. Turgor of the notochordal cells provides rigidity. The notochord is found during embryonic development in all chordates, but intervertebral disks are all that remain of the notochord

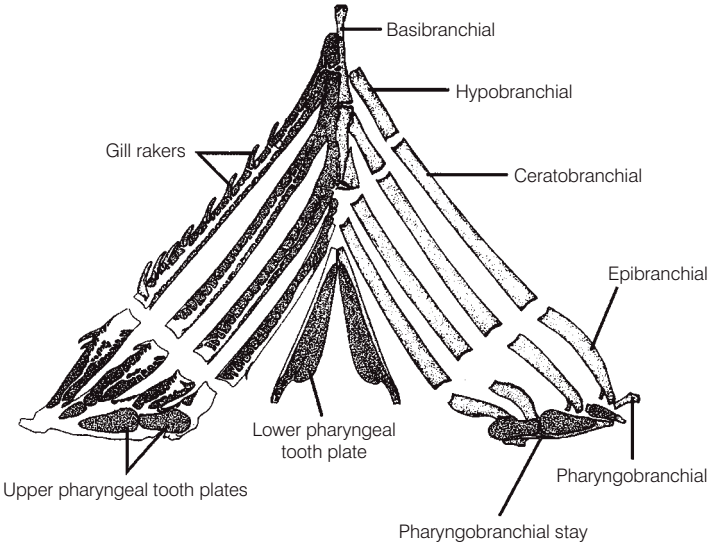


Figure 3.11
Branchial arch of a Spanish mackerel (*Scomberomorus semifasciatus*). Dorsal view of the gill arches with the dorsal region folded back to show their ventral aspect. The epidermis is removed from the right-hand side to reveal the underlying bones. From Collete and Russo (1985b).

in most adults. However, it is present in adult lancelets, Chondrichthyes, Dipnoi, sturgeons (Acipenseridae), paddlefishes (Polyodontidae), and coelacanths. A 1 m long sturgeon may have a notochord nearly as long and about 12 mm in diameter.

Vertebral column

Vertebrae arise and form around the notochord where muscular myosepta intersect with dorsal, ventral, and horizontal septa. Vertebrae form from cartilaginous blocks called **arcualia**. Typically, there is one vertebra per body segment, the **monospondylous** condition. The basidorsal, interdorsal, basiventral, and interventral arcualia all fuse together to form a single vertebra. In the **diplospondylous** condition, the basidorsal fuses to the basiventral and the interdorsal fuses to the interventral, producing two vertebrae per body segment. Diplospondyly is present in the tail region of sharks and rays, in lungfishes, and in the caudal vertebrae of the Bowfin (*Amia*). Diplospondyly is thought to increase body flexibility.

Vertebrae are usually divided into **precaudal** (anterior vertebrae extending posteriorly to the end of the body cavity and bearing ribs) and **caudal vertebrae** (posterior vertebrae beginning with the first vertebra bearing an elongate **haemal spine** surrounding a closed haemal canal through which the caudal artery enters) (Fig. 3.12).

Vertebrae may have various bony elements projecting from them. Dorsally, there is an elongate **neural spine** housing a **neural arch** through which the spinal cord passes (Fig. 3.13A). Ventrally, there may be **parapophyses** that extend ventrolaterally and to which the ribs usually attach. The main artery of the body, the dorsal aorta, passes ventral to the precaudal vertebrae and enters the closed **haemal canal** (Fig. 3.13B) toward the end of the abdominal cavity, at which point it is referred to as the caudal artery. Other projections include **neural prezygapophyses** and **postzygapophyses** on the dorsolateral margins of the vertebrae and **haemal prezygapophyses** and **postzygapophyses** on the ventrolateral margins (Fig. 3.13D).

Ribs and intermuscular bones

Pleural ribs form in the peritoneal membrane and attach to the vertebrae, usually from the third vertebra to the last precaudal vertebra. They are distinct from **intermuscular bones** and serve to protect the viscera. Terminology used for these bones, and for ribs, was confused until Patterson and Johnson (1995) clarified the situation. Patterson and Johnson recognized three series of intermuscular bones: epineurals, epicentrals, and epipleurals. Primitively, ossified **epineurals** may be fused with the neural arches. Some are autogenous (unfused) and may develop an anteroventral branch as in characins (see Fig. 3.13D). Epineurals usually start on the first vertebra (sometimes on the back of the skull; see Fig. 3.7) and continue along the vertebrae well posterior to the ribs. **Epicentrals** lie in the horizontal septum and are primitively ligamentous. **Epipleurals** start medially and move anteriorly and posteriorly. They lie below the horizontal septum and are posteroventrally directed. Epicentrals and epipleurals have been lost in many advanced

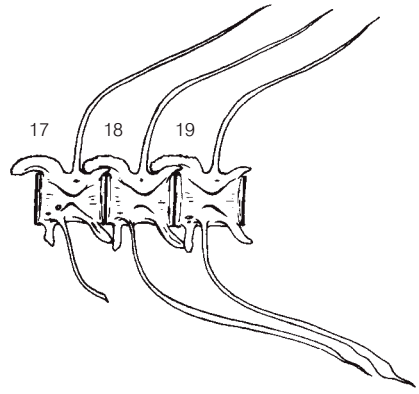


Figure 3.12

Junction of precaudal and caudal vertebrae in a left lateral view of the King Mackerel (*Scomberomorus cavalla*). The middle vertebra, with an elongate haemal spine, is the first caudal vertebra. Vertebrae numbered from the anterior. From Collete and Russo (1985b).

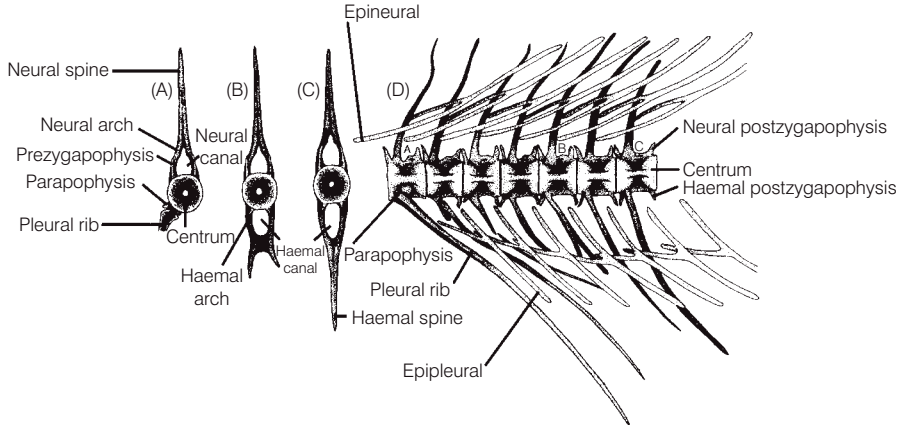


Figure 3.13

Representative precaudal and caudal vertebrae of a generalized characin (*Brycon meeki*). (A) Anterior view of the 20th precaudal vertebra. (B) Anterior view of the 24th precaudal vertebra. (C) Anterior view of the second caudal vertebra. (D) Lateral view of the 20th precaudal through second caudal vertebrae. From Weitzman (1962).

teleosts, leaving a series of short, straight epineurals lateral to the vertebral column and dorsal to the ribs. For these reasons, fillets taken from advanced teleosts such as perch and tuna contain fewer small bones then those from more primitive teleosts such as trout and herring.

Caudal complex

The tail of a fish is a complex of vertebral centra, vertebral accessories, and fin rays that have been modified during evolution to propel the fish forward in a linear fashion. The functional morphology of the fish tail and the history of its progressive change are discussed in Chapters 8 (Locomotory types) and 11 (Division Teleostei). The teleostean caudal skeleton was largely neglected as a source of systematic characters until Monod (1968) surveyed the caudal skeleton of a broad range of teleosts and established a coherent and homogeneous terminology. Schultze and Arratia (1989) further showed the value of the caudal skeleton in the classification of teleosts. In primitive teleosts, a number of **hypurals** (enlarged haemal spines) support most of the branched **principal caudal fin rays** that form the caudal fin (Fig. 3.14). **Epurals** (modified neural spines) and the last haemal spine support the small spinelike **procurrent** caudal fin rays. In many advanced teleosts, the number of hypurals has been reduced to five. In some groups, such as atherinomorphs, sticklebacks, sculpins, the Louvar, tunas and mackerels, and flatfishes, the posterior vertebrae have been shortened and some of the hypurals fuse to form a **hypural plate**. In scombrids, hypurals 3 and 4 are united into the upper part of the plate and hypurals 1 and 2 into the lower part (Fig. 3.15).

Caudal fin types

Caudal fins of fishes vary in both external shape and internal anatomy. The different types of caudal fins provide useful information about modes of swimming as well as about phylogeny. There are three basic types of fish tails, with an additional three types recognized for special groups of fishes.

The **protocercal** tail is the primitive undifferentiated caudal fin that extends around the posterior end in adult lancelets, agnathans, and larvae of more advanced fishes.

In the **heterocercal**, or unequal-lobed, tail, the vertebral column extends out into the upper lobe of the tail. This type of tail is found in Chondrichthyes and primitive bony fishes such as sturgeons (Acipenseridae) and is still recognizable in gars (Lepisosteidae). *Amia*, the Bowfin, has what has been termed a hemihomocercal tail (Harder 1975), intermediate between heterocercal and homocercal, with external but not internal symmetry.

Most advanced bony fishes have a **homocercal**, or equal-lobed, tail (see Figs. 3.14, 3.15). In this type of tail, the caudal fin rays are arranged symmetrically and attach to a series of hypural bones posterior to the last vertebra that supports the caudal fin rays. These plates are ventral to the upward-directed urostyle, so this type of tail could be considered to be an abbreviated heterocercal tail.

The **leptocercal** (or diphycercal) tail resembles the protocercal in having the dorsal and anal rays joined with the caudal around the posterior part of the fish, but this is considered to have been secondarily derived, not primitive. This type of tail is found convergently in lungfishes (Dipnoi), coelacanths, rattails (Macrouridae), and many eel-like fishes.

The last vertebra of the **isocercal** tail, not the original urostyle, has been secondarily modified into a small

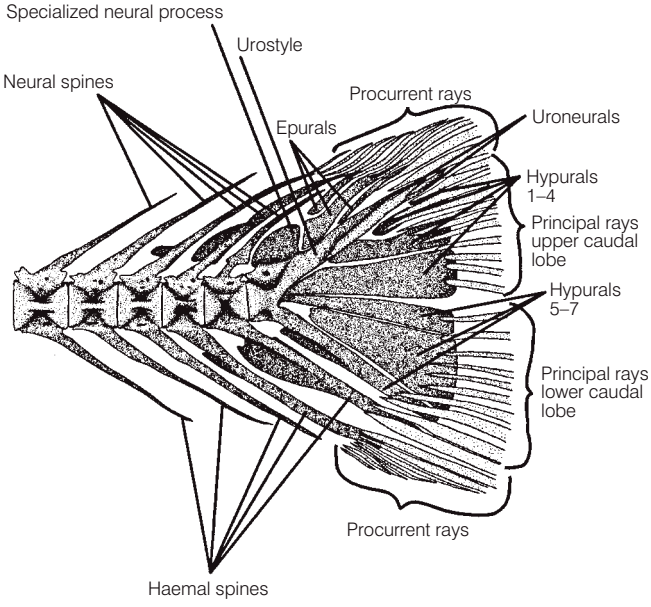


Figure 3.14
Posterior vertebrae and caudal complex of a generalized characin (*Brycon meeki*). From Weitzman (1962).

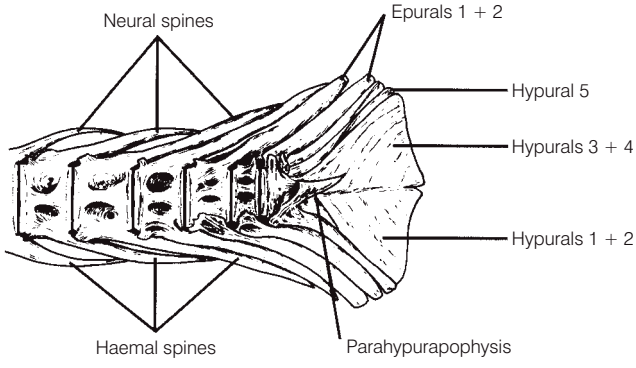


Figure 3.15
Caudal complex in left lateral view of a Spanish mackerel (*Scomberomorus semifasciatus*). From Collete and Russo (1985b).

flattened plate to which the caudal fin rays attach in the cods (Gadidae).

Ocean sunfishes (Molidae) have lost the posterior end of the vertebral column, including the hypural plate, i.e., they lack a true tail. A deep, abbreviated, caudal-fin-like structure extends between the dorsal and anal fins and has been termed a **clavus** forming a **gephyrocercal** (or bridge) tail. There are two hypotheses for the origin of this structure: (i) it is a highly modified caudal fin; or (ii) it is formed by highly modified elements of the dorsal and anal fins. By studying the ontogeny of the vertebral column and fins, Johnson and Britz (2005) have shown that the caudal fin is lost in molids and the clavus is formed by modified elements of the dorsal and anal fins. Because of this highly derived condition and other specialized osteological features, molids are considered to be the most advanced teleosts.

Appendicular skeleton

Pectoral and pelvic girdles are primitively absent in the hagfishes and lampreys. Sharks have a coracoscapular cartilage that hangs more or less freely inside the body wall and has no attachment to the vertebral column. In rays, the pectoral girdle is attached to the fused anterior section of the vertebral column (synarchial condition) and also, by way of the propterygium of the pectoral girdle and antorbital cartilage, to the nasal capsules of the skull.

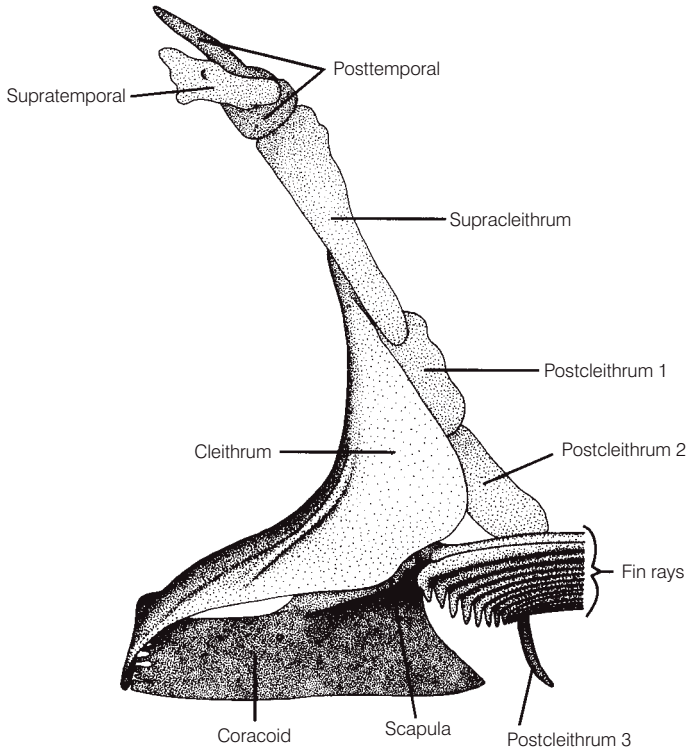


Figure 3.16
Left pectoral girdle of a generalized characin (*Brycon meeki*). From Weitzman (1962).

Pectoral girdle

Unlike the condition in tetrapods, the **pectoral girdle** in bony fishes usually has no attachment to the vertebral column and instead attaches to the back of the skull via the posttemporal bone. Rather than dividing bones into cartilage and dermal, as done for the skull, it seems more practical to present the bones in sequence from the skull to the girdle bones themselves.

Three dermal bones are involved in the suspension of the pectoral girdle from the skull. The **posttemporal** usually has two anterior projections that attach to the epioccipital and intercalar bones on the back of the skull. The **extrascapular** (or supratemporal) is a thin tubular bone, sometimes two bones, that carry part of the lateral line canal onto the body. They usually lie right under the skin dorsal to the posttemporal (Fig. 3.16). The **supracleithrum** is a heavy bone that lies between the posttemporal and the pectoral girdle.

The pectoral girdle is composed of two cartilage and one dermal bone in acanthopterygians. The dermal **cleithrum** is the largest, dorsalmost, and anteriormost element of the pectoral girdle. The **scapula** is a small bone, usually with a round scapular foramen, lying between the cleithrum and the radials. The **coracoid** is a long, thin bone that makes up the posterior part of the pectoral girdle and may support some of the pectoral fin radials. An additional element is found between the coracoid and cleithrum in many soft-rayed teleosts, the **mesocoracoid**. This bone is lost in spiny-rayed fishes as the pectoral fin moves up and assumes a vertical instead of oblique position.

The **actinosts** plus tiny **distal radials** are hourglass-shaped cartilage bones that connect to the pectoral fin rays. There are typically four in teleosts, attached to the coracoid and scapula.

Posterior and internal to the pectoral girdle are the dermal **postcleithra**. Soft-rayed teleosts typically have three; two are elongate and scalelike, and one is rodlike. Spiny-rayed teleosts typically have two, one scalelike, the other more riblike.

Pelvic girdle

The **pelvic girdle**, like the pectoral girdle, is usually not attached to the vertebral column in fishes as it is in tetrapods. In sharks, the pelvic girdle consists of the **ischiopubic cartilages** that float freely in the muscles of the posterior region of the body. In primitive bony fishes, there are paired pelvic bones, **basipterygia**, and radials to which the pelvic fin rays attach. In advanced bony fishes, both the pelvic bone itself and the radials are lost or fused so that the fin rays attach directly to the single remaining element, the basipterygium.

In soft-rayed teleosts, the pelvic fins are **abdominal** in position, ventrally located, slightly anterior to the anal fin. The pelvic fins move forward to a thoracic position, directly below the pectoral fins, in spiny-rayed fishes. In some fishes (i.e., ophidiiform cusk-eels and gadiform cods), the pelvic fins lie anterior to the pectoral fins, a condition known as **jugular** pelvic fins. Jugular pelvic girdles may have attachments to the pectoral girdle.

Pelvic fin rays are frequently lost, and in some cases, such as eels (Anguilliformes), the neotenic South American needlefish *Belonion apodion*, and puffers, the pelvic girdle has also been lost.

Median fins

The median or unpaired fins consist of the dorsal, anal, and adipose fins along the dorsal and ventral profiles of the fish. In jawless fishes, cartilaginous rods support the median fins. In Chondrichthyes, the median fins are supported by **ceratotrichia**, horny fin rays composed of elastin and supported by dermal cells. Below the ceratotrichia are three layers of **radials** – rodlike cartilages that support the fin rays and extend inward toward the vertebral column. If a spine is present at the anterior end of a median fin in a chondrichthyan such as the Spiny Dogfish (*Squalus acanthias*), it is not a true spine such as is found in spiny-rayed fishes (Acanthopterygii) but is rather a fusion of radials.

In bony fishes, the ceratotrichia are replaced during ontogeny by **lepidotrichia**, bony supporting elements that are derived from scales. Ceratotrichia are present in lungfishes and larval actinopterygians. Primitive actinopterygians such as the Bowfin (*Amia*) still have three radials supporting each median fin ray, but these are reduced to two and then one in advanced teleosts. The remaining element is then known as an **interneural bone** if it is under the dorsal fins or **interhaemal bone** if it is above the anal fin.

Primitive soft-rayed teleosts have a single dorsal fin that is composed entirely of soft rays. Advanced teleosts usually have two dorsal fins, with the anterior one (**first dorsal fin**) composed of spines and the posterior one (**second dorsal fin**) composed largely of soft rays, although there may be one spine at the anterior margin of the fin. Some soft-rayed fishes such as the Carp, the Goldfish, and catfishes may have a single spine at the anterior end of the dorsal fin, but this is a bundle of fused rays, not a true spine.

True **spines** differ from **soft rays** in several characters:

Spines	*Soft rays*
usually hard and pointed	usually soft and not pointed
unsegmented	segmented
unbranched	usually branched
solid	bilateral, with left and right halves

Some fast-swimming fishes such as the mackerels and tunas may have a series of **dorsal finlets**, small fins with one soft ray each, following the second dorsal fin.

Several groups of soft-rayed fishes have an additional fin posterior to the dorsal fin, the **adipose fin**, which varies greatly in size among different fishes. "Adipose" is a poor term for this fin because it is rarely fatty. The adipose fin usually lacks lepidotrichia and is supported only by ceratotrichia, although some catfishes have secondarily developed a spine, composed of fused rays, at its anterior margin. The function or functions of adipose fins remain something of a mystery, but their presence is useful in identifying members of five groups that usually have them: characins (Characiformes), catfishes (Siluriformes), trouts and salmons (Salmoniformes), lanternfishes and relatives (Myctophiformes), and trout-perches (Percopsidae).

The original function of the dorsal fin was as a stabilizer during swimming, but it has been modified in many different ways. It has been reduced or lost in rays (Batoidei) and South American knifefishes (Gymnotiformes). The dorsal and anal fins become **confluent**, joined with the caudal fin, around the posterior part of the body in many eels (Anguilliformes). The individual spines in the first dorsal fin have become shortened in fishes such as the Bluefish (*Pomatomus saltatrix*) and the Cobia (*Rachycentron canadum*). The first dorsal fin has been converted into a suction disk in the remoras (Echeneidae). The membranes between the spines have lost their attachment to each other in the bichirs (Polypteridae) and sticklebacks (Gasterosteidae). Venom glands have become associated with dorsal fin spines, and other spines, in fishes such as the stonefish (*Synanceia*), the weeverfishes (Trachinidae), and venomous toadfishes (Thalassophryninae). The spiny dorsal fin has been converted into a locking mechanism in the triggerfishes (Balistidae). It is depressible into a groove during fast swimming in the tunas (Scombridae). Perhaps the most extreme modification of a dorsal fin is the conversion of the first dorsal spine into an **ilicium**, or fishing rod, with an **esca**, or bait, at its tip in the anglerfishes (Lophiiformes).

The **anal fin** usually lies just posterior to the anus. In soft-rayed fishes, it is composed entirely of soft rays, as is the single dorsal fin of these fishes. In spiny-rayed fishes, the anal fin usually contains one or several anterior spines, followed by soft rays. Fast-swimming fishes that have dorsal finlets usually also have **anal finlets**, small individual fins following the anal fin.

The anal fin shows the least variation among fishes. It has been lost in the ribbonfishes (Trachipteridae). It is very long and serves as the primary locomotory fin in South American knifefishes (Gymnotiformes) and Afro-Asian featherfins (Notopteridae). The anterior part of the anal fin has been modified into a **gonopodium** for spermatophore transfer in male livebearers (Poeciliidae). It is also variously modified into what has been called an **andropodium** in males of *Zenarchopterus* and several related internally fertilizing genera of halfbeaks (Zenarchopteridae).

Integumentary skeleton

The **integument** is composed of the skin and skin derivatives, and includes scales in fishes and feathers and hair in birds and mammals. The integument forms an external protective structure parallel to the internal endoskeleton and serves as the boundary between the fish and the external environment. The structure of the skin in fishes is similar to that of other vertebrates, with two main layers: an outer epidermis and an inner dermis. See Elliott (2000) for a review of the integumentary system.

Epidermis

The epidermis is ectodermal in origin. In lampreys and higher vertebrates, the epidermis is stratified. The lowest layer is the **stratum germinativum**, composed of columnar cells (Fig. 3.17). It is the generating layer that gives rise to new cells. In hagfishes, lampreys, and bony fishes, there is an outer thin film of noncellular dead cuticle (Whitear 1970). The outer part of the epidermis in terrestrial vertebrates is the **stratum corneum**, which is composed of dead, horny, keratinized squamous cells that form hair and feathers. Breeding tubercles in fishes may also contain keratin (Wiley & Collette 1970).

The inner dermis contains blood vessels, nerves, sense organs, and connective tissue. It is derived from embryonic mesenchyme of mesodermal origin. It is composed of fibroelastic and nonelastic collagenous connective tissue with relatively few cells. Dermal layers include an upper, relatively thin layer of loose cells, the **stratum laxum** (or stratum spongiosum) and a lower, compact thick layer, the **stratum compactum** (Fig. 3.17). In adult fishes, the dermis is much thicker than the epidermis. The thickness of the integument depends on the thickness of the dermis. Scaleless species, such as catfishes of the genus *Ictalurus*, have relatively thick, leathery skin. The Ocean Sunfish (*Mola*) has the skin reinforced by a hard cartilage layer, 50–75 mm thick. Snailfishes (*Liparis*, Liparidae) have a transparent jellylike substance up to 25 mm thick in their dermis.

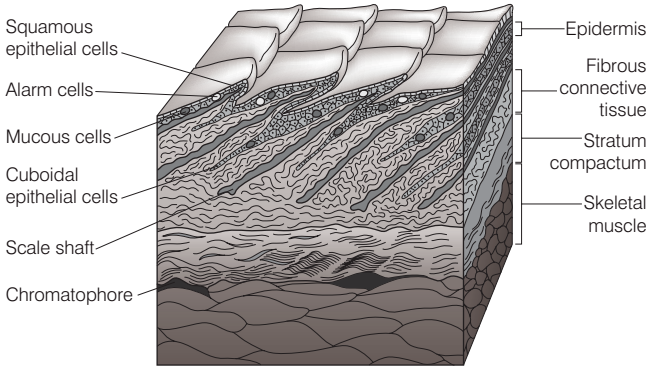


Figure 3.17
Structure of fish skin.

The chemical composition of fish skin is poorly studied, but some generalizations can be made. There is less water in fish skin than in fish muscle, a higher ash content, and similar amounts of protein. The main protein in skin is collagen, which is why fish skin has been used to manufacture glue. The chief minerals in fish skin are phosphorus, potassium, and calcium (Van Oosten 1957). The ash composition of the skin of the Coho Salmon (*Oncorhynchus kisutch*) is:

P_2O_5	33%	CaO	14%
Cl	21%	Na_2O	9%
K_2O	17%	MgO	2%

Among the functions of the skin are mechanical protection and production of mucus by epidermal mucous cells. **Mucin** is a glycoprotein, made up largely of albumin. Threads of mucin hold a large amount of water. It is possible to wring the water out of mucus, leaving threads of mucin. Among the first multicellular glands to evolve were the mucous glands of hagfishes (Myxinidae), called **thread cells** (Fernholm 1981). The oft-told story is that a hagfish + a bucket of water = a bucket of slime.

Other structures in the skin of fishes include epidermal venom glands associated with spines on fins (weeverfishes, Trachinidae; madtom catfishes, *Noturus*), opercles (venomous toadfishes, Thalassophryninae), and the tail (stingrays, Dasyatidae). **Photophores**, which produce bioluminescence, develop from the germinative layer of the epidermis. Color is due to **chromatophores**, which are modified dermal cells containing pigment. The skin also contains important receptors of physical and chemical stimuli.

Scales

Scales are the characteristic external covering of fishes. There are four basic types of scales.

1. **Placoid** scales are characteristic of the Chondrichthyes, although they have a more restricted distribution in rays and chimaeras than in sharks. This type of scale has been called a "dermal denticle", but this is not accurate terminology because there are both epidermal and dermal portions, as in mammalian teeth. Each placoid scale consists of a flattened rectangular basal plate in the upper part of the dermis, from which a protruding spine projects posteriorly on the surface. The outer layer of the placoid scale is hard, enamel-like **vitrodentine**, derived from ectoderm. Vitrodentine is noncellular and has a very low organic content. The scale has a cup or cone of **dentine** with a pulp cavity richly supplied with blood capillaries, just as in

mammalian teeth. Placoid scales do not increase in size with growth; instead, new scales are added between older scales. The teeth of elasmobranchs are evolutionary derivatives of placoid scales, and in fact placoid scales are homologous with teeth in all vertebrates.

2 **Cosmoid** scales were present in fossil coelacanths and fossil lungfishes. The scales of Recent lungfishes are highly modified by loss of the dentine layer. Cosmoid scales are similar to placoid scales and probably arose from the fusion of placoid scales. Cosmoid scales are composed of two basal layers of bone: **isopedine**, which is the basal layer of dense lamellar bone, and cancellous (or spongy) bone, which is supplied with canals for blood vessels. Over the bone layers is a layer of cosmine, a noncellular dentinelike substance. Over the cosmoid layer is a thin superficial layer of vitrodentine. Growth is by addition of new lamellar bone underneath, not over the upper surface.

3 **Ganoid** scales were present in primitive fossil actinopterygians and are found in Chondrostei. They are modified cosmoid scales, with the cosmine replaced by dentine and the surface vitrodentine replaced by **ganoine**, an inorganic bone salt secreted by the dermis. Ganoine is a calcified noncellular material without canals. Ganoid scales are usually rhomboidal in shape and have articulating peg and socket joints between them. The fossil palaeoniscoid scale is least modified in the bichirs, Polypteridae (three layers: ganoine, dentine, and isopedine). Ganoid scales are more modified in sturgeons (Acipenseridae) and paddlefishes (Polyodontidae), in which lamellae of ganoine lie above a layer of isopedine. Sturgeon scales are modified into large plates, with most of the rest of the body naked.

Scales of gars (Lepisosteidae) are similar to Polypteridae in external appearance but are more similar to those of the Acipenseridae and Polyodontidae in structure. In the Bowfin (*Amia*) the scale is greatly reduced in thickness to merely a collagenous plate with bony particles, very similar to the cycloid scales of Teleostei.

4 **Cycloid** and **ctenoid** scales are almost completely dermal. There is no enamel-like layer except perhaps the **ctenii** (teeth on posterior border) and the most posterior and superficial ridges of the scale. These types of scales evolved from ganoid scales by loss of the ganoine and thinning of the bony dermal plate. Two major portions make up these scales: (i) a surface "bony" layer, which is an organic framework impregnated with salts, mainly calcium phosphate (as hydroxyapatite) and calcium carbonate; and (ii) a deeper fibrous layer, or **fibrillary plate**, composed largely of collagen.

Cycloid or ctenoid scales are present in the Teleostei, the vast majority of bony fishes. They have the advantage of being imbricate, overlapping like shingles on a roof, which gives great flexibility compared with cosmoid and ganoid scales. Small muscles pull unequally on the dermis, causing the anterior portion of the scale to become depressed in the dermis and covered over by the posterior margin of the preceding scale. Cycloid scales lack ctenii. Breeding tubercles and contact organs (see Fig. 21.2) are present in many groups of fishes that lack ctenoid scales.

Including all scales with spines on their posterior margins under the term ctenoid is an oversimplification of the situation (Johnson 1984; Roberts 1993). Three different, general types of spined scales exist: (i) **crenate**, with simple marginal indentations and projections; (ii) **spinoid**, with spines continuous with the main body of the scales; and (iii) ctenoid, with ctenii formed as separate ossifications distinct from the main body of the scale (Roberts 1993). Crenate scales occur widely in the Elopomorpha and Clupeomorpha; spinoid scales occur widely in the Euteleostei; peripheral ctenoid scales (whole ctenii in one row) occur, probably independently, in the Ostariophysi, Paracanthopterygii, and Percomorpha; and transforming ctenoid scales (ctenii arising in two or three rows and transforming into truncated spines) are a synapomorphy of the Percomorpha.

As with fish skin, the chemical composition of scales is poorly known. About 41–84% is organic protein, mostly albuminoids such as collagen (24%) and ichthylepidin (76%). Up to 59% is bone, mostly $Ca_3(PO_4)_2$ and $CaCO_3$.

Phylogenetic significance of scale types

Scales have been used as a taxonomic tool since the beginnings of systematic ichthyology (Roberts 1993). For example, Louis Agassiz divided fishes into four groups based on their scale type. More recent classifications are based on more characters but are similar to the system used by Agassiz.

Agassiz system	*Recent classification*
a. Placodermi →	a. Chondrichthyes
b. Ganoidei →	b. Chondrostei
→	c. Holostei
	d. Teleostei:
c. Cycloidei →	malacopterygian grade (soft-rayed)
d. Ctenoidei →	acanthopterygian grade (spiny-rayed)

Whereas most groups of advanced acanthopterygian teleosts have ctenoid scales, some "ctenoid" groups may also have cycloid scales, and many species will have ctenoid scales on some parts of the body and cycloid scales on others. In the flatfishes, Pleuronectiformes, some species have ctenoid scales on the eyed side and cycloid scales on the blind side that is in contact with the bottom. Some

flatfishes are sexually dimorphic, males having ctenoid scales and females having cycloid scales.

Scale size varies greatly in fishes. Scales may be microscopic and embedded as in freshwater eels (Anguillidae), which led to their being classified as non-kosher because of the supposed absence of scales. Scales are small in mackerels (*Scomber*), "normal" in perches (*Perca*), large enough to be used for junk jewelry in Tarpon (*Megalops*), and huge (the size of the palm of a human hand) in the Indian Mahseer (*Tor tor*, a cyprinid gamefish reaching 43 kg in weight).

Development pattern of scales

In actinopterygian (ray-finned) fishes, scales usually develop first along the lateral line on the caudal peduncle, then in rows dorsal and ventral to the lateral line, and then spread anteriorly (see Fig. 9.8). The last regions to develop scales in ontogeny are the first to lose scales in phylogeny. Once the full complement of scales is attained in ontogeny, the number remains fixed. Therefore, the number of scales is a useful taxonomic character. Most scales remain in place for the life of the fish, which makes scales valuable in recording events in the life history of an individual fish, such as reduced growth that generally occurs during the winter or during the breeding season. Scales become deeply buried in the skin with age in the Swordfish, *Xiphias* (Govoni et al. 2004), leading some orthodox Jews to question if Swordfish are kosher, because kosher dietary laws require that a fish have both fins and scales.

Geographic variation can occur in the relative development of ctenoid scales in some species. For example, in the Swamp Darter (*Etheostoma fusiforme*) of the Atlantic Coastal Plain of the United States, the number of scales in the interorbital area increases from north to south (Collette 1962). In northern parts of the range, the few scales present are embedded and cycloid. Further south, there is an increase in number and in relative "ctenoidy" of the scales; more scales have the posterior surface of the scale projecting through the epidermis, and these scales have more ctenii on them.

Lateral line scales form pores on scales from head to tail. Most fishes have **complete** lateral lines, that is, pored scales extend from behind the opercular region all the way to the base of the caudal fin. Some species, such as the Swamp Darter, have **incomplete** lateral lines, with the pores extending only part way to the caudal base. Other patterns include **disjunct** where there is an interruption between the upper and lower portions of the lateral line, as in most members of the large family Cichlidae, **multiple** with several lateral lines, and **absent**, where the lateral line is missing on the body (Webb 1989).

Modifications of scales

Some fishes have scales that are **deciduous**, that is, easily shed. This is true of many species of herrings (Clupeidae) and anchovies (Engraulidae). It may be true of one species in a genus but not of another. For example, of two species of common Australian halfbeaks or garfishes (Hemiramphidae), scales remain in the River Garfish, *Hyporhamphus regularis*, but are easily lost in the Sea Garfish, *H. australis*.

Male darters of the genus *Percina* have **caducous scales**, a single row of enlarged scales along the ventral surface between the pelvic fins and the anus. Several structures in chondrichthyans may have arisen from fusions of modified placoid scales. These include the "spines" at the beginning of the first and second dorsal fins of the Spiny Dogfish, the prominent dorsal "spine" in some chimaeras (Holocephali), the caudal fin spine in stingrays (Dasyatidae), and the teeth on the rostrum of sawfishes (*Pristis*).

As mentioned earlier, the structure of placoid scales in Chondrichthyes is the same as the structure of teeth in vertebrates, leading to the question: Which came first? Did some primitive chondrichthyan ancestor develop teeth that then spread over the body? Or did the ancestor first develop scales that then spread into the mouth and became modified into teeth? Apparently, the dermal armor of the earliest known vertebrates, the ostracoderms, broke up into smaller units, and some of these scales in the mouth evolved into teeth (Walker & Liem 1994).

In many teleosts, there is an external dermal skeleton in addition to the internal supporting skeleton. This is composed of segmented bony plates in pipefishes (Syngnathidae) and poachers (Agonidae) and bony shields similar to placoid scales with vitrodentine in several South American armored catfish families such as the Loricariidae. The body is enclosed in a bony cuirass (armor) in the shrimpfishes (Centriscidae) and is completely enclosed in a rigid bony box in the trunkfishes (Ostraciidae).

Many fishes have protective scutes or spines. The ventral row of scales is modified into **scutes** with sharp, posteriorly directed points in herrings, such as the river herrings (*Alosa*) and the threadfins (*Harengula*). Some jacks (Carangidae) have lateral scutes along the posterior part of the lateral line. Sticklebacks (Gasterosteidae) have bony lateral plates. These plates vary in number and size in *Gasterosteus aculeatus*, roughly correlated with the salinity of the habitat and the presence or absence of predators. Sharp erectable spines derived from scales are present in porcupine fishes (Diodontidae). Large bony "warts" characterize lumpfishes (*Cyclopterus*). Surgeonfishes (Acanthuridae) are so named because of the pair of sharp, anteriorly directed spines on the caudal peduncle.

Three other modifications of scales are discussed elsewhere. Lateral line scales bear sensory structures (see Chapter 6). Lepidotrichia, fin rays supporting the fins, probably originated from scales (see above). The superficial bones of the skull originated as scales and have become modified into dermal bones (see above).

Scale morphology in taxonomy and life history

For studying taxonomy and life history, various parts of the scale are distinguished. Cycloid and ctenoid scales can be divided into four fields (Fig. 3.18): anterior (which is frequently embedded under the preceding scale), posterior, dorsal, and ventral. The focus is the area where scale growth begins. The position and shape of the focus may vary, being oval, circular, rectangular, or triangular. Radially arranged straight lines called radii may extend across any of the fields. A **primary radius** extends from the focus to the margin of the scale. A **secondary radius** does not extend all the way out to the margin of the scale. Radii may be present in different fields: only anterior, as in pickerels (*Esox*); only posterior, as in shiners (*Notropis*); anterior and posterior, as in suckers (Catostomidae); or even in all four fields, as in barbs (*Barbus*). Ctenii may occur in a single marginal row or in two or more rows located on the posterior field.

Circuli are growth rings around the scale. Life history studies, particularly those dealing with age and growth, utilize such growth rings. This is especially useful in temperate waters where pronounced retardation of growth of body and scales occurs in fall and winter, causing the spacing between the circuli to decrease and thus leaving a band on the scales called an **annulus**. However, interpreting such marks as annuli requires caution because any retardation in growth may leave a mark. The stress of spawning, movement from fresh to salt water, parasitism, injury, pollution, and sharp and prolonged change in temperature may all leave marks on the scales similar to annuli. Scales grow in a direct relationship with body growth, making it possible to measure the distance between annuli and back calculate the age at different body sizes. Other hard structures also show growth changes (see Chapter 10, Age and growth) and can be used for aging, such as fin spines, otoliths, and various bones such as opercles and vertebrae (DeVries & Frie 1996).

Scale morphology can also be useful in identification of fragments such as scales found in archeological kitchen middens or in stomach contents. An example of the latter is Lagler's (1947) key to the scales of Great Lakes families. Scale morphology is also useful in classification, as shown by McCully's (1962) study of serranid fishes, Hughes's (1981) paper on flatheads, Johnson's (1984) review of percoids, Coburn and Gaglione's (1992) study of percids, and Roberts' (1993) analysis of spined scales in the Teleostei.

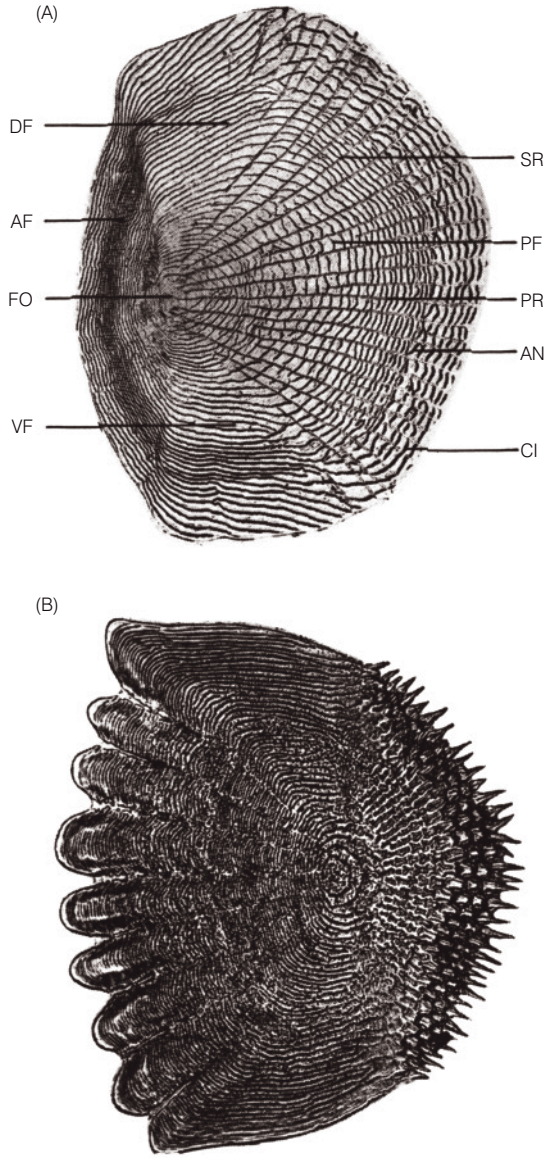
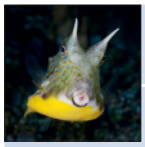


Figure 3.18

Fish scales. (A) A cycloid scale (length 3.14 mm) of the Shiner, *Notropis cornutus*. (B) A ctenoid scale (length 3.5 mm) of the Yellow Perch, *Perca flavescens*. The scales are oriented with the anterior field to the left; the lengths were measured along the anterior–posterior diameter. AF, anterior field; AN, annulus; CI, circulus (ridge); DF, dorsal field; FO, focus; PF, posterior field; PR, primary radius; SR, secondary radius; VF, ventral field. From Van Oosten (1957).



Summary

SUMMARY

1 Actinopterygians have more skull bones than do sarcopterygians. The skull encloses and protects the brain and is composed of the neurocranium and the branchiocranium. The neurocranium is derived from the chondrocranium (the original cartilaginous braincase) and the dermatocranium (dermal bones derived from scales). Actinopterygian skull bones can be divided into four regions: ethmoid, orbital, otic, and basicranial.

2 The branchiocranium consists of five series of endoskeletal arches (mandibular, palatine, hyoid, opercular, branchial) derived from gill arch supports.

3 The notochord of primitive chordates is replaced by the vertebral column in lampreys, Chondrichthyes, and osteichthyans. Vertebrae form around the notochord at intersections of myosepta with dorsal, ventral, and horizontal septa.

4 Posterior vertebrae support the caudal fin in most fishes. In teleosts, hypurals (enlarged haemal spines) support the branched principal caudal fin rays. Three basic types of caudal fins are: (i) protocercal, the primitive undifferentiated caudal fin of adult lancelets, hagfishes, lampreys, and larvae of more advanced fishes; (ii) heterocercal, or unequal-lobed tail, in Chondrichthyes and primitive osteichthyans; and (iii) homocercal, or equal-lobed tail, found in most teleosts.

5 Ribs (pleural ribs) attach to the vertebrae and protect the viscera. Intermuscular bones are segmental, serially homologous ossifications in the myosepta of teleosts.

6 Hagfishes and lampreys lack pectoral and pelvic girdles. Sharks have a coracoscapular (pectoral) cartilage with no attachment to the vertebral column. In osteichthyans, the pectoral girdle lacks a vertebral attachment but is connected with the back of the skull by the posttemporal bone.

7 The dorsal, anal, and adipose fins form the median or unpaired fins. Cartilaginous rods support the median fins of hagfishes and lampreys, whereas chondrichthyan fins are supported by ceratotrichia (horny fin rays). In osteichthyans, ceratotrichia are replaced during ontogeny by lepidotrichia, which are bony supporting elements derived from scales.

8 Primitive teleosts have a single dorsal fin composed of soft rays. Advanced teleosts usually have two dorsal fins: the anterior fin composed of spines and the posterior fin composed of soft rays.

9 The skin and its derivatives, such as scales in fishes, provide external protection. The five basic types of scales are placoid, cosmoid, ganoid, cycloid, and ctenoid.

Supplementary reading

SUPPLEMENTARY READING

Ostrander GK, ed. 2000. *The laboratory fish*. London: Academic Press.

Journal

Journal of Morphology.

Chapter 4

Soft anatomy

Chapter contents

CHAPTER CONTENTS

The organs and organ systems between the skin and scales on the outside of a fish and the axial skeleton on the inside (see Chapter 3) are termed the soft anatomy. Soft anatomy includes the muscles, cardiovascular system, alimentary canal, gas bladder, kidneys, gonads, and nervous system. The sense organs, although part of the nervous system, are treated in Chapter 6 in their functional context as receivers and integrators of information. For a comprehensive treatment of soft anatomy, see Harder (1975).

Muscles

Fish muscle is structurally similar to that of other vertebrates, and fishes possess the same three kinds of muscles, but differ in that a greater proportion (40–60%) of the mass of a fish's muscle is made up of locomotory muscle. Among the three types, **skeletal** muscle is striated and comprises most of a fish's mass, other than the skeleton. **Smooth** muscle is nonskeletal, involuntary, and mostly associated with the gut but is also important in many organs and in the circulatory system. **Cardiac**, or heart, muscle is nonskeletal but striated and is found only in the heart.

Hagfishes and lampreys have a simple arrangement of striated skeletal muscles. These primitive fishes have no paired appendages to interrupt the body musculature. Skeletal muscle behind the head is uniformly segmental and is composed of shallow W-shaped **myomeres**.

In jawed fishes, two major masses of skeletal muscle lie on each side of the fish, divided by the horizontal connective tissue septum. The **epaxial** muscles are the upper pair, and the **hypaxials** are the lower pair (see Fig. 8.1). A third, smaller, wedge-shaped mass of red muscle lies under the skin along the horizontal septum. This band of red muscle is poorly developed in most bony fishes although it is much more extensive and used for sustained swimming in fishes such as the tunas (see Chapter 7, Heterothermic fishes).

Cheek muscles

Seven principal muscles are involved in opening and closing the jaws, suspensorium, and operculum during feeding and breathing (Fig. 4.1). The major muscles are the **adductor mandibulae**, large muscles with several sections that insert on the inner surface of the upper and lower jaw and originate on the outer face of the suspensorium, the chain of bones that suspend the jaws from the neurocranium. The adductor mandibulae function to close the jaws (see also Fig. 8.4). The **levator arcus palatini** occupies the postorbital portion of the cheek. The **dilator operculi**, the **adductor operculi**, and the **levator operculi** insert on the opercle. The **adductor arcus palatini** originates from the ventrolateral margin of the parasphenoid and underlies the orbit. The **adductor hyomandibulae** originates on the prootic and exoccipital and inserts on the hyomandibula. In addition, **pharyngeal** muscles, or **retractores arcuum branchialium**, run from the upper pharyngeal bones to the vertebral column and function in operating the pharyngeal jaws.

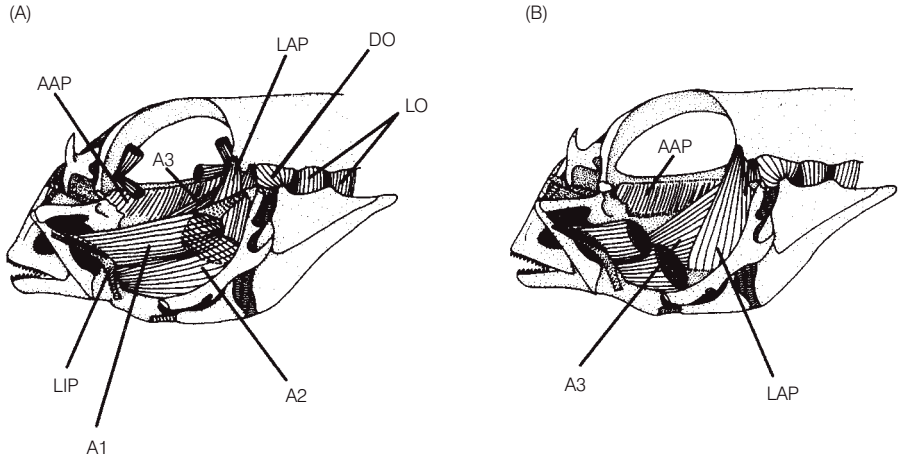


Figure 4.1
Cheek muscles of a sculpin, *Jordania zonope*. (A) Superficial musculature. (B) After removal of A1 and A2. A1, A2, and A3, adductor mandibulae; AAP, adductor arcus palatini; DO, dilator operculi; LAP, levator arcus palatini; LIP, ligamentum primordium; LO, levator operculi. From Yabe (1985).

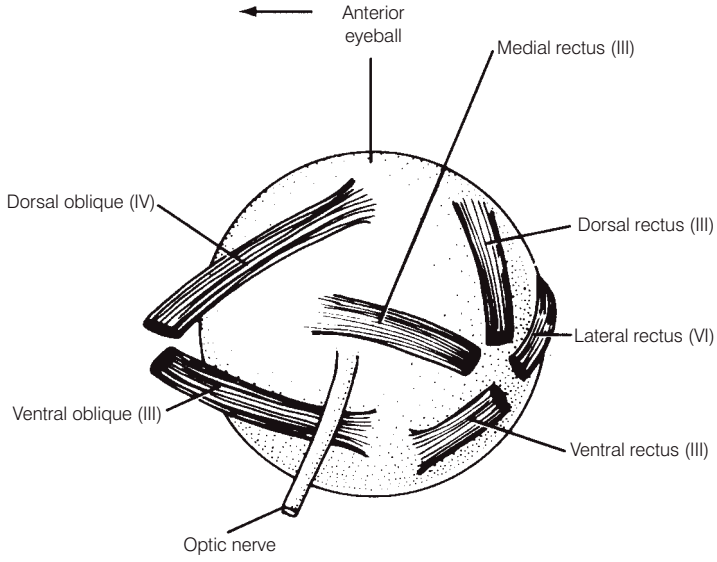


Figure 4.2
Extrinsic eye muscles of a fish. The cranial nerves that supply the muscles are indicated by Roman numerals. From Walker and Liem (1994).

Dorsal gill-arch muscles

The dorsal gill-arch musculature, aspects of the associated gill-arch skeleton, the **transversus ventralis 4**, and the semicircular ligament were recently described for many species of fishes in over 200 families and over 300 genera of bony fishes in a massive, superbly illustrated study by Springer and Johnson (2004). They found that the transversus dorsalis was much more complex than previously recognized and was useful for defining various groups of fishes. A cladistic analysis of the dorsal gill-arch musculature and gill-arch skeletal characters (Springer & Orrell 2004) showed groups such as the Percopsiformes and the Ophidiiformes to be monophyletic, whereas other groups such as the Paracanthopterygii and the Labroidei were polyphyletic.

Fin muscles

Muscles are arranged in pairs at the bases of the dorsal and anal fins: **protractors** erect the fins and **retractors** depress the fins. In addition, **lateral inclinators** function to bend the soft rays of the anal and second dorsal fins. For the paired fins, a single ventral **abductor** muscle pulls the fin ventrally and cranially. An opposing dorsal **adductor** muscle pulls the fin dorsally and caudally.

Eye muscles

Extrinsic eye muscles move the eye within its orbit. Eye muscles are evolutionarily very conservative, in that most vertebrates have the same three pairs of these striated muscles: **inferior** or **ventral** and **superior** or **dorsal oblique**; **inferior** or **ventral** and **superior** or **dorsal rectus**; and **external** or **lateral** and **internal** or **medial rectus** (Fig. 4.2). Eye muscles are innervated by three cranial nerves: superior oblique by the trochlear (IV), external rectus by the abducens (VI), and the other four by the oculomotor (III). Posteriorly, the eye muscles insert into dome-shaped cavities called **myodomes** in actinopterygian fishes. A **suspensory ligament** above the lens and a **retractor lentis** muscle below form the focusing muscle of the eye.

Eye muscles have been converted into two remarkable structures in fishes: an electric organ in the Electric Stargazer (*Astroscopus*, Uranoscopidae) and heater organs in two suborders of perciform fishes (Xiphioidei and Scombroidei). The upper edges of the four uppermost eye muscles form an electric organ in the Electric Stargazer. During development, the portion from the superior rectus loses its innervation from the trochlear nerve, and the portion from the external rectus loses its connection with the abducens, so that the electric organ in adult stargazers is innervated solely by the oculomotor nerve (Dahlgren 1927). Large stargazers can produce an electric discharge from these muscles strong enough to incapacitate a careless human handler. Their usual function is presumably to stun prey or deter predators. In billfishes (Istiophoridae and Xiphiidae), the superior rectus has been converted into a heat-producing muscle that keeps the eye warm during incursions into deep, cold waters (Box 4.1). In the Butterfly

Box 4.1

Brain heaters in "billfishes"

The largest, swiftest, widest ranging teleosts are the marlins and sailfishes (Istiophoridae) and swordfish (Xiphiidae). These "billfishes" maintain elevated brain and eye temperatures, perhaps allowing them to hunt in cold water without experiencing a decrease in brain and visual function (Block et al. 1993). During development, one of the eye muscles (the superior rectus) develops the capability of generating heat without contracting. This is the result of a loss of the contractile filaments, which take up most of the volume of normal skeletal muscle cells, and a dramatic increase in the amount of mitochondria, which may take up as much as one-half to two-thirds of the cell volume of these specialized thermogenic cells. In addition, these modified cells have high levels of myogoblin, an oxygen-storing protein indicative of high metabolic activity. They also have an unusually large sarcoplasmic reticulum, the organelle responsible for calcium storage in skeletal muscles. It seems that the central nervous system stimulates these thermogenic cells in the same way that normal skeletal muscle cells become activated. The release of calcium from the sarcoplasmic reticulum does not, however, lead to contraction. Because there are no contractile proteins and associated calcium-binding proteins, this excess calcium is rapidly pumped back into the sarcoplasmic reticulum. Heat is released by the addition of these ion pumps (Fig. 4.3). In addition, the high levels of intracellular calcium may stimulate metabolic activity of mitochondria, resulting in additional heat production (Block 1991).

Interestingly, modified, noncontractile muscle cells also make up the electricity-generating electroplaques of electric fishes (torpedo rays, knifefishes, Electric Eel, etc.). Hence two very different, specialized cell types – thermogenic and electrogenic – arise from alterations in developmental pathways associated with the basic muscle cell.

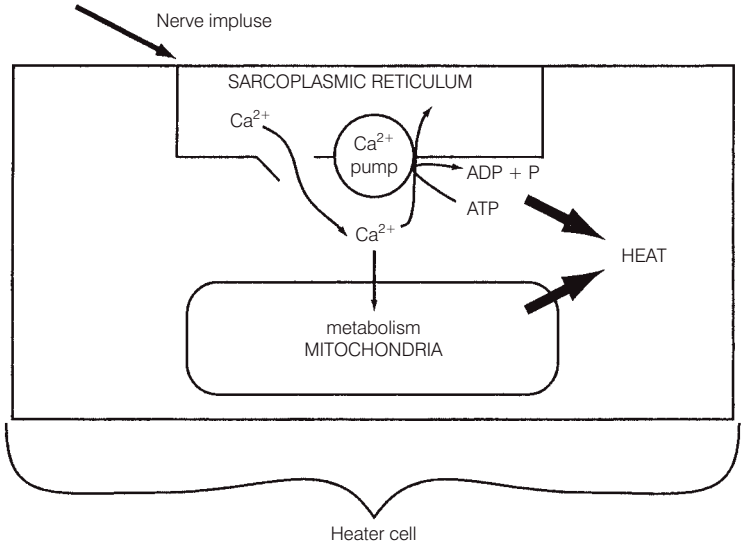


Figure 4.3
Stimulation of the modified muscle cells of the billfish brain heater releases calcium from the sarcoplasmic reticulum (SR), which is then transported back across the SR membrane. The cycling of calcium at the membrane generates heat. It is speculated that the excess calcium may also stimulate mitochondrial metabolism, generating heat.

Mackerel *Gasterochisma* (Scombridae), the external rectus is the muscle that becomes the heater organ (Block 1991), showing independent evolution of this character (see Chapter 7, Heterothermic fishes).

Sonic muscles

Fish sonic muscles are the fastest muscles in vertebrates (Parmentier et al. 2006). They are specialized fast-contracting striated muscles. Based on their origins and insertions, there are two types of sonic muscles. **Intrinsic** sonic muscles completely attach to the wall of the gas bladder as in toadfishes (Batrachoididae) and sea robins (Triglidae). **Extrinsic** sonic muscles have various origins and insertions but generally these paired muscles insert on the gas bladder or a neighboring structure. They are found in cusk-eels (Ophidiiformes), squirrelfishes (Holocentridae), and croakers (Sciaenidae).

Smooth muscle

Smooth muscles line the walls of the digestive tract. They are arranged in bundles of longitudinal and circular muscles that work in opposition to one another to permit peristaltic transport of food. Smooth muscles are associated with the swim bladder and move products along the ducts of the reproductive and excretory tracts. The lens muscle of the eye, also a smooth muscle, moves the lens, dilating or constricting it automatically in response to changing light.

Cardiac muscle

Cardiac or heart muscle is dark red involuntary muscle. It is thickest in the walls of the ventricle.

Ligaments

Ligaments are nonelastic strands of fibrous connective tissue that serve to attach bones and/or cartilages to one another. Names of ligaments usually include their initial and terminal points. Some, however, are named after their shape or after persons. **Baudelot's ligament** is a strong white ligament that originates on the ventrolateral aspect of an anterior vertebra (usually the first) in lower teleosts or on the posterior part of the skull (usually the basioccipital) in advanced teleosts and inserts on the inner part of the cleithrum. Baudelot's ligament helps anchor the pectoral girdles to the sides of the fish.

White muscle versus red muscle

Faced with the conflicting demands of low-speed, economical cruising versus short bursts of maximum speed, fishes have solved the problem by dividing the locomotory system into two systems with different fiber types, white and red (Bone 1978; Webb 1993). **White muscle** makes up the majority of the postcranial body of most fishes. It is used anaerobically in short-duration, burst swimming but fatigues quickly. White muscle gets its color because its fibers lack myoglobin and because it has comparatively little vascularization and hence a limited oxygen supply. White muscle fibers are relatively large in diameter, up to 300 μm. White muscle fibers have relatively few, small mitochondria, with energy resulting from anaerobic glycolysis. Muscle glycogen is depleted rapidly during contraction, producing large amounts of lactates that may require up to 12 h for full recovery after glycogen depletion (see Chapter 5, Respiration and ventilation).

Red muscle usually forms a thin, lateral, superficial sheet under the skin between the epaxial and hypaxial muscle masses on each side of the fish. Red muscle is much better developed in muscles involved in sustained swimming, such as lateral red muscle in tunas and pectoral fin muscles in wrasses and parrotfishes. Red muscle is hard to fatigue because it is highly vascularized and is therefore provided with a rich oxygen supply. The red color is caused by abundant myoglobin. In contrast with white muscle, red muscle has small-diameter fibers (18–75 μm) and high blood volume (three times the number of capillaries of white muscle per unit weight). Mitochondria in red muscle are large and abundant and energy is supplied by the aerobic oxidation of fats. During exercise, little change occurs in muscle glycogen or in the build-up of lactates; recovery after exercise is rapid. The strong taste of the prominent lateral red muscle in tunas (*chiai* in Japanese) leads to its being picked out from cooked tuna prior to canning for human consumption. (It is canned for cat food, which is why tuna cat food smells, and tastes, so strong.)

Lamnid sharks and advanced tunas (tribe Thunnini) have more and deeper portions of red muscle than other fishes. A countercurrent heat exchanger system (see Chapter 7, Heterothermic fishes) between the arterioles and venules of the cutaneous artery and vein ensures that the heat produced by muscular contraction remains in those tissues and is not carried off by the circulatory system to be lost at the gills. In at least the Atlantic Bluefin Tuna (*Thunnus thynnus*), this heat exchanger may function in actual regulation of body temperature (Carey & Lawson 1973). Cross-sections of the body in representative scombrids show increasing development and internalization of the red muscles phylogenetically from mackerels to tunas (Sharp & Pirages 1978).

Some fishes, such as the Scup (*Stenotomus chrysops*), also have another type of muscle. **Pink muscle** is intermediate between red and white muscle in levels of myoglobin, giving it a pink color, and is also intermediate in the other descriptive and metabolic qualities detailed above (Webb 1993). Like red muscle, pink muscle is used for sustained swimming and is recruited after red muscle but before white muscle.

Another variation on muscle color and function occurs in the Antarctic notothenioid family Channichthyidae (see Chapter 18, Polar regions). Many channichthyids have blood but lack hemoglobin, leading them to being called "bloodless". They even lack typical red muscle, instead having yellow muscle in the heart and in the adductor and abductor muscles of the pectoral fin. The protein composition of yellow muscle is similar to that of normal red muscle in fishes with hemoglobin (Hamoir & Geradin-Otthiers 1980).

Electric organ muscles

Fishes in six different evolutionary lineages have developed the ability to amplify the usual electrical production associated with muscle contractions (see Chapter 6, Electroreception). The muscles involved in electrogeneration are modified skeletal muscles. Caudal skeletal muscles, and sometimes lateral body muscles as well, are modified for electrogeneration in the Rajidae, Mormyridae, Gymnotiformes, and Malapteruridae. In torpedo rays (Torpedinidae, Narcinidae), hypobranchial muscles are involved, whereas an extrinsic eye muscle generates strong electrical discharges in the teleostean Electric Stargazer, *Astroscopus* (see above).

Only a few of the major muscles have been discussed here; see Stiassny (1999) and Winterbottom (1974) for a complete treatment.

Cardiovascular system

The cardiovascular system serves all bodily functions but is most closely associated with respiration, excretion, osmoregulation, and digestion. The cardiovascular system is the system of arteries, veins, and capillaries that carry respiratory gases, wastes, excretory metabolites, minerals, and nutrients. The cardiovascular systems of only a few fish species have been investigated extensively, most notably in hagfish, dogfish, skate, Port Jackson shark, trout, salmon, carp, cod, eel, and lungfishes (see Randall 1970; Satchell 1991; Farrell 1993).

Anatomy

The basic pattern of blood flow in fishes involves a single-pump, single-circuit system – from the heart to the gills to the body and back to the heart (Fig. 4.4).

The heart is located posterior and ventral to the gills in all fishes, although it is located farther anterior in teleosts than in chondrichthyans. It lies in a membranous **pericardial cavity** that is lined with **parietal pericardium**. The basic fish heart consists of four chambers in series: venous blood enters (i) the **sinus venosus** (a thin-walled sac) from the **ducts of Cuvier** and the **hepatic veins**; it next flows into (ii) the **atrium**; then into (iii) the **ventricle**, a thick-walled pump; and finally blood flows out of the heart into (iv) the **conus** or **bulbus arteriosus** (Farrell & Jones 1992). The conus arteriosus is a barrel-shaped chamber invested with cardiac muscle, present in Chondrichthyes and lungfishes (Dipnoi). The muscular conus arteriosus is replaced by the nonmuscular bulbus arteriosus in actinopterygian fishes. The bulbus is an onion-shaped elastic reservoir that is passively dilated with blood as it exits the ventricle. The bulbus dampens pressure oscillations, thereby providing continuous rather than pulsed blood supply to the body.

In lungfishes, the atrium and ventricle are partly divided by a partition, partially separating oxygenated and deoxygenated blood, a step toward development of the two-pump, four-chambered heart of tetrapods. This division is least complete in the Australian *Neoceratodus*, which is least dependent on atmospheric air, and is most complete in the South American *Lepidosiren*, which is most dependent on atmospheric air for respiration.

Heart valves prevent backflow of blood and maintain pressure in the circulatory system. Valves may be present between each of the sections of the heart. **Sinoauricular valves** (usually composed of both endocardial and myocardial muscle) separate the sinus venosus and atrium. **Auriculoventricular** or atrioventricular **valves** vary in number depending on the group: Chondrichthyes and most bony

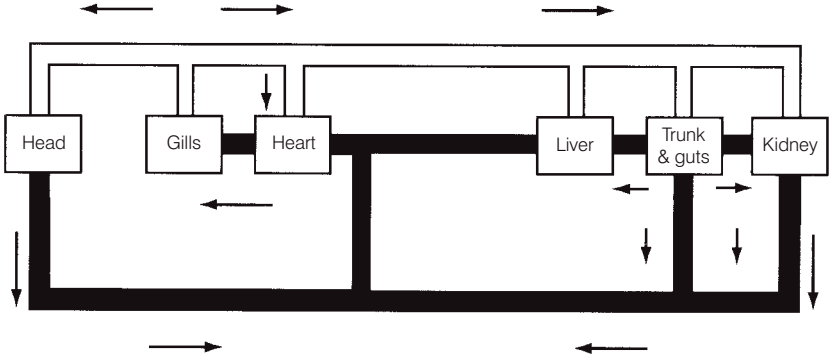


Figure 4.4
Block diagram showing the simplest type of fish circulatory system. Solid black vessels contain blood of lower oxygen content; white vessels contain blood with higher oxygen content. Arrows indicate direction of blood flow. From Mott (1957).

fishes have two rows of valves; the Bowfin has four rows, the North American Paddlefish has five rows, whereas gars and bichirs (*Polypterus*) have six rows. These valves are absent in lungfishes, which do have valves in the conus arteriosus. The number of **ventriculobulbar valves** is related to the length of the conus. There is usually one or, rarely, two in bony fishes, two to seven in Chondrichthyes, and up to 74 in eight rows in gars. Valves outside the heart region can occur in various parts of the circulatory system of fishes, such as segmental arteries and veins in the caudal regions of the Port Jackson Shark and teleost veins.

Blood is supplied to heart muscle from anterior hypobranchial arteries in Chondrichthyes, Actinopterygii, and *Neoceratodus*. In *Lepidosiren*, the coronary supply originates from the second afferent artery. Hagfishes have no special coronary circulation; they also differ in other regards. Nervous innervation of all fish hearts, except in the hagfish, is from the vagus. Hagfishes also have several accessory hearts in parts of the venous system (Farrell 1993).

Heart size as a proportion of body weight is lower in fishes than in other vertebrates. Inactive fishes have very small hearts, making up less than 1 part per 1000 parts body weight. More active fishes have relatively large hearts. For example, in mackerels and tunas, the heart makes up 1.2 parts per 1000 parts body weight, and in flying fishes (Exocoetidae), the heart constitutes 2.1 parts per 1000 parts body weight.

Blood vessels of the gills and head

The number of **afferent branchial arteries** bringing oxygen-deficient blood *to* the gills from the ventral aorta varies among different groups of fishes. Hagfishes and lampreys have seven to 14, the number depending on the number of gill pouches. Most Chondrichthyes have four, but sharks and rays with more gills have more arteries, such as *Hexanchus*, the Six-gilled Shark, which has five, and the Seven-gilled Shark, *Heptranchias*, which has six. Lungfishes have four to five afferent branchial arteries, whereas bony fishes have four (Fig. 4.5).

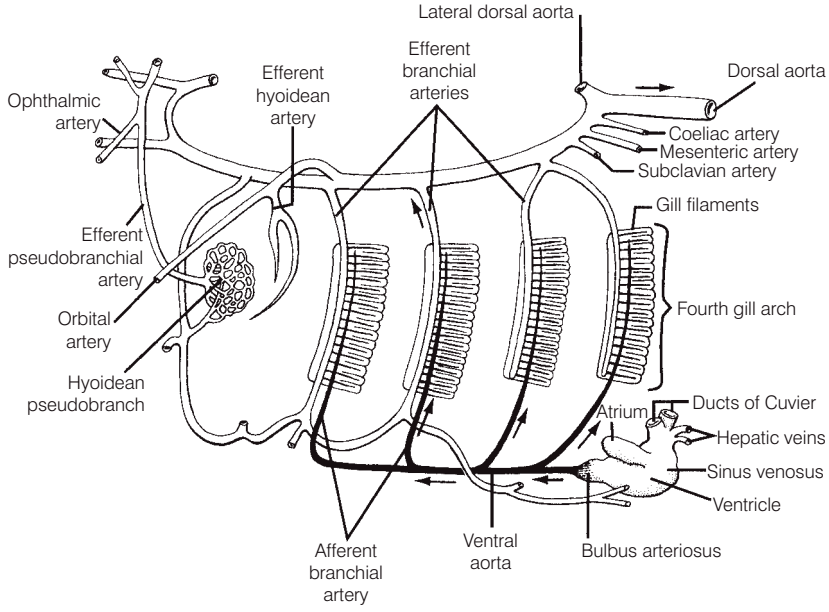
Efferent branchial arteries bring oxygenated blood from the gills to the rest of the body. These arteries merge to form the dorsal aorta, the largest and longest artery in a fish's body. Efferent branchial arteries number one per hemibranch in Chondrichthyes and one per holobranch in bony fishes. **Internal carotid arteries** run from the aorta to the brain. Major veins such as the facial, orbital, postorbital, and cerebral join into paired **anterior cardinal veins**, which empty into the **common cardinal** (also called the duct of Cuvier) and then into the heart. The jugular vein collects blood from the lower head and also empties into the common cardinal in Actinopterygii.

Many fishes have a pseudobranch, a small structure under the operculum composed of gill-like filaments that may provide oxygenated blood to the visual system (Box 4.2).

Blood vessels of the body

The **dorsal aorta** is the main route of transport of oxygenated blood from the gills to the rest of the body (Fig. 4.6). It lies directly ventral to the vertebral column in the trunk region and gives off major vessels and segmental arteries. The **subclavian artery** goes to the pectoral girdle, the **coeliaco-mesenteric artery** supplies the viscera, and the **iliac** or **renal artery** supplies the kidneys. The dorsal aorta becomes

Figure 4.5
Gills and blood vessels of the head of a cod (*Gadus*). From Lagler et al. (1977).



Box 4.2

The pseudobranch

Many fishes have a **pseudobranch**, a small structure under the operculum composed of filaments similar to those in the gills. It was named pseudobranch, or false gill, because, unlike the true gills, the blood reaching it is oxygen-rich blood, not venous oxygen-deficient blood. The history of the pseudobranch and speculations on its function make an interesting story (Laurent & Dunel-Erb 1984). In the 1700s, Broussenot thought it had a respiratory function; in the 1800s, Hyrtl noted that it receives arterial blood, and Müller believed it was associated with vision. Three important morphological features of the pseudobranch have fueled speculation about its function.

1. A pseudobranch covered with epithelium is rich in a respiratory substance, carbonic anhydrase. Is it, therefore, an endocrine organ?
2. The pseudobranch is associated with chloride cells (see Chapter 7, Control of osmoregulation and excretion). Does it have an osmoregulatory function?
3. The pseudobranch has rich nervous innervation. Could it have a sensory role?

The path of blood to and from the pseudobranch in Actinopterygii suggests that the pseudobranch is involved in providing oxygenated blood to the eye. Blood passes from the efferent hyoidean artery to the afferent pseudobranchial artery to the pseudobranchial capillaries to the ophthalmic artery to the choroid gland of the eye. The **choroid rete mirabile** is a large, discrete organ behind the retina of the eye. It is composed of several thousand capillaries arranged countercurrent to each other, a very effective mechanism for maximizing gas exchange. The pseudobranch, in combination with the countercurrent multiplier system of the choroid rete, modifies incoming oxygenated arterial blood by concentrating oxygen without building up carbon dioxide.

Not all fishes possess pseudobranchs (e.g., adult eels, Anguilliformes, and catfishes, Siluriformes, lack them). However, these fishes are mostly nocturnal in habit and rely heavily on non-visual senses. Hence it is not surprising that the complex circulatory apparatus that supplies highly oxygenated blood to the eye has been lost in these groups. Interestingly, larval eels do possess a pseudobranch, and it has been speculated that it serves a respiratory function in these larvae. It is generally accepted that the chondrichthyan spiracular gill is homologous to the actinopterygian pseudobranch.

known as the **caudal artery** upon entering the closed haemal canal of the caudal vertebrae.

The major return route of blood from most of the body is the **postcardinal vein.** It is best developed on the right side and empties into the common cardinal or ducts of Cuvier, then into the sinus venosus, and finally into the heart proper.

In the advanced tunas (tribe Thunnini), an additional pair of large arteries, the **cutaneous arteries**, exit the dorsal aorta posterior to the coeliaco-mesenteric artery and run laterally between the ribs. As these arteries approach the fish's skin, they divide into two vessels, each of which runs posteriorly, sending out arterioles to the underlying red muscle. After passing through an extensive network of capillaries – the countercurrent heat exchanger that retains metabolic heat in the red muscle – the cutaneous vein returns the unheated blood to the heart. Phylogenetically, the most advanced tunas show the greatest development of the subcutaneous circulatory system (Fig. 4.7).

Lymphatic system

The lymphatic system is derived from the venous part of the blood vascular system and is similar to that of other vertebrates. Lymph is collected by paired and unpaired ducts and sinuses that empty into the main blood system. Hagfishes and lampreys have more connections to the venous system; they essentially have a hemolymph system. At least some species of lampreys and bony fishes have contractile lymph "hearts". Chondrichthyes have lymph vessels but do not have sinuses or contractile lymph "hearts".

Blood

Paralleling the trend in heart size discussed above, the volume of blood in teleosts is less than in Chondrichthyes, and both have lower blood volumes than tetrapods. Hagfishes and lampreys have the greatest volume among fishes. Blood itself is composed of plasma and blood cells. Plasma contains dissolved minerals, digestive products,

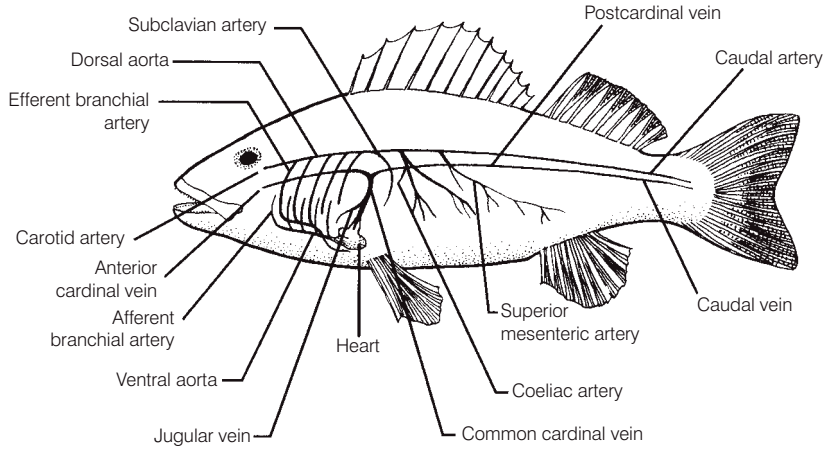


Figure 4.6
Main blood vessels of a bony fish. After Lagler et al. (1977).

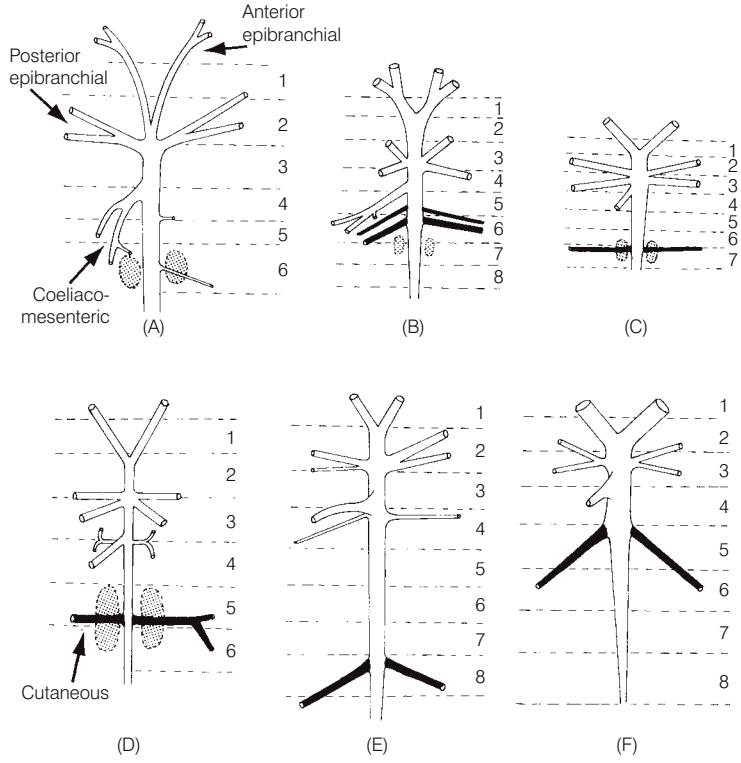


Figure 4.7
Anterior arterial system in ventral view in the Scombridae, showing the phylogenetic increase in development of the subcutaneous circulatory system (darkened vessels). Numbers indicate vertebrae; stippled areas show where pharyngeal muscles originate. (A) Wahoo (*Acanthocybium*); (B) Frigate tuna (*Auxis*); (C) Little tuna (*Euthynnus*); (D) Skipjack (*Katsuwonus*); (E) Longtail Tuna (*Thunnus tonggol*); (F) Albacore (*Thunnus alalunga*). From Collette (1979).

waste products, enzymes, antibodies, and dissolved gases, but few detailed analyses of fish blood have been published.

Solutes in the blood function to lower its freezing point. Freezing point depression of blood plasma is –0.5°C in freshwater bony fishes, –1.0°C in freshwater Chondrichthyes, –0.6 to –1.0°C in marine bony fishes, and –2.2°C in marine Chondrichthyes versus a freezing point of –2.1°C for sea water. Antarctic notothenioids (see Chapter 18) have additional blood antifreeze glycoproteins that reduce the freezing point of their blood to –0.9 to –1.5°C, with some notothenioids showing freezing points as low as –3°C.

Red blood cells (RBCs) account for nearly 99% of oxygen uptake. RBCs are nucleated, yellowish-red, oval cells in most fishes but are round in lampreys. Fishes have relatively fewer and larger RBCs than do mammals. Human RBCs measure 7.9 µm across, whereas fish RBCs range from 7 µm in some wrasses to relatively giant 36 µm cells in the African lungfishes, *Protopterus*. RBCs are absent in notothenioids (see above) and in the leptocephalus larvae of eels.

Alimentary canal

As in other vertebrates, the alimentary tract can be divided into anterior and posterior regions. The anterior part

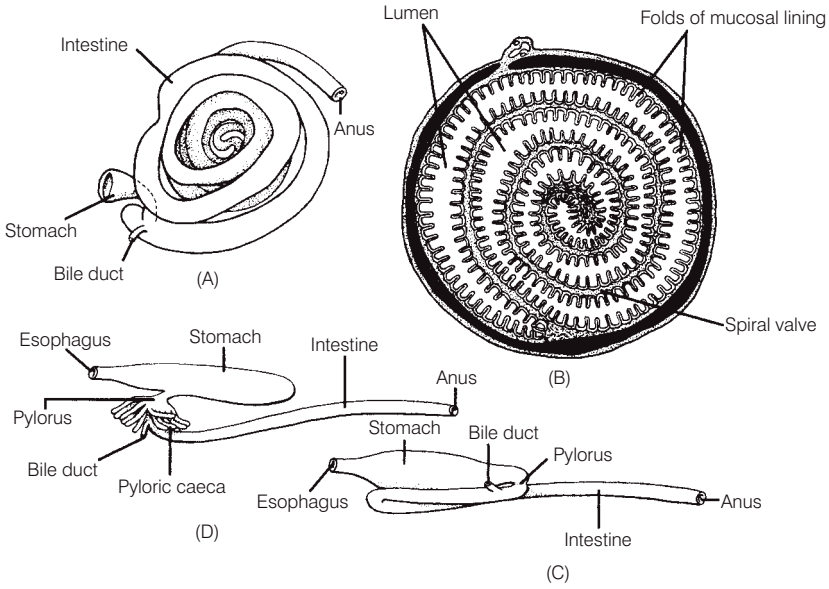


Figure 4.8

Variation in intestinal length and other features among carnivorous and herbivorous fishes. (A) An herbivorous catfish (Loricariidae). (B) Spiral valve in cross-section of intestine of a shark. (C) A carnivore, the Northern Pike (*Esox lucius*). (D) A carnivore, a perch (*Perca*). From Lagler et al. (1977).

consists of the mouth, buccal cavity, and pharynx. The posterior part consists of the foregut (esophagus and stomach), midgut or intestine, and hindgut or rectum. Voluntary striated muscle extends from the buccal cavity into the esophagus, involuntary smooth muscle from the posterior portion of the esophagus through the large intestine. Barrington (1957), Kapoor et al. (1975), and Fange and Grove (1979) provide detailed accounts of the alimentary tracts of fishes.

In hagfishes and lampreys, the absence of true jaws is correlated with the absence of a stomach. Presumably, the evolution of jaws permitted capture of larger prey, making a storage organ, the stomach, highly advantageous. Both hagfishes and lampreys have a straight intestine, but the surface area of the intestine is increased in the lampreys by the **typhlosole**, a fold in the intestinal walls. Chondrichthyes increase the surface area of the intestine by means of a **spiral valve**, a sort of a spiral staircase inside the intestine (Fig. 4.8).

The anatomy of the digestive tract in bony fishes deserves additional description. The buccal cavity (mouth) and pharynx lack the salivary glands present in mammals. These areas are lined with stratified epithelium, mucous cells, and, frequently, taste buds. This area is concerned with seizure, control, and probably also selection of food.

The **esophagus** is a short, thick-walled tube lined with stratified ciliated epithelium, mucous-secreting goblet cells, and, often, taste buds. The anterior portion has striated muscles, the posterior part smooth muscles that produce peristaltic movement of food toward the stomach. The esophagus is very distensible, so choking is rare, but miscalculation of prey size or armament can lead to the death of the predator, as in the case of a stickleback (Gasterosteidae) becoming stuck in the throat of a pickerel (*Esox*).

In predaceous fishes, the **stomach** is lined with columnar epithelium with mucous-secreting cells and one type of glandular cell that produces pepsin and hydrochloric acid. Although usually a fairly simple structure, evolutionary modifications of the fish stomach have led to some unusual functions. For example, the stomach, not the gas bladder, is used for defense by blowfishes and porcupinefishes (Tetraodontidae and Diodontidae), by taking in water or air (see Box 20.1). The stomach is modified into a grinding organ in sturgeons (Acipenseridae), gizzard shads (*Dorosoma*), and mullets (Mugilidae) and is used to extract oxygen in some of the South American armored catfishes (Loricariidae).

Many gnathostome fishes lack true stomachs. This is a secondary condition with no simple ecological explanation (Kapoor et al. 1975). Fishes without true stomachs include chimaeras (Holocephali) and lungfishes (Dipnoi). This condition is best documented in the Teleostei, including minnows (Cyprinidae) such as the European *Rutilus*, killifishes (Cyprinodontidae), wrasses (Labridae; see Chao 1973), and parrotfishes (Scaridae). Characteristics of the stomachless condition are both cytological and biochemical. Cytologically, no gastric epithelium or glands are present. The stratified epithelium of the esophagus grades into the columnar epithelium of the intestine. Biochemically, no pepsin or hydrochloric acid is produced, making it impossible to dissolve shells or bones.

The **intestine** of most fishes is lined with simple columnar epithelium and goblet cells. Usually no multicellular glands are present. The chief exception to this is in the cods (Gadidae), which have small tubular glands in the intestinal wall.

Pyloric caeca, fingerlike pouches that connect to the intestine near the pylorus, are often present. Pyloric caeca

may function in absorption or digestion. They vary in number from only three in a scorpionfish (*Setarches*) to thousands that form a caecal mass in tunas. The number of pyloric caeca is useful in the classification of some groups, like the Salmonidae.

The length of the intestine varies and is generally correlated with feeding habits (see Chapter 19, Scavengers, detritivores, and herbivores). Carnivores such as pickerels (*Esox*) and perches (*Perca*) have very short intestines, one-third to three-quarters of their body length. The intestine is much longer in herbivores and detritus feeders, 2–20 times the body length. In the herbivorous North American Stoneroller Minnow (*Campostoma*), the intestine is very long and wrapped around the swim bladder. The important factor is not only the actual length of the intestine but also the internal surface area of the intestinal mucosa. In addition to sharks, as mentioned earlier, some primitive bony fishes such as the Coelacanths (*Latimeria*), lungfishes, gars, and Ladyfish (*Elops*) have a spiral valve intestine that increases the surface area internally (see Fig. 4.8).

The **hindgut** or **rectum** is not as well defined externally in fishes as it is in tetrapods. Generally, the muscle layer near the rectum is thicker than in anterior regions, and the number of goblet cells in the large intestine increases in the rectal region. In Chondrichthyes, the hindgut is lined with stratified epithelium, contrasting with a single cell layer in the midgut. An iliocaecal valve between the small and large intestines is often found in teleosts, but this valve is absent in Chondrichthyes, Dipnoi, and *Polypterus*.

The liver and pancreas both participate in digestion. The **liver** develops as a ventral evagination of the intestine, as in other vertebrates. The anterior portion develops into the liver proper, and the posterior portion into the gallbladder and bile duct. The liver also stores fat in some fishes. Before vitamins A and D were synthesized, cods and sharks were harvested for their liver oil, which is rich in these vitamins. The **gallbladder** is a thin-walled temporary storage organ for the bile. It empties into the intestine near the pylorus by contraction of smooth muscles. Bile is usually green due to bile pigments (biliverdin and bilirubin) resulting from the breakdown of blood cells and hemoglobin, and also contains fat-emulsifying bile salts, which may assist in converting the acidity of the stomach to the neutral conditions in the intestine. The **pancreas** is both an endocrine organ and an exocrine organ that produces digestive enzymes. These enzymes include proteases such as trypsin, carbohydrases such as amylase and lipase, and, in some insect-feeding fishes, chitinase. The pancreas is a compact, often two-lobed structure in Chondrichthyes, is distinct in soft-rayed teleosts, but becomes incorporated into the liver as a hepatopancreas in most spiny-rayed teleosts (except for parrotfishes). The anatomically and histologically diffuse nature of the pancreas makes it difficult to study pancreatic function in these advanced fishes.

The various parts of the alimentary tract work together in conjunction with the feeding habits of a fish. For example, de Groot (1971) presented an instructive comparison of correlations between various organ systems and feeding in three families of flatfishes. The Bothidae, which are diurnal carnivores, possess a single loop of the intestine, heavily toothed gill rakers, small olfactory lobes of the brain, and large optic lobes. The Pleuronectidae are also diurnal but have complex loops of the intestine, less toothed gill rakers, medium olfactory lobes, and large optic lobes. The Soleidae, which are nocturnal feeders, have more complex intestinal loops, few gill raker teeth, large olfactory lobes, and small optic lobes.

Gas bladder

The **gas bladder** (swim bladder) is a gas-filled sac located between the alimentary canal and the kidneys (Jones 1957; Marshall 1960). It is filled with carbon dioxide, oxygen, and nitrogen in different proportions than occur in air, making the term "air bladder" inappropriate. The original function of the gas bladder was probably as a lung, but in most fishes today it functions mainly as a hydrostatic organ that helps control buoyancy. It also plays a role in respiration, sound production, and sound reception in some fishes. Some species in at least 79 of 425 families of extant teleosts have lost their gas bladders, at least as adults (McCune & Carlson 2004). Most of these fishes are either benthic or deepsea species. Billfishes (Istiophoridae) and two genera of halfbeaks (all 10 species of *Hemiramphus* and one of two species of *Oxyporhamphus*) have a vesicular gas bladder composed of many discrete gas-filled vesicles (Tibbetts et al. 2007).

Embryologically, the gas bladder is a two-layered (tunica externa and tunica interna), specialized outgrowth of the roof of the foregut and possesses tissues similar to those of the foregut, as shown here:

Tissue	*Layer*	*Embryological origin*
a. Peritoneal investiture b. collagenous layer	tunica externa	mesoderm
c. fibrous layer d. smooth muscle	tunica Interna	mesoderm
e. bladder epithelium	tunica Interna	entoderm

The structures and mechanisms by which gases enter and are released from the gas bladder differ in the major groups of teleosts. The **pneumatic duct** is a connection between the gas bladder and the gut. **Physostomous** fishes retain the connection in adults, whereas **physoclistous** fishes lose the connection in adults, if it is present at all during

development. In physostomous fishes, gas can be taken in and emitted through the pneumatic duct. More primitive soft-rayed teleosts have the primitive physostomous condition; whereas more advanced spiny-rayed fishes are physoclistous, lacking a pneumatic duct (see Chapter 5, Buoyancy regulation).

Another, more complex mechanism, which involves two distinct regions of the gas bladder, has evolved to allow gas exchange in these fishes (Fig. 4.9). The **anteroventral secretory region** contains the gas gland and the rete mirabile. The **gas gland** secretes lactic acid into the beginning of the capillary loop. This acidifies and reduces the solubility of all dissolved gases. A change of 1 pH unit releases 50% of the oxygen bound to hemoglobin. This raises the partial pressure of blood oxygen by the Root and Bohr effects (see Chapter 5, Gas transport).

The **rete mirabile**, or wonder net, is not actually a net but a looping bundle of arterial and venous capillaries associated with the gas gland that functions as a countercurrent multiplier. The rete is better developed in deep-dwelling fishes that have longer retial capillaries, thus providing more surface area and allowing a greater multiplying factor. Rattails (Macrouridae) and ophidioids living at abyssal depths of 4000 m and deeper have retial capillaries 25 mm in length or more; shallow water forms have retes only 1 mm long (Marshall 1971).

The posterodorsal resorptive region of the gas bladder is called the **oval**. It develops from the distal end of the degenerating pneumatic duct and consists of a thin, highly vascularized area. Circular muscles contract and close off the oval, preventing outflow of gases. Longitudinal muscles contract and expose the oval, permitting gas escape. The walls of the gas bladder are lined with a layer of cells containing crystals of guanine 3 μm thick, which decreases permeability by 40 times over an unlined membrane and thus limits gas escape except at the oval, when it is open.

The gas bladder of physostomous fishes receives blood from a branch of the coeliaco-mesenteric artery. Blood is returned to the heart through the hepatic portal system. The rete, oval, and gas bladder wall of physoclists are supplied by the coeliaco-mesenteric artery and blood is returned by a vein from the hepatic portal system. The oval and bladder wall are also supplied by intercostal branches of the dorsal aorta and returned through the postcardinal system.

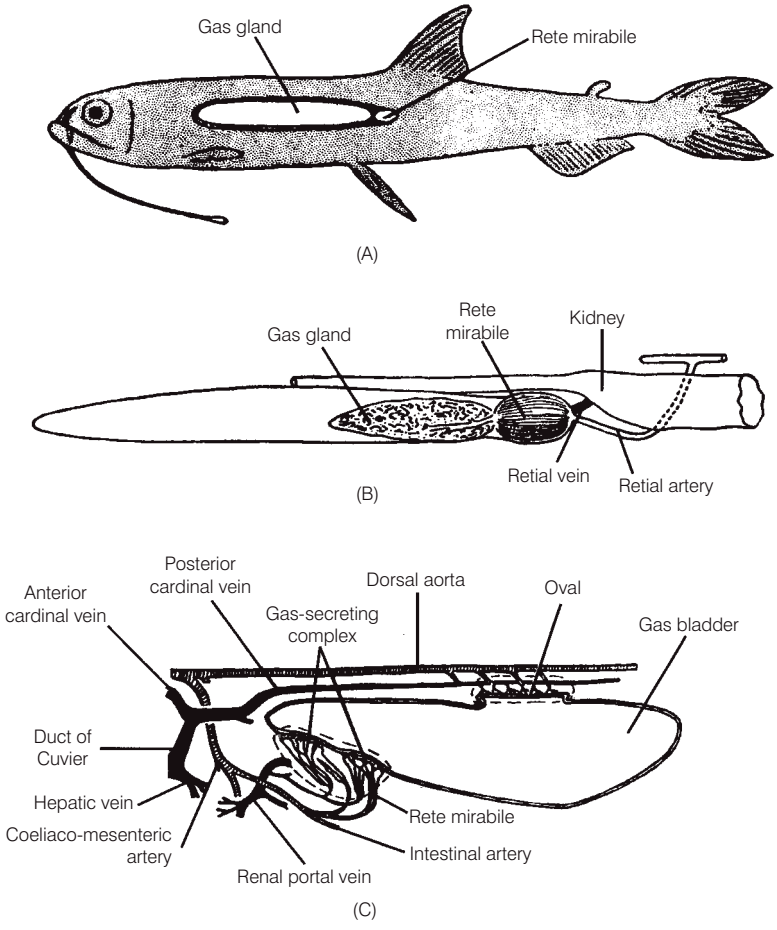


Figure 4.9

The gas bladder. (A) Position of gas bladder in a deepsea snagletooth (*Astronesthes*). (B) Details of the gas bladder in *Astronesthes*. (C) Generalized blood supply of the gas bladder in physoclistous bony fishes. From Lagler et al. (1977).

Nervous innervation of the gas bladder is sympathetic through a branch from the coeliaco-mesenteric ganglion and by branches of the left and right intestinal vagus (X) nerves. Cutting the vagus prevents gas secretion into the gas bladder. Gas secretion is also inhibited by atropine, a cholinesterase blocker. The gas gland has high cholinesterase activity, and the secretory fibers are probably cholinergic. Sensory nerve endings function as stretch receptors, responding to stretching or slackening of the gas bladder, thus providing information to the fish about the relative fullness of the gas bladder.

Kidneys

The **kidneys** are paired longitudinal structures located retroperitoneally (outside of the peritoneal cavity), ventral to the vertebral column. Left and right kidneys frequently join together to form soft black material under the vertebrae from the back of the skull to the end of the body cavity. The kidneys are one of the primary organs involved in excretion and osmoregulation (see Chapter 7, Osmoregulation, excretion, ion and pH balance). Three kinds of kidneys are present in vertebrates: pronephros, mesonephros, and metanephros. A pronephros is present in larval fishes, a mesonephros is the functional kidney in Actinopterygii, and the **metanephros** is the kidney present in tetrapods. Kidney tubules are involved with moving sperm in some fishes, so the two systems are sometimes discussed as the urogenital system.

The **pronephros** has **nephrostomes**, anterior funnels that empty into the body cavity by way of pronephric tubules. Adult hagfishes have an anterior pronephros and a posterior mesonephros, but it appears to be the mesonephros that is the functional kidney (Hickman & Trump 1969). Lampreys have a pronephros until they reach about 12–15 mm when they develop a mesonephros during metamorphosis. A pronephros is a transitional kidney that appears during ontogenetic development of actinopterygian larvae and then is replaced by a mesonephros as the fish grows.

The **mesonephros** is a more complex kidney that does not have funnels emptying into the body cavity. The mesonephros consists of a number of **renal corpuscles**, each composed of a glomerulus surrounded by a Bowman's capsule. The **glomerulus** receives blood from an afferent arteriole from the dorsal aorta. The glomerulus acts as an ultrafilter to remove water, salts, sugars, and nitrogenous wastes from the blood. The filtrate is collected in **Bowman's capsule** and then passes along a **mesonephric tubule** where water, sugars, and other solutes are selectively resorbed. Marine and freshwater fishes differ considerably in kidney structure, reflecting the different problems faced by animals living in solutions of very different solute concentrations (see Chapter 7, Osmoregulation, excretion, ion and pH balance). Freshwater fishes have larger kidneys with more and larger glomeruli, up to 10,000 per kidney and measuring 48–104 μm across (mean of several freshwater species = 71 μm). The glomeruli of marine fishes are only 27–94 μm across (mean of several marine species = 48 μm).

Urine contains water plus creatine, creatinine, urea, ammonia, and other nitrogenous waste products. Only 3–50% of the nitrogenous wastes are excreted through the urine (see Table 7.2), and much of this is as ammonia; most of the rest is excreted as ammonia at the gills during respiration. Some fishes have a storage organ for urine that has been called a "urinary bladder", but it is a posterior evagination of the mesonephric ducts, making it mesodermal in origin and not homologous with the entodermally derived urinary bladder of tetrapods.

Freshwater fishes produce copious amounts of highly dilute urine to avoid "waterlogging" by the large amount of water diffusing in through all semipermeable membranes (see Fig. 7.3). Marine fishes drink sea water to correct dehydration and excrete a low volume of highly concentrated urine. Most nitrogenous wastes are excreted extrarenally through the gills.

Some fishes are **aglomerular**, lacking glomeruli in their kidneys. At least 30 species of aglomerular teleosts are known from seven different families of mostly marine fishes, such as Batrachoididae, Ogcocephalidae, Lophiidae, Antennariidae, Gobiesocidae, Syngnathidae, and Cottidae (Hickman & Trump 1969; Bone et al. 1995). Aglomerular kidneys are unable to excrete sugars and so are therefore of great interest to physiologists studying the function of glomeruli. It would be particularly interesting to study kidney function of freshwater members of the above families to see how they meet the problem of bailing out excess water if they lack glomeruli in their kidneys.

Gonads

As in tetrapods, the sexes in fishes are usually separate (**dioecious**), with males having testes that produce sperm, and females having ovaries that produce eggs. "Fishes as a group exemplify almost every device known among sexually reproducing animals; indeed, they display some variations which may be unique in the animal kingdom" (Hoar 1969, p. 1). Only basic anatomy is treated here; other aspects of reproduction are discussed in Chapters 9, 10, and 21.

Testes

The **testes** are internal, longitudinal, and usually paired. They are suspended by lengthwise mesenteries known as **mesorchia**. The testes lie lateral to the gas bladder when one is present. Kidney tubules and ducts serve variously among different groups of fishes to conduct sperm to the

outside. Testes may constitute as much as 12% of body weight in some species at sexual maturity, although this proportion is usually smaller.

Hagfishes and lampreys have a single testis. Sperm is shed into the peritoneal cavity and then passes through paired genital pores into a urogenital sinus and out through a urogenital papilla.

Among Chondrichthyes, internal fertilization is universal, males using modified pelvic fins, termed **claspers**, to inseminate females. Sperm leave the testis through small coiled tubules, **vasa efferentia**, which are modified mesonephric (kidney) tubules. Sperm pass through **Leydig's gland**, which consists of small glandular tubules derived from the kidney. Secretions of Leydig's gland are involved in spermatophore production. The sperm then go through a **sperm duct**, which is a modified mesonephric duct, and into a **seminal vesicle**, a temporary storage organ that is also secretory.

Among Actinopterygii, the situation is similar, but no true seminal vesicles or sperm sacs are present. Marine catfishes (Ariidae), gobies (Gobiidae), and blennies (Blenniidae) have secondarily derived structures that have also been called seminal vesicles, but these are glandular developments from the sperm ducts and are not comparable to structures with the same names in tetrapods. These vesicles provide secretions that are important in sperm transfer or other breeding activities.

Lungfishes, sturgeons, and gars make varying use of kidney tubules and mesonephric (Wolffian) ducts (Fig. 4.10). In the Bowfin (*Amia*), vasa efferentia bypass the kidney and go to a Wolffian duct. In *Polypterus* and the Teleostei, there is no connection between the kidney and gonads at maturity. The sperm duct is new and originates from the testes. Thus the sperm duct of more primitive fishes such as the Chondrichthyes and Chondrostei is not homologous with that in the Teleostei.

The tubular structure of the teleost testis has two basic types distinguished by the distribution of spermatogonia, the sperm-producing cells. In most teleosts, **spermatogonia** occur along the entire length of the tubules, but in atherinomorph fishes the spermatogonia are confined to the distal end of the tubules (Grier 1981).

Ovaries

The **ovaries** are internal, usually longitudinal, and primitively paired but are often variously fused and shortened. Sometimes only one ovary is present in adults, as in some needlefishes (Belonidae). The number or relative lengths of the ovaries are a useful taxonomic character in some fishes, such as the needlefishes. The ovaries are suspended by a pair of lengthwise mesenteries, the **mesovaria**. The ovaries are typically ventral to the gas bladder. Kidney tubules and

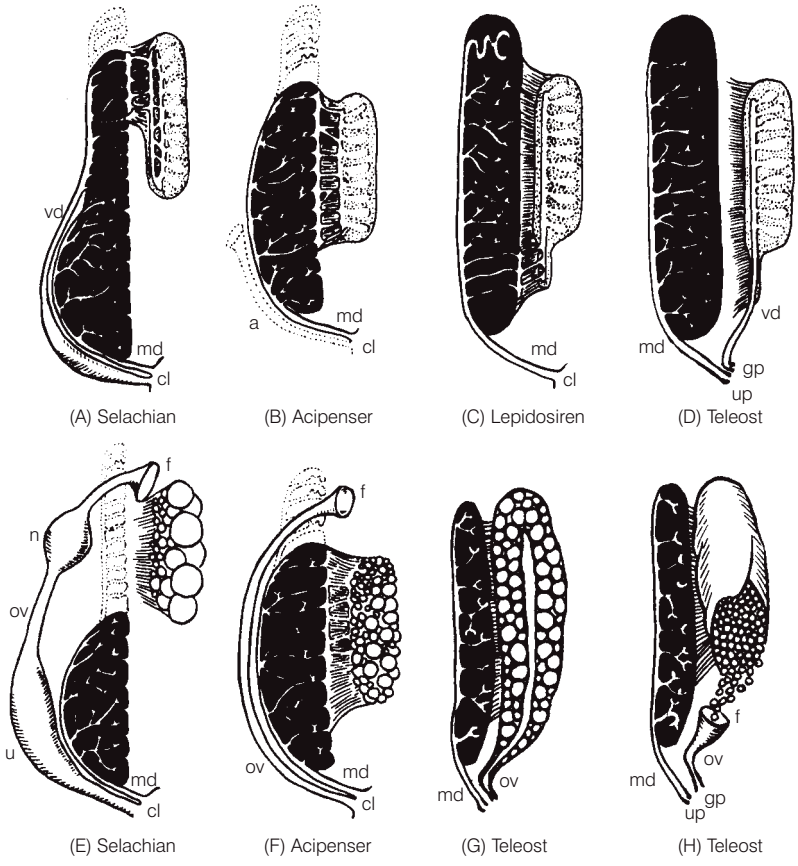


Figure 4.10

Representative types of urogenital systems in fishes. Upper series (A–D), males; lower series (E–H), females; black organs, mesonephric kidneys; stippled organs, testes; organs with circles, ovaries; stippled lines, vestigial structures; a, Müllerian duct; cl, cloaca; f, open funnel of oviduct; gp, genital papilla; l, Leydig's gland; md, mesonephric duct; n, nidamental gland; ov, oviduct; u, uterus; up, urinary pore; vd, vas deferens. From Hoar (1957).

ducts are not used to transport eggs. Ovary mass can be as high as 70% of body weight and tends to increase with body size of individual females.

Ovaries of hagfishes and lampreys have the same basic structure as do the male testes. There is a single ovary, and the eggs are shed into the body cavity and then pass through paired genital pores and out through a urogenital papilla.

In Chondrichthyes, the ovarian capsule is not continuous with the oviduct so eggs are shed into the body cavity, the **gymnovarian** condition. The eggs enter the funnel of the oviduct, which is a **Müllerian duct**, not a modified mesonephric duct; it develops as a posterior continuation of the ovarian tunic. The anterior part of the oviduct is specialized to form a **nidamental** or shell gland where fertilization takes place. The nidamental gland secretes a membrane around the fertilized egg. In **oviparous** (egg-laying) taxa, the membrane is horny, composed of keratin. The nidamental gland may function as a seminal receptacle where sperm are nourished before fertilization. In **viviparous** (live-bearing) species, the posterior part of the oviduct is modified to form a **uterus**, which houses the developing embryo.

In osteichthyan fishes, the primitive gymnovarian condition is found in lungfishes, sturgeons, and the Bowfin. In gars and most teleosts, the lumen of the hollow ovary is continuous with the oviduct, termed the **cystovarian** condition. In trouts and salmons (Salmonoidei) and some other teleosts, the oviducts have been secondarily lost in whole or in part, so the eggs are shed into the peritoneal cavity and reach the outside through pores.

Nervous system

The nervous system can be divided into the cerebrospinal and autonomic systems. The **cerebrospinal** system is composed of the central nervous system and the peripheral nervous system. The **central nervous system** is further subdivided into the brain and the spinal cord (Healey 1957; Bernstein 1970; Northcutt & Davis 1983). The **peripheral system** is composed of the cranial and spinal nerves and the associated sense organs (vision, smell, hearing, lateralis system, touch, taste, and electrical and temperature detection; see Chapter 6). The **autonomic** nervous system is composed of sympathetic and parasympathetic ganglia and fibers.

Central nervous system

Fish brains are on average only 1/15 the size of the brain of a bird or mammal of equal body size. Sharks have much larger brains relative to body size than teleosts and pelagic sharks have larger brains than pelagic teleosts (Linsey & Collins 2006). In pickerels (*Esox*), the brain is only 1/1305 of body weight. Elephantfishes (Mormyridae) have the largest brains among fishes, 1/52 to 1/82 of body weight. This large brain is associated with electroreception, as we shall see later. In the Ocean Sunfish (*Mola mola*), the spinal cord is even shorter than the brain: a 1.5 ton fish, 2.5 m long, has a spinal cord only 15 mm long.

The **brain** can be divided into five parts from anterior to posterior (Fig. 4.11). The most anterior part is the **telencephalon**, or forebrain, which becomes the cerebrum of tetrapods. Its function in fishes is primarily associated with reception and passage of olfactory stimuli. The olfactory nerve (cranial nerve I) runs from the nostrils to the olfactory lobe of the brain. The olfactory lobe is large in hagfishes and lampreys, huge in sharks such as the hammerheads (Sphyrnidae), and moderately large in teleosts such as catfishes that rely heavily on odors when foraging (Fig. 4.11E).

The **diencephalon**, or 'tween brain, lies between the forebrain and the midbrain and is also known as the saccus dorsalis. It functions as a correlation center for incoming and outgoing messages regarding homeostasis and the endocrine system. The **pineal body** is a hollow, invaginated, well-vascularized structure dorsal to the diencephalon and connected to it by a narrow hollow stalk. It frequently underlies a more or less unpigmented area of the cranial roof and is light-sensitive in some if not all fishes. Pineal functions are diverse, including light detection, circadian and seasonal clock dynamics, and color change. The pineal contains neurosensory cells that resemble cones in the retina. Photosensitivity of the pineal has been demonstrated by behavioral tests in Rainbow Trout. Light sensitivity of the pineal may allow it to play a navigation role in the cross-ocean migrations of large tunas such as the Atlantic Bluefin, *Thunnus thynnus* (Rivas 1954; Holmgren 1958; Murphy 1971). The pineal may regulate color change associated with background matching. It also produces an apocrine secretion containing glycogen. There is a possibility that the pineal may also play an endocrine role, in that it produces the hormone melatonin, implying a potential pineal–pituitary relationship.

The **mesencephalon**, or midbrain, is important in vision. The optic nerve (cranial nerve II) brings impulses from the eyes and enters the brain here. The midbrain is also a correlation center for messages coming from other sensory receptors. Fishes have two optic lobes, which are relatively large in sight-feeding species such as trouts and minnows (Fig. 4.11C, D).

The **metencephalon**, or hindbrain, functions in maintaining muscular tone and equilibrium in swimming. The **cerebellum**, a large single lobe, is the largest component of the fish brain. Cranial nerve IV (trochlear) runs from the metencephalon to the eye muscles. The metencephalon is small in lampreys (Petromyzontidae) and almost absent in hagfishes (Myxinidae). In elephantfishes (Mormyridae), the cerebellum is hypertrophied to form the valvula cerebelli (Fig. 4.11F), which extend over the dorsal surface of the telencephalon. This large cerebellum is related to reception of electrical impulses.

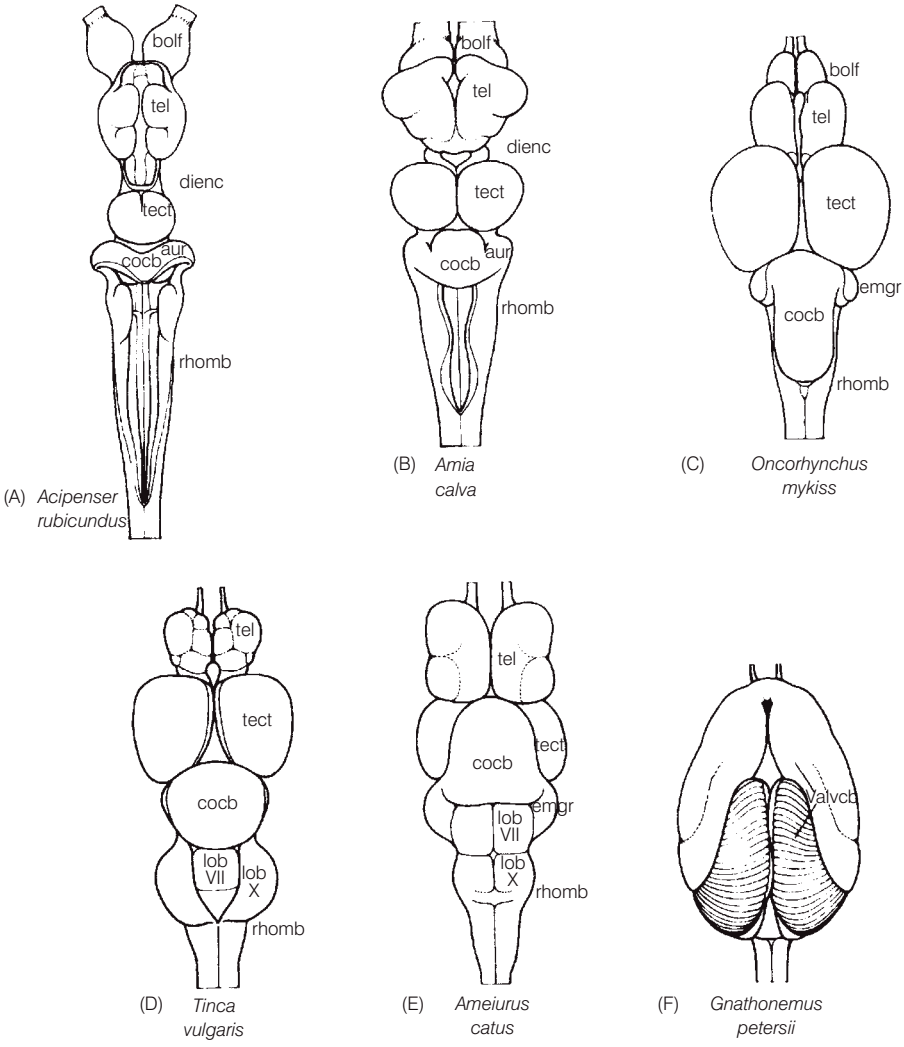


Figure 4.11

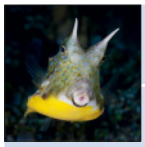
Dorsal views of brains of representative fishes: (A) sturgeon; (B) Bowfin; (C) trout; (D) minnow; (E) catfish; (F) elephantfish (Mormyridae). Major brain parts from anterior to posterior: bolf, olfactory lobe; tel, telencephalon; dienc, diencephalon; tect, optic lobe; aur, auricular cerebelli; cocb, cerebellum; emgr, eminentia granularis; rhomb, myelencephalon; valvcb, valvula cerebelli. From Nieuwenhuys and Pouwels (1983).

The **myelencephalon**, brainstem, or medulla oblongata is the posterior portion of the brain and the enlarged anterior part of the **spinal cord**. Cranial nerves V through X arise here. The myelencephalon serves as the relay station for all the sensory systems except smell (cranial nerve I) and sight (cranial nerve II). It contains centers that control certain somatic and visceral functions. In bony fishes, it also contains respiratory and osmoregulatory centers.

A series of investigators have correlated brain morphology with ecology and behavior: H. M. Evans (1940) studied European freshwater species, H. E. Evans (1952) investigated four species of American minnows (Cyprinidae), and R. J. Miller and H. E. Evans (1965) studied the brains of suckers (Catostomidae).

Peripheral nervous system

The 10 **cranial nerves** in fishes are similar to those in other vertebrates. Cranial nerve I, the **olfactory nerve**, is a sensory nerve that runs from the olfactory bulb to the olfactory lobes. The **optic nerve** (cranial nerve II) runs from the retina to the optic lobes. As in other vertebrates, cranial nerves III (**oculomotor**), IV (**trochlear**), and VI (**abducens**) are somatic motor nerves that innervate the six striated muscles of the eye: IV, the superior oblique; VI, the external rectus; and III, the other four eye muscles. Unlike in most other vertebrates, four cranial nerves (VII through X) innervate parts of the lateral line system. The **trigeminal**, V, is a mixed somatic sensory and motor nerve serving the anterior portion of the head. Cranial nerve VII, the **facial**, and VIII, the **acoustic**, usually join to form the **acousticofacialis** nerve, which then subdivides into four groups of mixed nerves serving the temporal and branchial regions of the head. Patterns of nerves, such as that of the ramus lateralis accessorius of the facial nerve (which innervates taste buds on the posterior head and body), have proved to be useful in assessing relationships of teleosts (Freihofer 1963). The **glossopharyngeal**, IX, is a mixed nerve that supplies the gill region. It often fuses with cranial nerve X, the anterior ramus of the vagus. The **vagus** is a mixed nerve connected to the body lateral line and viscera.



Summary

SUMMARY

1. Fishes have three kinds of muscles (skeletal, smooth, and cardiac, or heart, muscle) and have relatively more skeletal muscle than do other vertebrates.
2. In the locomotory system, white muscle forms most of the postcranial body and is used anaerobically for burst swimming but fatigues quickly. Red muscle usually forms thin, lateral, superficial sheets under the skin; it is used in sustained swimming and fatigues slowly.
3. The basic pattern of the cardiovascular system is a single-pump, single-circuit system that goes from the heart to gills to body and back to the heart. Many fishes have a pseudobranch, a small structure under the operculum composed of gill-like filaments that may provide oxygenated blood to the visual system.
4. The anterior region of the alimentary tract consists of the buccal cavity (mouth) and the pharynx. The posterior region consists of the foregut (esophagus and stomach), midgut or intestine, and hindgut (rectum). Alimentary tract length and structure differ as a function of feeding habits.
5. The gas or swim bladder is a gas-filled sac located between the alimentary canal and the kidneys. It develops from the roof of the foregut. A pneumatic duct connects the gas bladder and the gut in primitive teleosts (physostomous condition). Physostomous fishes can take gas in and emit it through the mouth and pneumatic duct. Advanced teleosts are physoclistous, losing the connection in adults. Physoclistous fishes have a secretory region containing a gas gland and a rete mirabile to produce gas, and an oval where gas is resorbed.
6. Kidneys, paired longitudinal structures ventral to the vertebral column, are one of the primary organs involved in excretion and osmoregulation. A pronephros is present in hagfishes and larval fishes, whereas a mesonephros is the functional kidney in Actinopterygii.
7. The sexes in fishes are usually separate, and the gonads are usually paired. Males have testes that produce sperm, and females have ovaries that produce eggs. In Chondrichthyes and primitive osteichthyans, eggs are shed into the body cavity – the gymnovarian condition. In gars and most teleosts, the lumen of the hollow ovary is continuous with the oviduct – the cystovarian condition.
8. The fish brain can be divided into five parts, from anterior to posterior: (i) the telencephalon, or forebrain, primarily associated with smell; (ii) the diencephalon, a correlation center for messages regarding homeostasis and the endocrine system; (iii) the mesencephalon, or midbrain, important in vision; (iv) the metencephalon, or hindbrain, which maintains muscle tone and equilibrium in swimming and has a large median lobe (cerebellum), which is the largest component of the fish brain; and (v) the myelencephalon, brainstem, or medulla oblongata, the posterior portion of the brain and enlarged anterior portion of the spinal cord that relays input for all sensory systems except smell and sight.
9. Fishes have small brains but sharks have larger brains than teleosts. The largest brains occur in elephantfishes (Mormyridae), which have a large proportion of their brain devoted to electroreception.

Supplementary reading

SUPPLEMENTARY READING

Ostrander GK. 2000. *The laboratory fish*. London: Academic Press.

Journal

Journal of Morphology.

Chapter 5

Oxygen, metabolism, and energetics

Chapter contents

CHAPTER CONTENTS

Fishes, like all eukaryotic life forms, require oxygen to produce sufficient energy to support their metabolic needs. Although acquiring sufficient oxygen from water is challenging, fishes have evolved a range of morphological and physiological adaptations that increase the efficiency of oxygen uptake and delivery to help them succeed in a wide range of aquatic environments. The demands of the aquatic environment also have prompted a range of adaptations that decrease metabolic costs through improved energetic efficiency. In this chapter we will explore the metabolic and energetic challenges fishes face and the mechanisms they use to succeed and diversify. Because fishes were the first vertebrates, these adaptations provided a physiological foundation upon which other adaptations eventually brought about the success of tetrapods and endothermy.

Respiration and ventilation

Fishes must extract oxygen from the water and distribute it to the cells of the body fast enough to meet the demands of metabolism. The oxygen maximizes the amount of adenosine triphosphate (ATP) that can be generated from glucose, the primary metabolic fuel of cellular metabolism. This ATP is needed for many biochemical reactions, so maximizing its production is beneficial to the fish. Oxygen permits the aerobic completion of cellular respiration (glycolysis, Krebs cycle, and oxidative phosphorylation). If oxygen is not present, oxidative phosphorylation and the Krebs cycle cannot proceed, and the only energy available from the metabolism of glucose is from the small amount of ATP released during the initial glycolysis reaction.

For glycolysis to continue producing some ATP, the pyruvate that also is produced is often converted to lactate and stored temporarily. If lactate levels get too high, however, glycolysis can be inhibited, no ATP will be produced, and cellular metabolism will cease. When oxygen next becomes available, such as following bursts of activity, the stored lactate can be converted back to pyruvate and oxidative metabolism may proceed. However, lactate conversion bears a metabolic cost and a period of elevated oxygen consumption is required to pay off the **oxygen debt** accumulated during the period of insufficient oxygen. This may not have an adverse effect on swimming, however, as adult Pacific salmon (*Oncorhynchus*) exercised to exhaustion in a swim tunnel showed no decrease in swimming ability when tested a second time less than 1 h after the initial test (Farrell et al. 2003). The less active Goldfish (Cyprinidae) can avoid lactate build-up altogether through an alternative biochemical pathway that converts excess pyruvate to alcohol which can then be excreted (Hochachka & Mommsen 1983; Hochachka & Somero 1984). This can be quite useful in regions where Goldfish are likely to be trapped under ice with little or no oxygen through a long winter; Goldfish can continue producing ATP by glycolysis without suffering the problems associated with decreasing pH and lactate build-up.

Water as a respiratory environment

Terrestrial organisms live in an oxygen-rich environment, but water contains considerably less oxygen than air – less than 1% by volume, as opposed to over 20% for air. Flowing or turbulent water may be well mixed, so oxygen may be somewhat evenly distributed. Still water, however, may have more oxygen at the surface due to diffusion from the air. Some fishes take advantage of this by coming toward the surface to breathe when oxygen is limited. For example, Sailfin Molly (Poeciliidae) use aquatic surface respiration (ASR) as well as an increase in ventilation frequency to cope with hypoxic conditions (Timmerman & Chapman 2004). The use of ASR diminishes, however, after a period of acclimation to the low oxygen conditions.

Gas solubility in liquids diminishes with increasing temperature. Warm water, therefore, contains less oxygen than cool water, making the challenges of meeting metabolic needs far greater for warm water fishes. Fresh water can hold about 25% more oxygen than sea water due to the diminished solubility of gases in water as the concentration of salts or other solutes increases. This **salting out effect** is true for all water solutions, including natural aquatic environments, blood plasma, cytoplasm, or a glass of carbonated beverage (just add some table salt and see what happens). The combined effects of temperature and salinity make oxygen availability especially low in warm, marine environments.

The relatively high density and viscosity of water means that more energy is required to simply move water across the respiratory surfaces than is true of air. A fish may use as much as 10% or more of the oxygen that it gets from the water simply keeping the breathing muscles going (Jones & Schwarzfeld 1974), whereas for air-breathing animals the relative cost is much lower, around 1–2%.

Aquatic breathing

The **gills** of fishes are very efficient at extracting oxygen from the water because of the large surface area and thin epithelial membranes of the **secondary lamellae** (Fig. 5.1). Diffusion of gases across the gill membrane is further enhanced by blood in the secondary lamellae flowing in the opposite direction to the water passing over the gills, thereby maximizing the diffusion gradient across the entire lamellar surface. This **countercurrent flow** ensures that as the blood picks up oxygen from the water it moves along the exchange surface to an area where the adjacent water has an even higher oxygen concentration.

Gills will function efficiently only if water is kept moving across them in the same direction, from anterior to posterior. This is accomplished in one of two ways. First, the great majority of fishes pump water across their gills by increasing and decreasing the volume of the **buccal** (mouth) **chamber** in front of the gills and the **opercular chamber** behind them. The expansion and contraction of these two chambers is timed so that the pressure in the

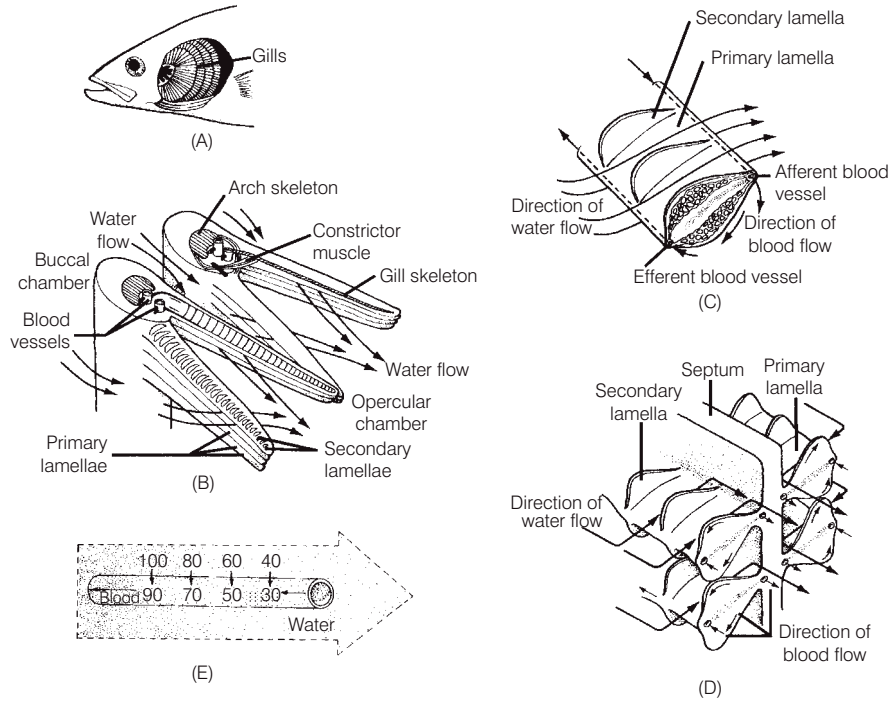


Figure 5.1

(A, B) The gill arches of a fish support the gill filaments (also called the primary lamellae) and form a curtain through which water passes as it moves from the buccal cavity to the opercular cavity. (C) As water flows across the filaments of a teleost, blood flows through the secondary lamellae in the opposite direction. (D) In elasmobranchs, even though septa create some structural differences in gill filaments, water flow across the secondary lamellae is still countercurrent to blood flow. (E) The countercurrent flow of water and blood at the exchange surface of the secondary lamellae ensures that the partial pressure of oxygen in the water always exceeds that of the blood, thereby maximizing the efficiency of oxygen diffusion into the blood.

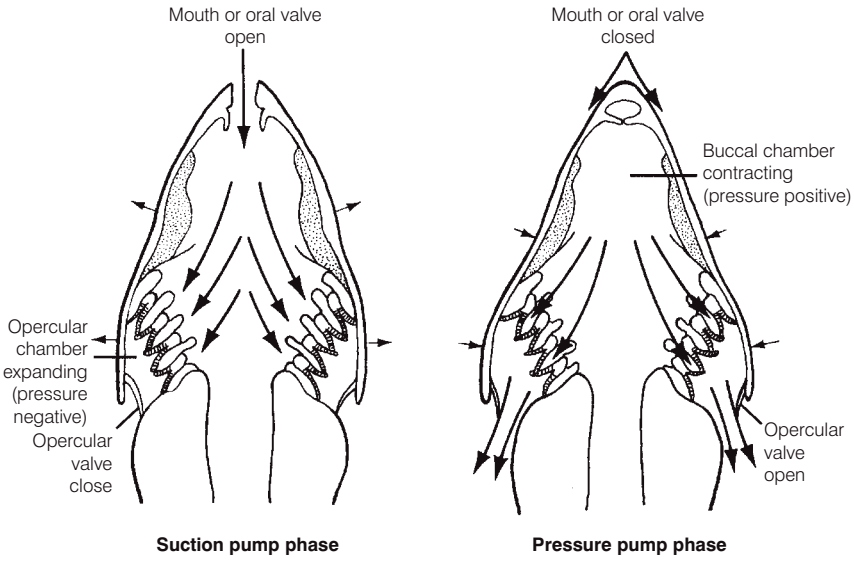


Figure 5.2

The timing of the expansion and contraction of the buccal (oral) and opercular cavities ensures that the pressure in the buccal chamber exceeds that of the opercular chamber throughout nearly all of the respiratory cycle. This creates a nearly steady flow of water from the buccal chamber to the opercular chamber, passing over the gill lamellae, which have blood flowing through them in the opposite direction. The fish is viewed from below. Adapted from Hildebrand (1988).

buccal chamber is greater than the pressure in the opercular chamber, thereby ensuring that the water flows in the anterior to posterior direction throughout the breathing cycle (Fig. 5.2).

A second method of gill ventilation, called **ram ventilation**, consists simply of keeping the mouth slightly open while swimming. The forward movement of the fish keeps water flowing over the gills. This is an efficient way to ventilate the gills because the work of ventilation is accomplished by the swimming muscles, but it can only be used by strong swimmers while they are moving at relatively high speeds. Some predatory pelagic fishes, such as tunas (Scombridae), rely exclusively on ram ventilation and must therefore swim constantly. It had been thought that sharks also had to swim constantly in order to breathe. However, observations of so-called "sleeping" sharks on the ocean floor, including relatively sedentary species such as Whitetip Reef Sharks and Nurse Sharks, indicate they too use a gill pumping mechanism similar to the one described above for teleosts. Many larger fishes use ram ventilation while swimming at moderate to high speeds, but rely on pumping of the buccal and opercular chambers while still or moving slowly. As speed increases they can switch from gill pumping to ram ventilation (Roberts 1975a).

The total surface area of the gills is considerable and active fishes with higher metabolic demands generally have larger gill surface areas than less active fishes. For example, Skipjack Tuna are active pelagic predators and have about 13 cm^2 of gill area per gram of body weight (Roberts 1975b). Scup (Sparidae) are nearshore, active fish and have about 5 cm^2/g. Benthic, yet active, plaice (Pleuronectidae) have a little over 4 cm^2/g, whereas the sluggish, benthic Oyster Toadfish (Batrachoididae) has about 2 cm^2/g. Fishes with large gill areas control how much of the gills are receiving blood at any given time by constricting or dilating blood vessels in the gill filaments (see Jones & Randall 1978). This allows a fish to meet its oxygen needs without experiencing needlessly high osmotic stress. (Because the gill epithelium is so thin, water and ions also are exchanged with the surrounding environment; see Chapter 7, Osmoregulation, excretion, ion and pH balance.)

Agnathans have a very different gill structure and rely on different means of ventilation. Hagfishes (Myxinidae) have a muscular, scroll-like flap known as a **velum** which moves water in through the single median nostril and over the gills (Fig. 5.3). When the hagfish's head is buried in food, water enters and leaves the gill area via the external opening behind the last gill pouch. Lampreys (Petromyzontidae) expand and contract the branchial area causing water to flow in and out through the multiple gill openings. This method of ventilation is especially practical when the lamprey's buccal funnel is attached to the substrate or a host organism.

Although gills typically are identified as the respiratory organ of most fishes, any thin surface in contact with the respiratory medium is a potential site of gas exchange. Gas exchange across the skin (cutaneous respiration) can be important to some fishes, particularly in young fish whose gills have not yet developed fully. Newly hatched alevins of Chinook Salmon (Salmonidae) rely on cutaneous respiration for up to 84% of their oxygen (Rombough & Ure 1991). As the fish develop and their gills increase in size and efficiency, dependence on cutaneous respiration decreases to about 30% of total uptake in the fry and later stages. Adult eel (Anguillidae), plaice, Reedfish (Polypteridae), and mudskipper (Gobiidae) gain about 30% or more of their oxygen through their skin (Feder & Burggren 1985; Rombough & Ure 1991).

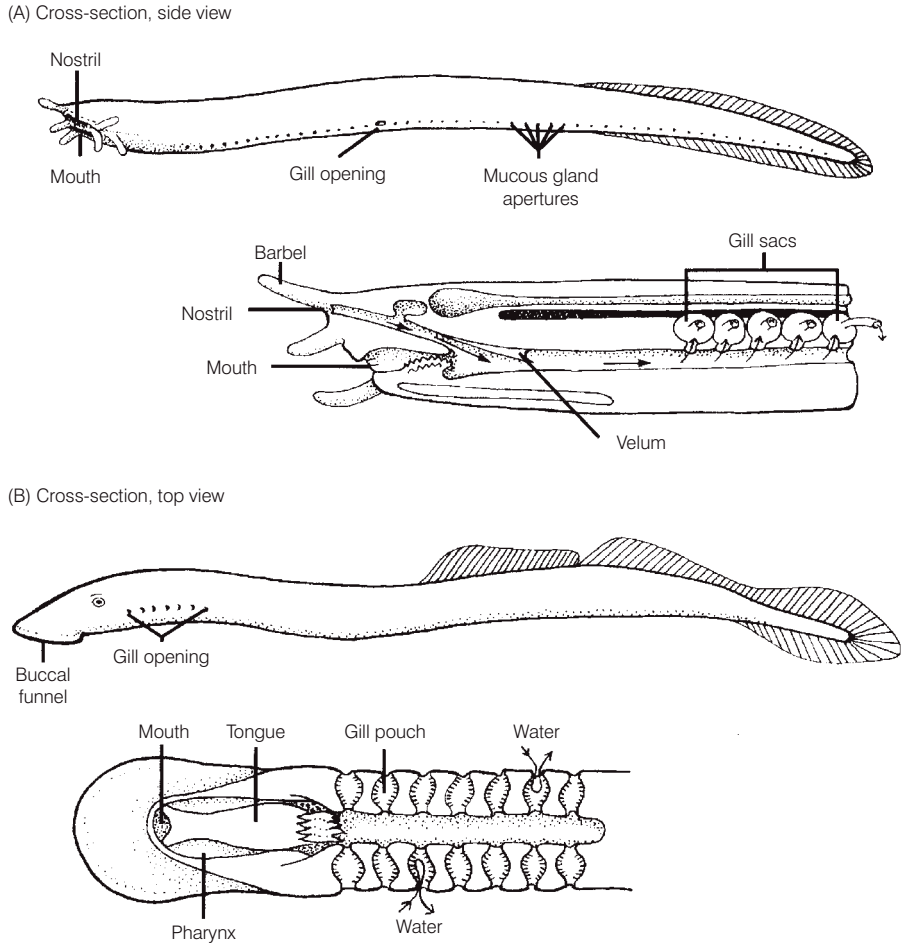


Figure 5.3
(A) Hagfishes have one or more external gill openings on each side. Movement of the scroll-like velum draws water in through the nostril and pushes it through the pharynx and branchial pouches. Excurrent branchial ducts then direct the water to the gill openings. (B) Lampreys have multiple external gill openings on each side. Expansion and contraction of the branchial pouches provides ventilation through each external opening. This permits continued breathing while the mouth is attached to substrate or a host.

Air-breathing fishes

At least 370 extant species of fishes in 49 families have some capacity to obtain oxygen from the air, and the numbers are likely to increase with further study (Graham 1997a; Graham & Lee 2004) (Table 5.1). Most air-breathing fishes remain in water all of the time (**aquatic air breathers**). Among these some only supplement gill respiration when necessary (**facultative air breathing**), whereas others must have access to air or they will drown (**obligate air breathing**). Although there are some temperate air-breathing fishes, such as the Bowfin (*Amia*), gars (*Lepisosteus*), mudminnow (*Umbra*), and Tarpon (*Megalops*), most live in tropical habitats where high temperatures dramatically reduce dissolved oxygen levels in water. Many of these tropical air-breathing fishes live in freshwater habitats in which high rates of decomposition further decrease the amount of oxygen available and a thick forest canopy inhibits aquatic photosynthesis, which would add some oxygen to the water.

Some fishes also have the ability to survive, and even remain active, while out of the water due to their ability to breathe air (**amphibious air breathers**). These include some tropical freshwater species in habitats that may become dry seasonally (providing additional selective pressure for aerial respiration) and marine intertidal species that leave the water to forage. Air breathing in these fishes is not a mechanism to survive low oxygen in the water, but instead provides a means to take advantage of a habitat not available to other fishes.

Air breathing evolved among fishes over 400 million years ago, and at least some members of extinct groups such as the placoderms and acanthodians may have been air breathers (Graham 1997a). Early sarcopterygians gave rise to early tetrapods, which have since successfully colonized terrestrial habitats. But long after the tetrapods began their invasion of the land, air breathing continued to develop independently in many other groups of fishes. Although the high salinity and temperatures of tropical oceans could create low oxygen levels and lead to the origins of air breathing, it is more likely that tropical freshwater habitats with persistent low oxygen and periodic drying provided the long-term evolutionary pressure to drive this adaptation (Graham & Lee 2004). Air-breathing organs of fishes today fall into three broad categories: (i) those that are derived from the gut, such as the lungs, gas bladder, stomach, or

Table 5.1

Diversity of fishes with air-breathing capabilities. Modified from Graham 1997a.

Order and family	No. genera/species	Habitat	Air-breathing organ	Respiratory pattern
Ceratodontifomes				
Ceratodontidae	1/1	F	Yes	AF
Lepidosireniformes				
Lepidosirenidae	1/1	F	Yes	AC, AmS
Protopteridae	1/4	F	Yes	AC, AmS
Polypteriformes				
Polypteridae	2/11	F	Yes	AC, AmV
Lepisosteiformes				
Lepisosteidae	2/7	F, B	Yes	AC
Amiiformes				
Amiidae	1/1	F	Yes	AC
Osteoglossiformes				
Osteoglossidae	2/2	F	Yes	AC (?)
Pantodontidae	1/1	F	Yes	AC
Notopteridae	3/5	F	Yes	AC
Gymnarchidae	1/1	F	Yes	AC/AF?
Elopiformes				
Megalopidae	1/2	F, M	Yes	AC
Anguilliformes				
Anguillidae	1/1	F	(Yes/no?)	AmV
Gonorhynchiformes				
Phractolaemidae	1/1	F	Yes	AC/AV?
Cypriniformes				
Cobitididae	4/7	F	Yes	AC + AF
Characiformes				
Erythrinidae	2/2	F	Yes	AC
Lebiasinidae	2/2	F	Yes	AC
Siluriformes				
Pangasiidae	1/4	F	Yes	AC
Clariidae	3/44	F	Yes	AC + AF, AmV + AmS
Heteropneustidae	1/2	F	Yes	AC, AmV + AmS
Aspredinidae	1/2	F	Yes	AF
Trichomycteridae	2/2	F	Yes	AF
Callichthyidae	4/131	F	Yes	AC
Loricariidae	10/14	F	Yes	AF
Gymnotiformes				
Hypopomidae	1/3	F	(Yes/no?)	AF
Gymnotidae	1/1	F	Yes	AF
Electrophoridae	1/1	F	Yes	AC
Salmoniformes				
Umbridae	2/5	F	Yes	AF
Lepidogalaxiidae	1/1	F	No	AF, AmS
Galaxiidae	3/10	F	No	AmV
Gobiesociformes				
Gobiesocidae	5/7	F, M	No	AmS

Table 5.1

Diversity of fishes with air-breathing capabilities. Modified from Graham 1997a.

Order and family	No. genera/species	Habitat	Air-breathing organ	Respiratory pattern
Cyprinodontiformes				
Aplocheilidae	1/5	F	No	AmV
Cyprinodontidae	1/4	F, M	No	AmV + AmS
Scorpaeniformes				
Cottidae	2/4	M	No	AmV
Perciformes				
Stichaeidae	4/5	M	No	AmS
Pholididae	3/5	M	No	AmS
Tripterygiidae	1/1	M	No	AmV
Labrisomidae	2/2	M	No	AmV
Blenniidae	7/32	M	No	AmV
Eleotridae	2/2	M	No	AF
Gobiidae	15/40	M, B	Yes/no	AF, AmV
Gobioididae	1/1	M, B	No	AF, AmS
Mastacembelidae	2/3	F, B	No	AmS
Anabantidae	3/24	F, B	Yes	AC, AmV + AmS
Belontiidae	12/44	F, B	Yes	AC, (AmV?)
Helostomatidae	1/1	F	Yes	AC
Osphronemidae	1/1	F	Yes	AC
Luciocephalidae	1/1	F	Yes	AC
Channidae	1/12	F	Yes	AC, AmS
Synbranchidae	3/14	F, B	Yes	AC + AF, AmV + AmS

Habitats: B, brackish; F, fresh water; M, marine.
Respiratory pattern: AC, aquatic continuous; AF, aquatic facultative; AmS, amphibious stranded; AmV, amphibious volitional.

intestine; (ii) structures of the head and pharynx, such as modifications of the gills, mouth, pharynx, or opercles; and (iii) skin, which can be very effective for gas exchange if it is well vascularized and kept moist.

An analysis of the relationships among the known air-breathing fishes led Graham (1997a) to conclude that air breathing probably evolved independently at least 38 times, and quite possibly over 65 times. Air-breathing fishes are found in 18 orders, 49 families, and in freshwater, brackish, and marine ecosystems (Graham 1997a). Most are aquatic air breathers, including those that continuously breathe air and those that only do so occasionally, but some are amphibious species that regularly breathe air during seasonal aestivation, occasional strandings, or intentional excursions onto land. Air-breathing fishes show great diversity in size, from as small as 3 cm up to some that may exceed 2 m, including *Arapaima gigas*, one of the largest freshwater fishes in the world.

Despite the great diversity of air-breathing fishes, 39% of known species are found in just seven families (Graham 1997a) – the Callichthyidae and Clariidae (both in the order Siluriformes), and the five families of anabantoids (in the order Perciformes). Among the anabantoids, changes in the jaws and branchial region that allow for air breathing also provide enhanced capabilities for sound reception and production, bubble-nest construction, and mouth brooding. There also is evidence of evolutionary regression as members of the anabantoid genus *Sandelia* have less well-developed air-breathing organs than other members of their highly specialized family who are obligatory air breathers. This regression may be due to radiation of members of an ancestral group into habitats with more oxygen available (Graham 1997a).

Two main factors probably have driven the evolution of air breathing: (i) persistent or occasional low oxygen levels in freshwater habitats; and (ii) emergence during low tides among littoral and intertidal marine and brackish water habitats (Graham 1997a). In both habitats, the ability to make excursions onto land provides access to resources that non air breathers cannot reach.

Lungs were present in many primitive fishes, and became more specialized and efficient among the sarcopterygians as they evolved and one lineage became the modern tetrapods. As the actinopterygians evolved and became more advanced, the lung lost its respiratory function and became the gas bladder, which functions for buoyancy control and, in some fishes, enhances hearing (see Chapter 6, Hearing). Subsequently, some of the more advanced fishes developed alternative mechanisms to once again take advantage of the oxygen available in air.

Freshwater air-breathing fishes show a wide array of adaptations for aerial gas exchange. Gills are not well suited

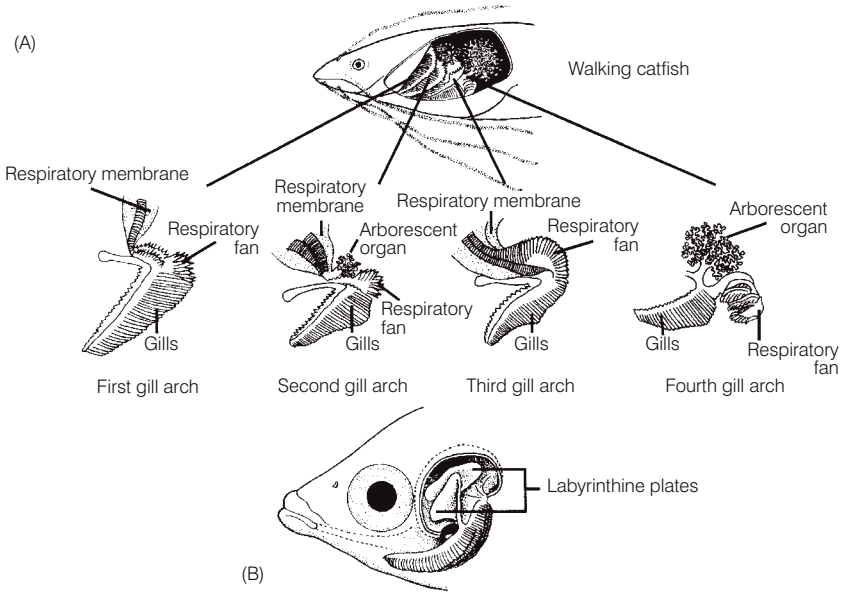


Figure 5.4

(A) Lateral views of the gill arches of the Walking Catfish (*Clarias batrachus*) show the respiratory fans, respiratory membranes of the suprabranchial chamber, and treelike extensions (arborescent organs) that permit the fish to extract oxygen from air when it is out of water. (B) A cut-away view of the branchial region of the Giant Gourami (*Osphronemus goramy*) shows a labyrinth of platelike extensions to accomplish the same goal. A, from Munshi (1976); B, from Peters (1978).

for aerial respiration because they collapse and stick together when not supported by the buoyancy of water. There are, however, a few fishes that have modified gill structures that assist with aerial respiration, such as the modified treelike branches found above gill arches two and four of the Walking Catfish (Clariidae) or the complex platelike outgrowths of the gill arches of anabantoids such as the Giant Gourami (Osphronemidae) and several other Asian perciforms (Fig. 5.4). Other respiratory structures include highly vascularized surfaces such as the skin, mouth, and opercular cavity, or modifications of the gut, such as the stomach, intestine, modified gas bladder, or lungs. Gas bladders of most fishes are not well vascularized except in the regions designed for gas deposition or removal (discussed elsewhere in this chapter), but several air breathers have highly vascularized and subdivided gas bladders designed for gas exchange. These include the very large South American osteoglossiform *Arapaima* (Osteoglossidae), as well as the North American Bowfin (Amiidae) and gars (Lepisosteidae). The gills of these aquatic air breathers are still important for getting rid of metabolic wastes, such as carbon dioxide and ammonia, and for regulating ionic and acid–base balance (see Chapter 7).

The lungfishes (Dipnoi) have true lungs. The Australian Lungfish (Ceratodontidae) is a facultative air breather with a single lung, whereas the African and South American lungfishes (Protopteridae and Lepidosirenidae, respectively) are both obligate air breathers with bilobed lungs (see Chapter 13, Subclass Dipnoi, Order Ceratodontiformes: the lungfishes). The gills of the South American Lungfish (*Lepidosiren paradoxa*) are of so little value for gas or ion exchange that the respiratory physiology of this species is more similar to that of an amphibian than to most other fishes (de Moraes et al. 2005).

A strong reliance on air breathing among some freshwater fishes aids survival in oxygen-poor habitats, but it also helps some cope with drought. When rivers and ponds dry up, African lungfishes burrow into the sediment, dramatically slow their metabolism, and can remain in this torpid state for years. When the rains return and water levels rise, they leave their mud cocoons and become active (see Chapter 13). When the Walking Catfish is confronted with drought conditions, it "walks away" to find another pond, using a side-to-side lurching action supported by its stout pectoral spines.

Many intertidal fishes also demonstrate some air-breathing capability, so this should not be seen as an anomaly but rather a part of the broad range of capabilities of fishes in this extreme habitat. Oxygen can become limited in tidepools due to increasing temperature and salinity and the ongoing respiration of animals and plants. Most marine air-breathing fishes evolved from relatively advanced fishes, so they do not have lungs and instead rely on modification of existing aquatic breathing structures such as gills and skin (Martin & Bridges 1999). Gills often are modified with structural support to prevent collapsing in air, and the skin often is well vascularized, has few scales, and is kept moist. Zhang et al. (2003b) provide evidence that mudskippers (Periopthalmidae) rely on cutaneous respiration to support their amphibious lifestyle. Some emergent intertidal species decrease their oxygen consumption rate by using anaerobic respiration to support activity, whereas other species simply reduce their activity until the next high tide (Martin & Bridges 1999). Although most marine air-breathing fishes are emergent or amphibious and rely on their skin for respiration while in air, notable exceptions include the Longjaw Mudsucker (*Gillichthys mirabilis*), which has a highly vascularized mouth and

pharynx (Martin & Bridges 1999), and the Pacific Tarpon (*Megalops cyprinoides*), which uses its gas bladder to augment respiration when oxygen levels in the water are low (Seymour et al. 2004).

Although aquatic air breathers rely on gills for the release of carbon dioxide, ion regulation, and nitrogen excretion, the capability of some air-breathing fishes to tolerate extended periods of low oxygen availability, and in some cases aestivation, would require some biochemical means of either preventing or tolerating low blood pH (due to elevated carbon dioxide) and elevated levels of nitrogen wastes. Ip et al. (2004a) found several different adaptations for protecting against ammonia toxicity among five tropical air-breathing fishes, with most fish utilizing at least two mechanisms. These included reducing ammonia production by reducing amino acid catabolism, converting ammonia to less toxic compounds such as urea or glutamine, excreting ammonia through the skin or digestive tract by increased volatilization, and increasing tolerance to ammonia at the cellular and subcellular level. Slender Lungfish (*Protopterus dolloi*) apparently convert ammonia to urea when exposed to air for 21–30 days (Wood et al. 2005). The Swamp Eel (*Monopterus alba*) converted ammonia to glutamine when exposed to air for 6 days, but suppressed ammonia production during aestivation in mud for 6 or 40 days (Chew et al. 2005). However, the African Sharptooth Catfish (*Clarias gariepinus*) survived 4 days of air exposure by tolerating very high levels ammonia in its tissues (Ip et al. 2005). When exposed to elevated ammonia levels, the Giant Mudskipper (*Periopthalmodon schlosseri*) increased levels of cholesterol and saturated fatty acids in its skin, thereby decreasing skin permeability (Randall et al. 2004). In addition, exposure to the low oxygen or high sulfide found on mudflats induces an enzyme system in some mudskippers to detoxify the sulfur (Ip et al. 2004b). There is still much more to learn about the physiological specializations of these amphibious fishes.

Because some air-breathing fishes can tolerate low oxygen levels and poor water quality, they are good species for high-density, low-maintenance aquaculture in warm climates (Graham 1997a). Understanding more about their physiology, therefore, would not only be intellectually interesting, but also has the potential of being economically valuable.

Gas transport

Oxygen enters the blood at the respiratory surfaces and is transported via the circulatory system to tissues and released (see Chapter 4, Cardiovascular system). Some oxygen simply is dissolved in the blood plasma. This is not enough, however, to support the level of the metabolism of most large organisms, except in some Antarctic icefishes (Channichthyidae). The red blood cells of most fishes and other vertebrates contain **hemoglobin**, an oxygen-carrying protein that increases the overall capacity of the blood to transport oxygen. Each hemoglobin molecule has four subunits, each of which can bind a single molecule of oxygen. The packaging of hemoglobin within red blood cells permits intracellular biochemistry to optimize the binding and releasing of oxygen without affecting molecules carried in the plasma or in other cells in the blood stream.

For hemoglobin to work well as an oxygen-transporting protein it must alter its oxygen-binding ability so that it can bind oxygen at the respiratory surface and release it at the tissues elsewhere in the body. Like many proteins, hemoglobin is sensitive to the physical and chemical conditions of its environment, such as temperature and pH. At the tissues, blood pH tends to be lowered by the presence of carbon dioxide because it combines with water to form carbonic acid (H_2CO_3). At the respiratory surfaces, however, carbon dioxide is released to the environment, thereby decreasing the level of carbonic acid in the blood and raising the pH. Hemoglobin's structure is affected by the changing pH conditions such that it has a higher affinity for oxygen (can bind more easily) at higher pH but has a lower affinity when pH decreases (Fig. 5.5A). This phenomenon, known as the **Bohr effect**, is caused by changes in the structure of the hemoglobin subunits that alter oxygen's access to the binding sites. In some cases, the structure of hemoglobin can become altered so much that oxygen cannot bind to all potential binding sites and the total capacity of the blood to carry oxygen is decreased (the **Root effect**, Fig. 5.5B). These phenomena become very important in understanding the function of the teleost gas bladder, discussed later.

Hemoglobin can be affected by changes in temperature also, with affinity for oxygen decreasing as temperature increases. This is one reason why cold water fishes often cannot survive at higher temperatures, even if the oxygen content of the water is increased. At these higher temperatures, the structure of the fish's hemoglobin may be altered to the point where the fish simply cannot pick up enough oxygen at its gills, and could therefore suffocate even though sufficient oxygen was present in the water. The blood of a coelacanth, for example, has its highest affinity for oxygen at 15°C, and the fish suffers from hypoxic stress at temperatures above 25°C (see Fricke & Hissmann 2000).

Hemoglobins of different fish species may have different affinities for oxygen. For example, the higher affinity of toadfish hemoglobin makes it better adapted for low oxygen environments. Mackerel (Scombridae), however, require more oxygen in their environment for their hemoglobin to become saturated enough to support their active lifestyle (Hall & McCutcheon 1938) (Fig. 5.5C). The higher affinity for oxygen of hemoglobin of the Largemouth Bass (*Micropterus salmoides*, Centrarchidae) makes this species better adapted to somewhat warmer, lower oxygen environments, and less sensitive to hypoxia than its close relative the Smallmouth Bass (*M. dolomieu*; Furimsky et al. 2003)

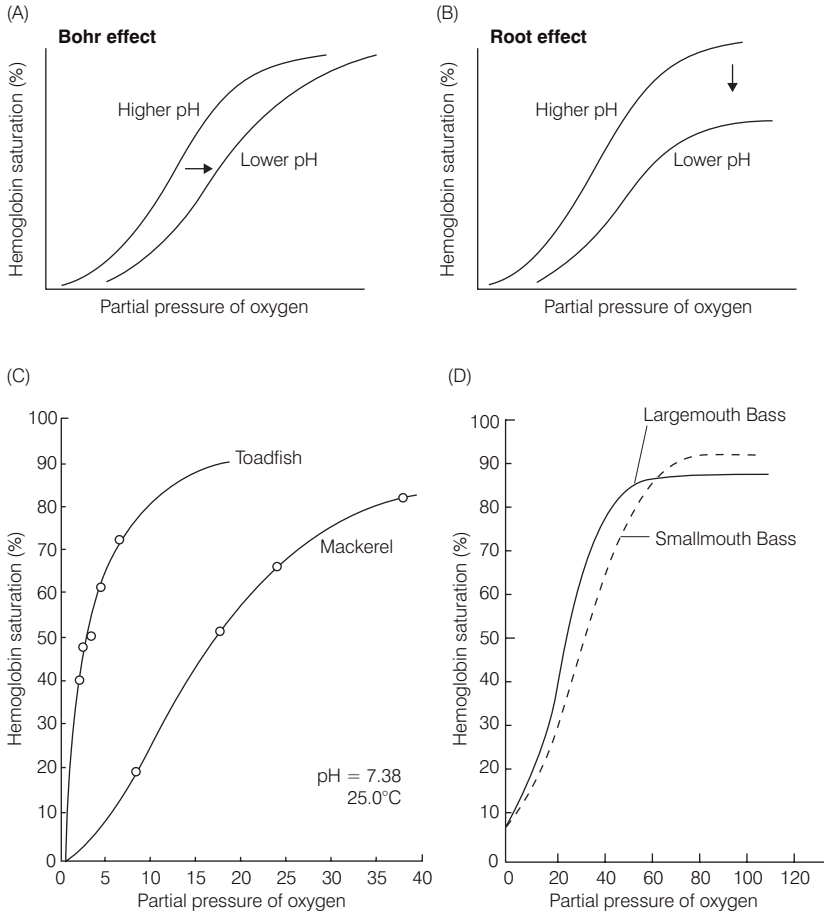


Figure 5.5

Oxygen dissociation curves. Vertical axes indicate the percent of total oxygen-binding sites that are occupied by oxygen. The horizontal axes indicate the concentration of oxygen dissolved in the solution surrounding the hemoglobin, typically blood plasma. A decrease in pH results in a shift of the curve to the right (the Bohr shift, A), and may also prevent full saturation of hemoglobin with oxygen (the Root effect, B). (C) Toadfish can survive better than mackerel in low oxygen conditions because their hemoglobin has a higher affinity for oxygen than mackerel hemoglobin. After Hall and McCutcheon (1938). (D) Largemouth Bass are better suited for warmer water with somewhat less oxygen than are Smallmouth Bass because the hemoglobin of the Largemouth Bass has a higher affinity for oxygen. After Furimsky et al. (2003).

(Fig. 5.5D). Different fish hemoglobins also may show different temperature sensitivities. Antarctic fishes (Nototheniidae) possess hemoglobins that are effective at temperatures well below the effective temperature range of hemoglobins of temperate fishes (Hochachka & Somero 1973). The hemoglobins of the warm-bodied tunas and lamnid sharks are less sensitive to temperature changes than are hemoglobins of many other species. This is adaptive because blood temperatures in these fishes may increase as much as 10°C or more as blood travels from the gills to the warm swimming muscles (see Chapter 7). If the hemoglobins were not thermally stable, arterial blood might unload its oxygen as it warmed in the countercurrent heat exchanger, resulting in loss of oxygen to venous blood and depriving the highly active swimming muscles that need the oxygen most (Hochachka & Somero 1984).

Some fishes, such as trouts (Salmonidae) and suckers (Catostomidae) have more than one type of hemoglobin. The different hemoglobins exhibit different degrees of sensitivity to decreased pH, therefore providing a "back up" system to ensure some oxygen transport even if blood pH drops considerably. If all of the hemoglobins were sensitive to the Bohr effect, a substantial drop in blood pH, perhaps due to a burst of swimming activity, might inhibit oxygen loading at the gills (Brunori 1975; Hochachka & Somero 1984).

In addition to transporting oxygen, the blood must pick up the carbon dioxide that is produced in cellular metabolism and transport it back to the gills for release to the environment. If excess carbon dioxide is not removed, blood and tissue pH will drop and interfere with normal metabolic processes. Because of this link between carbon dioxide levels and pH, the transport of carbon dioxide and oxygen are linked.

Carbon dioxide can be carried in the blood in three forms. A relatively small amount is simply dissolved carbon dioxide in the plasma. A greater amount is bound to hemoglobin to form **carbaminohemoglobin**. Although carbon dioxide does not bind to the oxygen-binding sites on hemoglobin, carbaminohemoglobin has a lower affinity for oxygen than does hemoglobin without carbon dioxide bound to it. The greatest proportion of carbon dioxide in the blood is carried as **bicarbonate ion** (HCO_3^-) resulting from the dissociation of carbonic acid.

At the tissues, carbon dioxide diffuses down its concentration gradient into the blood (Fig. 5.6). In the plasma

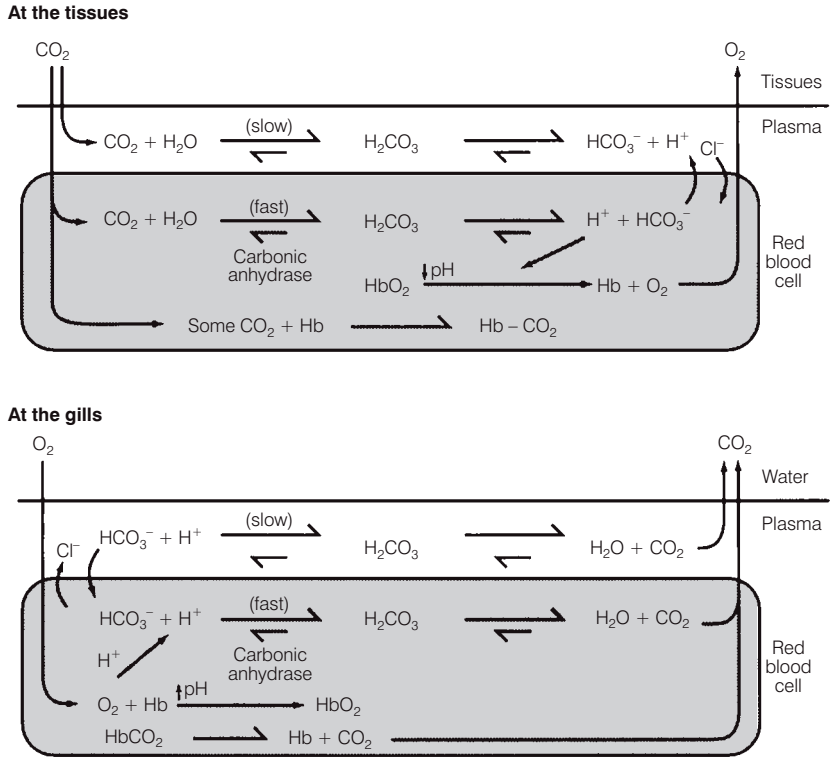


Figure 5.6

The uptake of carbon dioxide at the tissues is enhanced by the presence of carbonic anhydrase in the red blood cells. This enzyme catalyzes the conversion of CO_2 to carbonic acid (H_2CO_3), which dissociates to form bicarbonate (HCO_3^-) and a hydrogen ion (H^+). The increase in intracellular levels of H^+ causes a drop in pH, causing hemoglobin (Hb) to lose its oxygen (the Bohr effect). Hemoglobin can bind some CO_2, as well as some H^+ to help buffer against too great a drop in pH. Bicarbonate diffuses out of the red blood cell into the plasma, permitting further uptake of CO_2. To balance the loss of negative charges, chloride (Cl^-) diffuses into the cell (the chloride shift). These reactions occur in reverse at the gills.

some carbon dioxide combines with water to form carbonic acid, which dissociates to bicarbonate and hydrogen ions. Most of the carbon dioxide, however, is drawn into the red blood cells where this same reaction is taking place at a faster rate due to the presence of the enzyme carbonic anhydrase. The rapid production of H^+ from the dissociating carbonic acid inside the red blood cells causes the intracellular pH to drop. This, in turn, alters hemoglobin and causes the release of oxygen, which then diffuses out of the red blood cells and into the tissues. In addition, some carbon dioxide binds to hemoglobin, forcing the release of oxygen from the hemoglobin molecule. Some hemoglobin also binds some of the excess hydrogen ions, thereby preventing the blood pH from dropping too low.

The dissociating carbonic acid also causes the concentration of bicarbonate (HCO_3^-) inside the red blood cell to increase. Much of this HCO_3^- diffuses across the membrane of the red blood cell and into the plasma, keeping intracellular HCO_3^- levels from getting so high that they would inhibit further carbon dioxide uptake. In response to this loss of negative ions from inside the cell, chloride (Cl^-) from the plasma diffuses into the red blood cell, thereby balancing the distribution of charges (Cameron 1978). The net result of all of these reactions is that the blood has taken up carbon dioxide and become slightly acidified, oxygen has been released from hemoglobin, the hemoglobin molecule itself has helped buffer against too much of a pH drop by taking up some carbon dioxide and H^+, and the bicarbonate level in the plasma has increased.

When blood gets to the respiratory surface where carbon dioxide levels are low and oxygen levels are high, these reactions occur in the opposite direction, resulting in the release of carbon dioxide, a slight increase in blood pH, and the binding of oxygen to hemoglobin within the red blood cells.

Metabolic rate

Metabolism is the sum total of all biochemical processes taking place within an organism. Since these reactions give off heat as a byproduct, measuring the heat lost by an animal probably is the best way to measure its metabolism. This can be a difficult process, however, so frequently another parameter related to metabolism serves as an indirect measure. In fishes the rate of oxygen consumption is frequently used as an indicator of metabolic rate, but we must assume that no significant anaerobic metabolism takes place during the measurement period.

Metabolic rates can be influenced by a variety of factors, including age, sex, reproductive status, food in the gut, physiological stress, activity, season, and temperature. For this reason, it is useful to define metabolic terms. **Standard metabolic rate** is often defined as the metabolic rate of a fish while it is at rest and has no food in its gut. However, Belokopytin (2004) points out that many fishes under natural conditions feed regularly and therefore almost always have some food in the gut, so some amount of

digestion is likely to be part of a fish's metabolism at all times. Fishes rarely remain still while metabolic rates are being measured, so the term **routine metabolic rate** is often used to indicate that the rate was measured during routine activity levels. The resulting estimates of metabolic rate are therefore higher than what might be expected for a resting fish. Sometimes researchers will measure metabolism at several levels of activity and extrapolate back to zero activity to estimate standard metabolic rate. Because metabolism is affected by temperature, the temperature should be recorded whenever measuring fish metabolism.

Metabolic rate increases with activity until a fish reaches the point at which it is using oxygen as rapidly as its uptake and delivery system can supply it. This is its **maximum** (or active) **metabolic rate**. The difference between the standard metabolic rate and the maximum metabolic rate at any given temperature is known as the **metabolic scope**. The concept of metabolic scope can be important in trying to understand a fish's metabolic limits. Any factors that increase standard or routine metabolic rates, such as stress due to disease, handling, reproduction, or environmental conditions, narrow this scope and may limit other activities.

In general, fishes tend to have higher metabolic rates at higher temperatures, so as temperature increases a fish's need for oxygen also increases. Because the availability of oxygen in water decreases with increasing temperature, warm conditions stress most fishes. This stress probably was an important selection factor favoring the evolution of air breathing in many tropical fishes.

Under laboratory conditions fish acclimated to low temperatures consume less oxygen than fish of the same species acclimated to higher temperatures (see, for example, Beamish 1970; Brett 1971; Kruger & Brocksen 1978; DeSilva et al. 1986). The rates of many biochemical reactions increase with temperature, thereby increasing the need for oxygen to provide the energy needed to support increased levels of cellular metabolism. However, trends such as this observed in laboratory studies may not reflect seasonal changes in metabolic rate. Under natural environmental conditions, the gradual **acclimatization** of a fish to seasonal changes involves many physiological processes, each of which can have an impact on overall metabolism. Therefore, the results of temperature **acclimation** studies during a single season may not represent true seasonal changes in metabolic rates (Moore & Wohlschlag 1971; Burns 1975; Evans 1984; Adams & Parsons 1998; Gamperl et al. 2002).

Temperature–metabolic rate generalizations based on studies of individual species acclimated to different temperatures should not be applied across species, especially those adapted to very different thermal environments. At low temperatures, for example, polar fishes have metabolic rates considerably higher than those of temperate species acclimated to the same low temperatures (Brett & Groves 1979). Metabolic rates of tropical fishes and those of temperate species acclimated to high temperatures differ only slightly.

Size also can have a considerable effect on metabolism. Not surprisingly, large fishes generally will have higher overall metabolic rates than small fishes, assuming other factors such as activity are constant. However, the metabolic rate per unit of mass, often called the mass-specific metabolic rate or **metabolic intensity**, is higher for smaller fishes. This relationship seems to hold true for other animal groups as well.

Among the more metabolically costly things that a fish does is to swim. Because water is 800 times denser than air, more energy is required to move through it. There is a trade-off, however, in that the density of water also provides buoyancy so that fishes do not have to utilize as much energy fighting gravity as they would in a less dense medium. Not surprisingly, oxygen consumption in fishes increases with swimming velocity. The increase is exponential, starting out quite slowly at first, but increasing dramatically at higher velocities (Fig. 5.7). Such oxygen consumption curves probably underestimate the true metabolic cost of swimming at high speeds because of the increased use of anaerobic metabolism by swimming muscles at higher velocities.

The evolution of a torpedo-shaped, fusiform body undoubtedly is the result of its energetic advantages. Fin

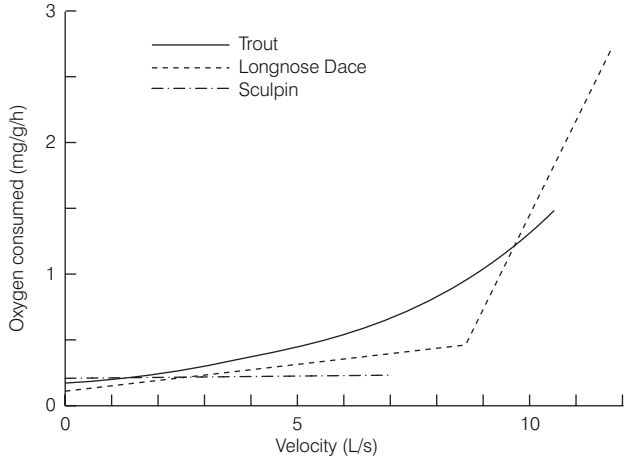


Figure 5.7

The amount of oxygen used by stream fishes while holding position at different water velocities varies with fish morphology and lifestyle. Water column species, such as Rainbow Trout (*Oncorhynchus mykiss*) must increase swimming effort as water velocity increases. The resulting exponential increase in oxygen consumption rates with increasing velocity has been shown in numerous studies of swimming fishes. Mottled Sculpin (*Cottus bairdi*) are benthic fish that lie on and cling to the substrate. Hence, their oxygen consumption rates do not change with increasing water velocity. Longnose Dace (*Rhinichthys cataractae*) combine tactics. At low and moderate velocities they remain on the substrate, and oxygen consumption rates do not change much. At higher velocities, however, they must swim, and oxygen consumption increases dramatically. After Facey and Grossman (1990).

shape and placement also are important considerations, as well as body flexion during the act of swimming. The fastest, most active swimmers are streamlined, with high, thin caudal fins that oscillate rapidly while the rest of the body remains fairly rigid. This eliminates the drag that would be created by throwing most of the body into curves while swimming forward. The relationship between body shape, fin placement, and swimming style are addressed in more detail in Chapter 8 (Locomotion: movement and shape).

Body shape and other morphological features also are important to the energetics of many benthic fishes. Bottom-dwelling stream fishes, for example, are able to hold their position in a high-flow environment without much energetic cost due to body shape and judicious use of their fins. Mottled Sculpin (Cottidae) can use their pelvic fins to hold to the rocky substrate of swift mountain streams. They can even hold position in a plexiglass swimming tunnel, apparently by using their large pectoral fins to create downward force as the water flows over them (Facey & Grossman 1990). Their overall body shape of a large head and a narrow, tapering body may also help them remain on the bottom as water flows over them. These morphological adaptations give sculpins the ability to hold position in moderate currents without a significant energetic cost (Fig. 5.7). The bottom-foraging Longnose Dace (Cyprinidae) responds similarly at low to moderate velocities, showing no change in oxygen consumption. At higher velocities, however, it must resort to swimming to hold its position and its oxygen consumption increases dramatically. This change in behavior breaks the oxygen consumption curve into two distinct segments (Fig. 5.7).

Energetics

Swimming

Water is a viscous medium and therefore presents considerable resistance to animals moving through it. It is not surprising, therefore, that fishes have evolved a variety of mechanisms to minimize the cost of swimming. Variations in body shape, fin shape and location, and swimming style are addressed in Chapter 8. Fishes also can utilize vortices in their environment to reduce the cost of swimming (Liao et al. 2003). These vortices may be created by either water moving past an obstacle or by the movement of other fishes, such as those in a school. By carefully positioning themselves fishes can use the vortices to "slalom" ahead while reducing the activity of trunk muscles normally used in propulsion, thereby conserving energy (see Chapter 22).

Buoyancy regulation

For fishes that are not benthic, maintaining vertical position in the water column has the potential for being energetically expensive. This is not the case for most teleosts, however, because of their ability to regulate buoyancy by regulating the size of the **gas bladder**, a flexible-walled, gas-filled chamber in the body cavity. This structure is often referred to as the "swim bladder", but it has nothing to do with generating propulsive forces for the act of swimming and instead saves energy by regulating buoyancy. The gas bladder also is important in hearing by some fishes (see Chapter 6, Hearing).

The need to regulate the volume of the gas bladder is a result of the effect of changing pressure as a fish changes depth. If a fish is neutrally buoyant at a given depth and descends in the water column, the increase in pressure decreases the volume of the gas bladder, making the fish negatively buoyant and the fish begins to sink. If the fish continues to descend, the gas bladder shrinks even more and the fish would have to expend energy to prevent further sinking. Conversely, if a fish ascends in the water column, the gas bladder expands and the fish becomes positively buoyant. It would now have to either expend energy to swim downward in the water column or continue to float toward the surface with the gas bladder continuing to increase in size as the pressure decreases. Therefore, to save energy fishes must be able to regulate the volume of the gas bladder by the release or addition of gases in order to maintain neutral buoyancy at a variety of depths.

The gas bladder is derived as an outpocket from the esophagus, and in some groups retains its connection to the gut via the **pneumatic duct** (the **physostomous** condition). In **physoclistous** fishes, which include the higher teleosts (Paracanthopterygii and Acanthopterygii), the gas bladder is initially open to the esophagus, but becomes sealed off once the gas bladder is initially filled during the larval stage. Czesny et al. (2005) showed that larval Yellow Perch (Percidae) that did not inflate their gas bladder fed less efficiently, used more energy, grew more slowly, were more susceptible to predation, and had higher overall mortality than those with properly inflated gas bladders.

We will consider function of the teleost gas bladder in two parts – those of gas release and gas addition. Consider first the case of gas release. A fish swimming upward experiences increasing gas bladder volume, and to remain neutrally buoyant the fish must release some of the gas. In physostomes, gas can be released directly via the pneumatic duct. In some physostomes, however, such as eels (Anguillidae, Congridae), the pneumatic duct serves as a resorptive area for slow gas release via the blood, but can release gas rapidly via the esophagus if necessary (Fig. 5.8A). In physoclists, the gas must be released via the blood. Although most of the wall of the gas bladder is not permeable to gases because it is poorly vascularized and lined with sheets of guanine crystals, there is a modified area (called the oval in some species) where gas can diffuse into the blood when the gas bladder expands (Fig. 5.8B). The blood carries the excess gas to the gills where it is released to the surrounding

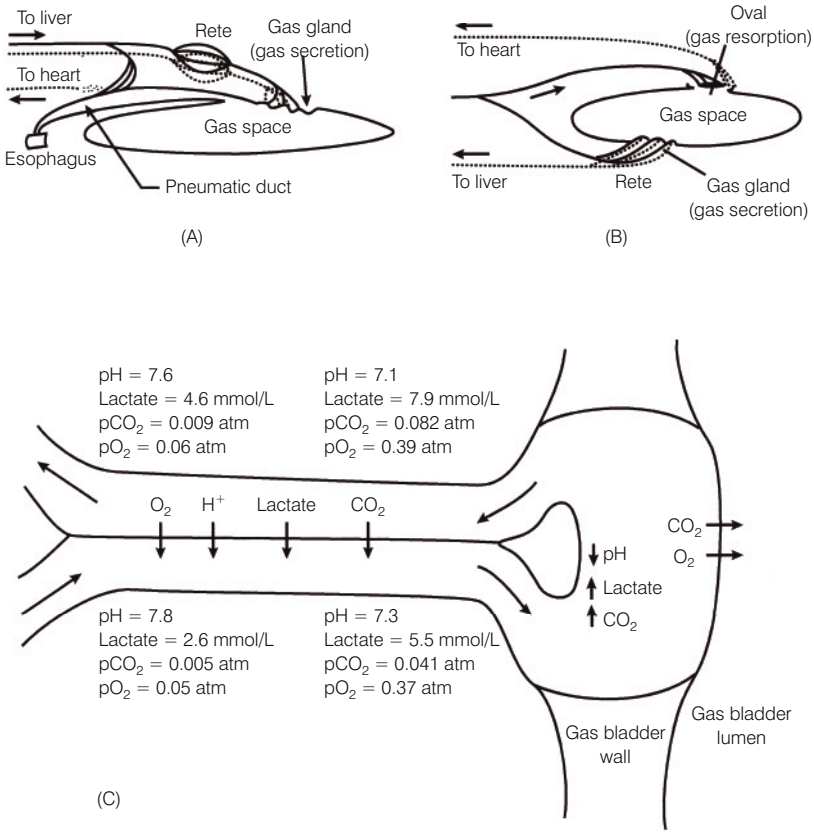


Figure 5.8

Schematic representation of the gas bladders of a physostome (A) and a physoclist (B). The pneumatic duct permits gas release via the esophagus in a physostome, whereas a physoclist must rely on a specialized area of the bladder wall for gas resorption. Both have gas glands with associated retia for gas addition. (C) Production of lactate and hydrogen ions by gas gland tissue triggers the hemoglobin's release of oxygen (the Bohr and Root effects) and a decrease in gas solubility (the salting-out effect). Countercurrent exchange of ions and dissolved gases in the rete creates very high gas pressures in the gas gland, thereby facilitating the diffusion of gases into the gas bladder. (A, B) after Denton (1961); data presented in (C) are for eels (*Anguilla*), from Kobayashi et al. (1989, 1990).

water. Fishes regulate the loss of gas by controlling the flow of blood to the resorption area and by using muscles to regulate the amount of gas entering the resorptive region.

The addition of gas to the gas bladder is more complex. As a fish descends, the volume of the gas bladder decreases due to increasing pressure, and the fish must add gas to maintain neutral buoyancy. A physostome could theoretically swim to the surface, gulp air and force it into the gas bladder via the pneumatic duct. However, the change in pressure with depth would affect any air gulped at the surface, making this impractical, if not impossible. Hence, a physostome is in the same predicament as a physoclist. The addition of gas takes place by the diffusion of gases from the blood into the gas bladder at a special vascularized region of the bladder wall known as the **gas gland**. The process of inflating the gas bladder occurs by diffusion and not by active transport, therefore a dramatic increase in the amount of gas in solution in the blood must occur. Three general physiological phenomena discussed earlier act together to bring this about (Fig. 5.8C). First is the effect of acidification on hemoglobin's ability to hold oxygen. The tissues of the gas gland produce lactic acid, which dissociates to lactate and hydrogen ions. The increase in hydrogen ion concentration decreases the blood pH, and the Bohr and Root effects cause unloading of oxygen from hemoglobin when pH decreases. This oxygen goes into solution in the blood, increasing the amount of dissolved oxygen. The second phenomenon is the reduced solubility of gases in an aqueous solution as the concentration of lactate and hydrogen ions increases (the **salting-out effect**). This helps to drive the dissolved gases out of solution and into the gas bladder through the formation of small bubbles (Copeland 1969). The combined effect results in the diffusion of gas from the blood and into the gas bladder. Elevated levels of plasma carbon dioxide also enhance the addition of this gas into the gas bladder (Pelster & Scheid 1992).

The third phenomenon that makes the gas gland so effective is the efficiency of countercurrent exchange. The blood vessels leading to and from the gas gland are divided into a network of small capillaries that run countercurrent to one another. Such a bundle of capillaries is called a **rete mirabile** ("wonderful net"), or rete for short. As blood leaves the gas gland and travels through the rete, lactate, hydrogen ions, and dissolved gases diffuse down their concentration gradients into the blood coming toward the gas gland. Hence, the countercurrent arrangement of the rete capillaries helps build up the levels of diffusible gases in the gas gland.

The reason that the blood can give up oxygen in the gas gland and enter the rete with a higher partial pressure of oxygen than it had when it entered the gas gland, is that

partial pressure only indicates the amount of gas in solution; oxygen bound to hemoglobin is not in solution and therefore is not accounted for in the partial pressure. So blood leaving the gas gland actually has less total oxygen than when it entered because some of the oxygen has diffused into the gas bladder. However, the partial pressure is higher because the oxygen that is present is in solution. Hemoglobin cannot bind much because the pH is low.

One other important factor is the timing of the release of oxygen by hemoglobin under acidic conditions (the **Root-off shift**) and the binding of oxygen by hemoglobin when pH increases (the **Root-on shift**). The Root-off shift occurs nearly instantaneously whereas the Root-on shift takes several seconds. Therefore, hemoglobin in blood in the rete that is leaving the gas gland area does not increase its affinity or capacity for oxygen until it is already out of the rete.

Understanding how the rete mirabile functions to build up high gas pressures in the gas gland helps explain why fishes with a long rete can build up higher gas pressures than those with a shorter rete. Deepsea fishes (see Chapter 18, The deep sea), which must deposit gas under high pressure conditions, tend to have a longer rete than shallow water fishes (Alexander 1993). The rete associated with the gas bladder of migratory eels (Anguillidae) lengthens as fish metamorphose from their shallow water, freshwater or estuarine juvenile phase to their deep water, oceanic reproductive phase (Kleckner & Kruger 1981; Yamada et al. 2004).

Because the main purpose of the gas bladder is to maintain buoyancy at a given depth, several groups of teleosts find it more adaptive to have greatly reduced gas bladders, if they have one at all. Many benthic fishes, such as sculpins and flounders, either have gas bladders that are greatly reduced in size or lack gas bladders altogether. The absence of a gas float makes it that much easier to remain on the bottom. Fishes that constantly swim and change depth rapidly and frequently, such as some tunas, also lack gas bladders. Herring (Clupeidae) are marine physostomes that lack a gas gland. Their high body lipid content, however, also provides buoyancy, so decreasing gas bladder volume with depth is less of a problem (Brawn 1962).

Gas bladders are found only in the bony fishes, so the elasmobranchs must utilize other means to reduce their buoyancy. A cartilaginous skeleton helps because cartilage is much less dense that bone (the specific gravity of cartilage is 1.1, as opposed to 2.0 for bone), and the constant swimming of pelagic sharks helps prevent sinking by providing upward lift (see Chapter 8). Pelagic elasmobranchs also maintain high levels of low-density lipids in their large livers, which may make up 20–30% of their total body mass (Alexander 1993). Livers of other, more benthic, sharks make up only about 5% of their body mass. The Basking Shark (Cetorhinidae) has a large liver that contains much squalene (specific gravity = 0.86), which is less dense than most other fish oils (specific gravities around 0.92). Another low-density, oily compound, wax esters (specific gravity = 0.86), has been found in the livers of some benthopelagic sharks (Van Vleet et al. 1984).

Some teleosts also utilize lipids to reduce body density. The skin, muscles, and even the bones of the Oilfish (Gempylidae) contain deposits of lipids, including wax esters (Bone 1972). Wax esters have also been found in the muscles and adipose tissues of coelacanth (Nevenzel et al. 1966), and in some mesopelagic lanternfishes (Myctophidae) that lose their gas bladders as adults (Capen 1967). Other tactics to reduce body density include reduced ossification of bone and increased water content of tissues. This is true in the Lumpfish (Cyclopteridae; Davenport & Kjorsvik 1986), a coastal teleost, and in some bathypelagic species (Gonostomatidae and Alepocephalidae; Denton & Marshall 1958) (see Chapter 18, The deep sea).

Energy intake

Fishes obtain the energy needed to meet metabolic demands through feeding. The diversity of feeding adaptations found among fishes is discussed in Chapter 8. The emphasis here is on postingestion processes.

Food is taken into the **mouth** and passed down the **esophagus** into the **stomach**. Secretion of mucus by the epithelial lining of the esophagus helps to lubricate the passage of food along the gut. Most fishes lack a mechanism for chewing food in the mouth, so food items are swallowed whole or in large chunks and much of the physical breakdown takes place in the stomach. However, many fishes, such as minnows (Cyprinidae), suckers, croakers (Sciaenidae), cichlids (Cichlidae), wrasses (Labridae), and parrotfishes (Scaridae), have bony arches or toothed pads deep in the pharynx that are equipped with toothlike projections. These pharyngeal teeth grind up food before it reaches the stomach (see Chapter 8, Pharyngeal jaws).

The stomach is often highly distensible and can store food. Tough ridges along the internal wall of the stomach, along with contractions of the muscular wall, aid in the physical breakdown of foods. Acidic secretions of the stomach help to further break down foods; proteolytic enzymes also function more efficiently at lower pH. The combined physical and chemical activity of the stomach creates a soupy mixture which is released into the small intestine in small amounts.

Chemical digestion continues in the **intestine**, aided by **bile** from the liver, which helps emulsify lipids, and by secretions from the pancreas. **Pancreatic juice** contains bicarbonate to neutralize the acid from the stomach and a wide variety of enzymes to complete the process of chemical digestion.

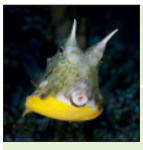
The **small intestine** is also the primary site of absorption of the products of digestion, and mechanisms exist for maximizing this uptake. Elasmobranchs have a short, thick intestine with a large, spiraling fold of tissue (the **spiral**

valve) to increase absorptive surface area. Teleosts generally have longer intestines, often with numerous side pouches (**pyloric caecae**) to increase the absorptive area (Buddington & Diamond 1987). Herbivorous and microphagous teleosts have particularly long, often coiled, intestines to increase the opportunity to extract nutrients (see Fange & Grove 1979; Lobel 1981) (Box 5.1). Some of these fishes, such as minnows, suckers, and topminnows (Cyprinodontidae), and several tropical marine fishes, including wrasses and parrotfishes, have reduced stomachs or lack them altogether (Fange & Grove 1979; Lobel 1981; Buddington & Diamond 1987). Transgenic Coho Salmon (Salmonidae) have more than two times the intestinal surface area than do their control counterparts, which may help explain how these fish are so effective in extracting the nutrients needed to maintain their high rate of growth (Stevens & Devlin 2000). Although some nutrient absorption may continue in the large intestine, this last major portion of the gut functions primarily in water absorption.

Once basic metabolic demands are met, excess nutrients can be accumulated. **Carbohydrates** are stored as **glycogen** either in the liver or in muscle tissue. **Lipids** and **proteins** also are stored, resulting in an increase in mass that we refer to as growth. Lipids tend to accumulate either in the liver, in muscles, or as distinct bodies of fat in the visceral cavity. Protein often goes into tissue growth. All of these potential energy sources are mobilized when needed, although carbohydrates are metabolized first. In prolonged periods of starvation, such as during the migration of salmonids, body lipids and proteins will also be used. Stored lipids yield considerably more energy per gram than stored carbohydrates or proteins.

Bioenergetics models

Bioenergetics models can aid in understanding energy intake and utilization. The construction of a bioenergetics model is a complex process because the energetic costs and benefits of all physiological activities must be accounted for if the model is to provide a reasonably realistic view of how energy is being allocated. In addition, each individual organism is different. Consequently, bioenergetics models, like any physiological model, provide a broad conceptual framework, rather than a precise prediction of what will happen in any particular organism. Bioenergetics models can, however, be useful in understanding how energy is allocated, and may be used to estimate the impacts of environmental alterations on rare species (Petersen & Paukert 2005). In addition, bioenergetics models of individual species can be used to construct community bioenergetic models, thereby providing some understanding of energy flow through ecosystems and estimating how fish populations may be impacted by factors such as predators, invasive species, and climate change (see Bajer et al. 2003). But such models should be used cautiously – Bajer et al. (2003) applied two bioenergetic models to a controlled study of



Box 5.1

BOX 5.1

Herbivory in fishes

Although carnivory is more common than herbivory among fishes, herbivorous species can have a substantial effect on macrophyte or algal communities in both marine (Alcoverro & Mariani 2004) and freshwater (Nurminen et al. 2003) environments. Herbivorous fishes may depend in part on fermentation by symbiotic microorganisms in their guts to digest the plants they consume. Many of 27 primarily herbivorous tropical marine fishes from five families (Pomacanthidae, Scaridae, Kyphosidae, Acanthuridae, Siganidae) showed elevated levels of short-chained fatty acids (SCFAs) in the posterior gut segments (Clements & Choat 1995). SCFAs are produced by microbial digestion of plant matter in the guts of terrestrial vertebrate herbivores. Most species examined also showed elevated SCFA levels in their blood, suggesting a direct contribution of metabolic fuel by microbial fermentation.

Fermentation digestion may not only benefit herbivorous fishes, however, as some planktivorous fishes studied by Clements and Choat (1995) also showed elevated SCFA levels. The relative contribution of gut microorganisms to digestion and nutrition in fishes deserves further study.

Some herbivorous fishes seem to rely on physical grinding or low stomach pH to break through plant cell walls (Lobel 1981). Of the 27 herbivores studied by Clements and Choat (1995), the six showing the lowest SCFA levels all possessed some mechanism for mechanically grinding ingested plant material.

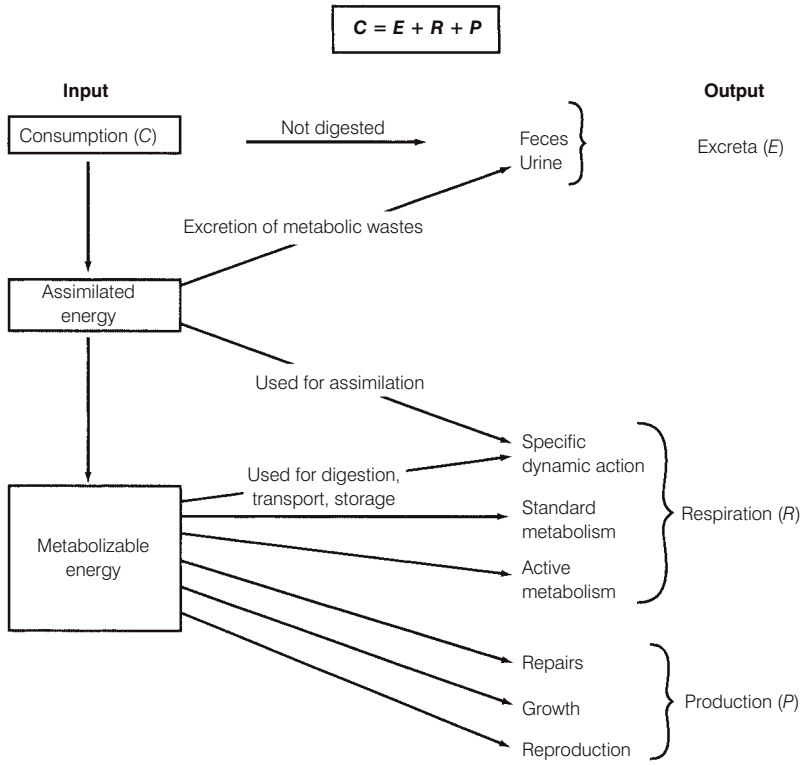


Figure 5.9
Partitioning of the energy consumed by a fish. Only energy not required to meet basic physiological needs (digestion, standard metabolism, repairs) or needed for activity is available for growth and gametes. Adapted from Videler (1993).

Yellow Perch, found deficiencies in both, and concluded that such models should be evaluated in lab and field studies and refined accordingly before being applied.

Several methods can be used to determine the energetic content of food items, waste products, or components of fish growth such as tissue or gametes (see Wootton 1998). The energetic costs of different activities can be estimated either by direct calorimetry (measuring the heat produced by an organism) or some form of indirect calorimetry, such as measuring oxygen consumption (discussed earlier in this chapter). We can then construct a conceptual model (Fig. 5.9) to represent how energy may be partitioned. The energy equation is often represented as:

$$C = E + R + P,$$

where C is the energy **consumed**, E is the energy **excreted**, R is the energy used in **respiration**, and P is the energy remaining for **production**.

Some of the potential energy in food will never be digested and is therefore lost in the feces. The proportion that is digested is sometimes represented by the **absorption efficiency** (or "digestibility") and varies for different food types. Carnivorous fishes feeding on soft-bodied, highly digestible prey may have absorption efficiencies as high as 90% or more, whereas herbivores tend to have considerably lower absorption efficiencies (e.g., 40–65%; see Wootton 1998). In general, foods high in lipids and proteins have much higher absorption efficiencies than foods high in carbohydrates.

Of the energy that is absorbed during digestion, some is subsequently lost through the excretion of nitrogenous wastes. An additional 10–20%, depending on the amount and type of food consumed, is used in providing the energy needed for digestion (Jobling 1981). Larger meals and foods with higher protein content require more energy to digest and assimilate.

The remaining absorbed energy must be allocated among maintaining metabolism, swimming or other forms of activity, and the production of gametes or new somatic tissue (growth). Only energy remaining after other physiological maintenance needs have been met is available for growth or reproduction. Therefore, any factors that increase other metabolic demands can ultimately decrease growth or reproduction. Environmental factors affect the amount of energy needed to sustain metabolism. Increased temperature often elevates metabolism and increases the need for energy. Other energetic costs include the maintenance of proper salt and water balance (osmoregulation) and the costs of health maintenance by the immune system. Energy requirements for basic maintenance may increase due to changes in salinity, or energy diverted to fighting infections, diseases, or parasites. In addition, exposure to contaminants that affect ion or water balance or that diminish the effectiveness of a fish's immune system can indirectly divert more energy away from growth and reproduction.

Summary

SUMMARY

1. Fishes need oxygen to provide energy for physiological function. In the presence of oxygen, far more energy can be derived from the metabolism of glucose than is possible in the absence of oxygen. Although anaerobic metabolism can provide some energy, it also results in the build up of lactate, which can inhibit further metabolism.
2. Water's high density and viscosity, as compared to air, make it a difficult medium to move across respiratory surfaces. Water also contains considerably less oxygen than air, especially at elevated temperatures. Fish gills provide a large surface area for gas exchange, and the countercurrent flow of blood and water across the lamellae maximizes the efficiency of gas exchange by diffusion. Some fishes have special adaptations to allow them to breathe air.
3. Blood transport of carbon dioxide and oxygen is closely linked because of hemoglobin's sensitivity to pH. At metabolically active tissues, high levels of carbon dioxide result in lower pH, which enhances the release of oxygen by hemoglobin. The loss of carbon dioxide to the surrounding water at the gills results in an increase in pH, enhancing hemoglobin's ability to bind oxygen.
4. Metabolism is influenced by a wide variety of factors, including the presence of food in the gut, activity, age, sex, reproductive status, temperature, and season. Because of the impacts of these numerous factors, metabolic studies of fishes acclimated to controlled laboratory conditions may not accurately represent the metabolic rates of fishes in nature.
5. Many fishes that live in the water column use buoyancy control mechanisms, such as the addition or release of gases from the gas bladder, to save energy.
6. Energy in food is made available by digestion. Although some mechanical breaking down of food is accomplished in the mouth or pharynx of some fishes, most digestion takes place in the stomach and intestine. The intestines also function in nutrient uptake. Some fishes that feed on plants rely on symbiotic microorganisms in the gut to help break down their food.
7. Energy budgets indicate how the energy that is consumed is allocated. Some of the energy in food is not digestible and is subsequently excreted. Of the energy that is digested and absorbed, some must be used for basic metabolism and maintenance. Energy remaining after basic needs have been met can be used for growth and reproduction.

Supplementary reading

SUPPLEMENTARY READING

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Chapter 6

Sensory systems

Chapter contents

CHAPTER CONTENTS

The sensory environment of fishes is quite different than what we experience. Vibrations such as sound may travel long distances under water, but certain wavelengths of light attenuate rapidly. Fishes are surrounded by molecules in solution, so chemoreception (taste and smell) can take place almost anywhere on their body that has appropriate receptors. And water's conductive properties surround fishes with electric impulses, making electroreception not just a possibility, but a reality for many species. It should not be surprising, therefore, that more than 400 million years of natural selection have resulted in a remarkable array of sensory abilities and adaptations. In this chapter we will explore the fundamentals of fish sensory systems as well as some specific examples, recognizing that the full diversity of fish sensory capabilities is well beyond the reach of these pages.

Sensory organs are basically accessories to the nervous system that act as transducers. They capture specific types of signals, such as light, sound, molecular shapes, or electricity, and convert them into changes in action potentials, which are then carried by sensory neurons to the brain where the information is interpreted. Sensory systems may show ontogenetic changes because larvae, juveniles, and adults must be prepared to deal with different sensory environments. We will consider the following categories of fish sensory systems: **mechanoreception** (lateral line, hearing), **electroreception**, **vision**, **chemoreception** (taste and smell), and **magnetic reception**. In addition, we consider the question of whether or not fishes detect **pain** (Box 6.1). Finally, we will explore how signals from various sensory organs are integrated to help fishes survive and thrive in their environments.

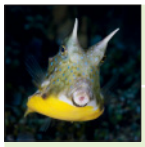
Mechanoreception

Water's density makes it an excellent conductor of vibrations. It is not surprising, therefore, that aquatic organisms have come to rely heavily on detecting these signals in a variety of ways. These mechanisms evolved early in the long history of vertebrates, and have become highly modified and specialized in the fishes.

Mechanoreception among fishes involves the detection of the movement of the water. Fishes have two major mechanosensory systems: the **lateral line system** and the **inner ear**. Both of these rely on **sensory hair cells** (Fig. 6.1) which include an array of cilia on their apical surface. Displacement of the shorter stereocilia with respect to the much longer kinocilium alters the rate of nerve impulses sent to the brain by the nerve cells associated with each hair cell – a higher rate if the stereocilia move toward the kinocilium and a lower rate if they move in the opposite direction. The lateral line system detects disturbances in the water, thereby helping a fish detect currents, capture prey, maintain position in a school, and avoid obstacles and predators, whereas the inner ear is responsible for fish equilibrium and balance, as well as hearing (Schellart & Wubbels 1998).

Lateral line system

The lateral line system is an old feature in the history of vertebrates, as indicated by its presence in fossil jawless



Box 6.1

A "sense" of pain?

Sneddon et al. (2003) attempted to address the question of whether fish can detect pain by studying neural and behavioral responses of Rainbow Trout (*Oncorhynchus mykiss*) to noxious stimuli. Monitoring nerve activity in the brain of decerebrated trout revealed 22 areas of nociceptors (receptors that respond to noxious stimuli) on the mouth, face, and head. Some of these responded to pressure, some to heat, some to acetic acid, and some responded to all of these (polymodal nociceptors). Behavioral studies showed that trout that had bee venom or acetic acid injected into their lip had significantly higher breathing rates and took much longer to resume feeding after treatment than did fish that were injected with saline or fish that were just handled and had nothing injected. The fish injected with acetic acid also rubbed their lips in the gravel and against the sides of the tank. In a related study, the effects of noxious stimuli were reduced when the fish were administered morphine (Sneddon 2003). The combination of the facts that these fish detected noxious stimuli, that the noxious stimuli caused fish to rub their jaws in the gravel and stop eating, and that these effects could be reduced by the use of an analgesic led Sneddon (2004) to the conclusion that criteria for nociception and pain were met, and that bony fishes, as represented by Rainbow Trout, can feel pain. Studies of elasmobranchs, however, have not shown nociception (see Rose 2002; Sneddon et al. 2003), and it is therefore presumed that they do not have the capability to sense pain. In a more recent review of related studies, Braithwaite and Boulcott (2007) also conclude that bony fishes may be able to sense pain, and perhaps fear.

Rose (2002, 2007), however, argues that just because fish detect and react to noxious stimuli, does not mean that they necessarily feel pain. His argument comes down to a few main points: (i) sensing pain requires a level of cognition and awareness that can only be achieved by animals that have a complex neocortex of the brain, which fishes do not have; (ii) responses to noxious stimuli can occur without a level of awareness that could be perceived as pain; and (iii) analgesics such as morphine act at the subcortical level of the brain, and in the spinal cord, so their effects on nociception should not be seen as evidence for an animal's ability to perceive pain. Rose recognizes that fishes have been shown to learn, but feels that the type of learning seen in fishes can occur without conscious awareness, so it should not be used as an argument that fishes possess higher level cognition. This leads Rose to the conclusion that fishes simply do not have the brain structure necessary to process and perceive pain.

Rose's argument, however, is based on a definition of pain that requires a conscious awareness of the stimuli, and also on the argument that this can only be achieved in a brain that has a neocortex, which fishes lack. The assumption, therefore, is that animals lacking a brain structure similar or equivalent to the area associated with pain detection in humans must not be able to perceive pain. This seems to be a case of humans defining pain in terms that can only apply to animals with brains similar to ours, and then concluding that animals with a much simpler brain structure cannot detect pain. Fishes can detect noxious stimuli, react to it, and have it affect their behavior.

As Rose points out, however, it would be anthropomorphic to presume that a fish's perception of pain is similar to ours, and we should make no presumptions about the emotional or psychological impacts of noxious stimuli on fishes, as we have no data to suggest that they have the capability for such cognition and their brain structure seems to make it unlikely that that they could. Iwama (2007) points out that we will never be able to know enough about the mental processing of stimuli to determine whether or not fishes may experience something similar to what we would describe as pain. He suggests, therefore, that the scientific community not be drawn into this debate, but instead focus on testable aspects of fish biology and physiology, while recognizing our "ethical responsibility to respect the life and well-being of all organisms".

fishes from the Silurian. The system is only useful in water, and is therefore restricted to fishes and larval and permanently aquatic amphibians. The hair cells of the lateral line system are organized into **neuromasts**, which allow fishes to detect vibrations in the water that originate from or reflect off prey, predators, other fishes in a school, and environmental obstacles. These neuromasts are clusters of cells that are typically covered by a gelatinous cupula (Fig. 6.2), which can be displaced by water movement, thereby moving the cilia of the hair cells and initiating a change

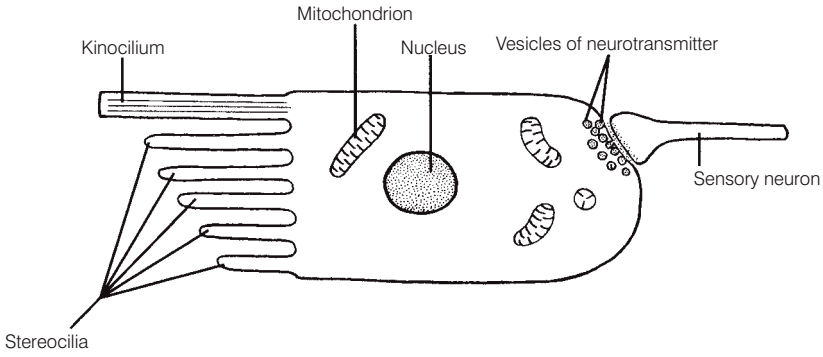


Figure 6.1

Mechanoreception involves sensory hair cells, which are found in the lateral line system of fishes and the inner ear of fishes and other vertebrates. The apical surface of a sensory hair cell usually has numerous stereocilia and a single, much longer kinocilium. Deflection of the stereocilia toward or away from the kinocilium causes an increase or decrease in the firing rate of the sensory neuron innervating the hair cell at its basal surface.

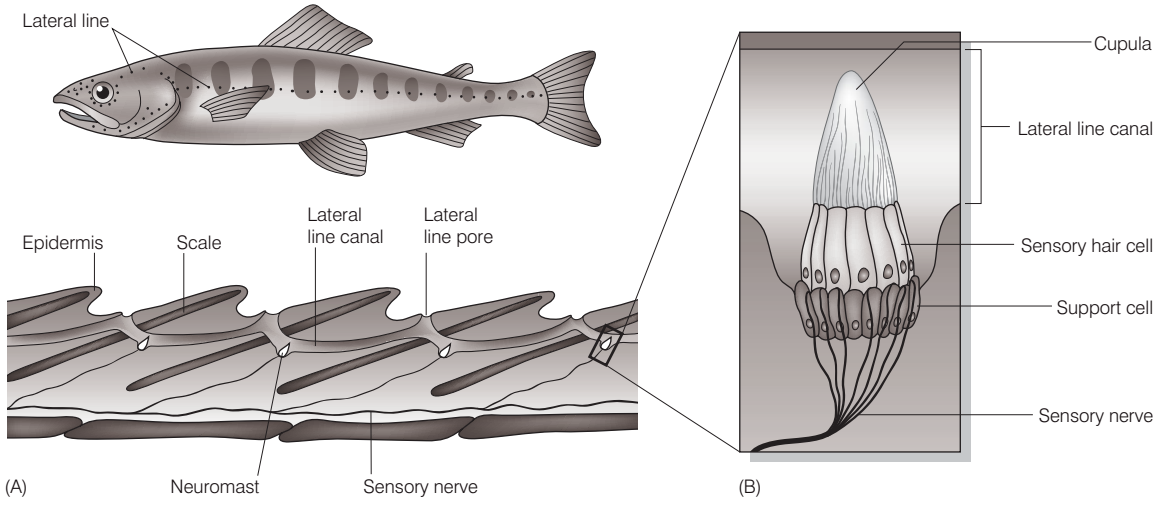


Figure 6.2

(A) Cross-section of the lateral line on the trunk of a fish showing the distribution and innervation of neuromast receptors and the location of pores that connect the canal to the external environment. (B) Each neuromast is composed of several sensory hair cells, support cells, and innervating sensory neurons. The apical kinocilia and stereocilia project into a gelatinous cupula which overlays the entire neuromast.

in signals to the brain (Schellart & Wubbells 1998). The cupula helps screen out background "noise" by preventing the hair cells from being affected by small vibrations – only vibrations strong enough to move the entire cupula will be detected by the hair cells within it.

The lateral line system has two main subdivisions – superficial neuromasts, which are free-standing on the skin, and canal neuromasts, which are located in channels beneath the scales of the trunk (the "lateral line") and in dermal bones of the head ("cephalic lateral line canals") and which open to the surrounding water via small pores (Fig. 6.2). Early in development all neuromasts are superficial and tend to be concentrated around the head, but as development progresses they spread along the trunk and in many fishes they become incorporated into canals that run below the skin or scales (Poling & Fuiman 1998; Diaz et al. 2003; Gibbs & Northcutt 2004). Superficial neuromasts are more exposed, making them quite sensitive to water movement across the skin. This makes them particularly effective for detecting water currents for orientation (rheotaxis) or movement of the fish itself in areas with little water velocity, but not very useful for detecting small stimuli in areas of swift or turbulent water (Engelmann et al. 2000, 2002). They also are most effective in detecting currents that are unidirectional or at frequencies below 20 Hz (Braun et al. 2002). Superficial neuromasts are more abundant in fishes that are sedentary or slow swimmers and that inhabit quiet areas, such as the Goldfish (*Carassius auratus*). Canal neuromasts, however, are shielded from constant stimulation by water moving across the skin and are better at detecting stimuli if the fish or the water around it is moving quickly. Therefore, they are more effective in detecting transient currents, or currents of higher frequency (20–100 Hz; see Braun et al. 2002). These, therefore, tend to be better developed in fishes that are fast swimmers or that live in fast or turbulent water. Rainbow Trout (*Oncorhyunchus mykiss*), for example, often inhabit running water and have very few superficial neuromasts

but have well-developed neuromasts in narrow canals (Engelmann et al. 2002). And the canal neuromasts of the Mottled Sculpin (*Cottus bairdi*) help the fish locate prey by filtering out background stimuli due to water currents (Kanter & Coombs 2003).

As an example of the relationship between the lateral line system and habitat use, Poling and Fuiman (1998) studied the development of lateral line systems and vision in juveniles of three species of drum (family Sciaenidae). As in other fishes, the superficial neuromasts develop first, and then some become incorporated into canals as development continues and the fishes become more active. However, the relative abundance of the two types of neuromasts differed among species and correlated well with juvenile habitat and the relative role that vision might also play. Juveniles of Spotted Seatrout (*Cynoscion nebulosus*), which inhabit shallow, murky, and often weedy inshore areas where mechanoreception would be more critical to predator and prey detection, had significantly more superficial neuromasts on their heads than did juveniles of Red Drum (*Sciaenops ocellatus*) or Atlantic Croaker (*Micropogonis undulatus*). Juveniles of Atlantic Croaker settle the furthest offshore, where the water is clearer and deeper, and they are larger and have the best developed eyes of the three species. Red Drum juveniles are somewhat intermediate in both their habitat (bays and nearshore areas) and their sensory development.

There are other examples of fishes in which mechanoreception helps compensate for a poor visual environment. Under experimental conditions, Lake Trout (*Salvelinus namaycush*) detected and followed the hydrodynamic trails left by prey fishes in total darkness, and their ability to capture prey was significantly inhibited when the lateral line system was rendered ineffective (Montgomery et al. 2002). Mottled Sculpin feed in low light conditions and rely on their lateral lines to detect and locate prey (Braun et al. 2002). And Blind Cave Fish (*Astyanax fasciatus mexicanus*/*Anoptichthys jordani*) have many superficial neuromasts, as well as taste buds, on their heads to help compensate for the inability to see (Schellart & Wubbells 1998). They rely more on their lateral line system than any other sense (Montgomery et al. 2001a).

Some fish predators have learned that their prey can be attracted to vibrations and have used this to their advantage. Several species of piscivorous birds, including herons and egrets (family Ardeidae) have been observed creating disturbances in the water's surface by tongue-flicking or bill-vibrating in order to attract fishes (Davis 2004). In addition, the recreational angling industry designs lures that create vibrations in the water, and even fishing rods have been developed that have built-in, battery-operated vibration devices that claim to enhance angling success.

Equilibrium and balance

Hair cells also can detect movement of fluid or objects within organisms, and therefore play an important role in the ability of fishes to maintain their equilibrium and orientation within the water column (Schellart & Wubbels 1998). Postural equilibrium and balance are maintained by the **pars superior**, a portion of a fish's inner ear that, in jawed fishes, consists of three **semicircular canals** and an additional chamber known as the **utricle** (Fig. 6.3). Lampreys (Petromyzontidae) have only two semicircular canals, and hagfishes (Myxinidae) have one. The semicircular canals are filled with a fluid (endolymph) and have sensory hair cells in their terminal ampullae. Changes in acceleration or orientation set the endolymph in motion and cause displacement of a gelatinous cupula that encloses the cilia of the hair cells. Lateral displacement of the cilia results in changes in the firing rate of the sensory neurons innervating the hair cells, thereby signaling the fish's brain about changes in acceleration or orientation. The utricle contains a solid deposit, or **otolith** ("ear stone"), the lapillus, which rests on a bed of sensory hair cells. The downward pull of gravity on the lapillus triggers impulses from the sensory cells and provides the fish with information regarding its vertical orientation in the water. The utricle works in coordination with the detection of light from above the fish by the retina of the eyes and together they help keep the fish upright in the water (the **dorsal light reflex**). Goldfish with the utricle and semicircular canals removed on one side initially lost their ability to orient

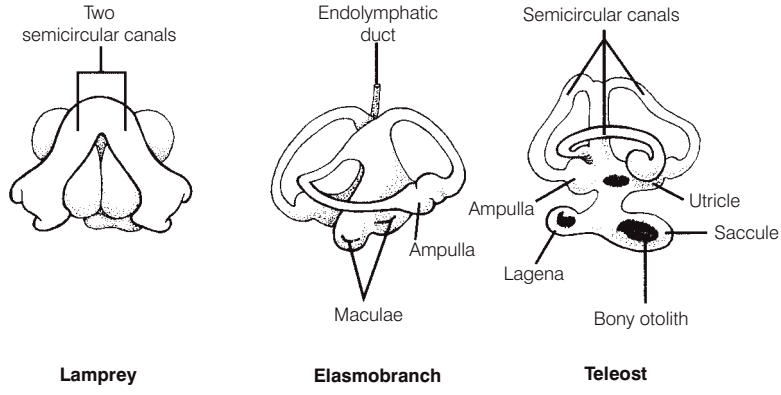


Figure 6.3
The inner ear of fishes. After Hildebrand (1988).

vertically, although this was often regained after several days (Ott & Platt 1988).

Hearing

Hearing in fishes is primarily the responsibility of the inner ear, including the utricle of the pars superior and the **saccule** and **lagena** of the **pars inferior** (see Fig. 6.3). Each chamber contains an otolith (the lapillus, sagitta and astericus, respectively) and is lined with patches of tissue composed of sensory hair cells. An otolithic membrane provides a mechanical linkage between the otolith and the cilia of the sensory hair cells.

Most fish tissue is transparent to sound because its density is similar to that of the water. Structures that are significantly different in density, however, will vibrate differently from the rest of the fish's tissues and provide an opportunity for sensory detection of sound. As sound vibrations pass through a fish, the otoliths lag behind in their vibration due to their greater density. The relative difference in vibration between the fish's sensory hair cells and the otoliths excites the sensory hair cells and triggers action potentials in the sensory neurons of the auditory nerve (Schellart & Wubbels 1998).

Aquatic environments are quite varied in the levels of background sound, and not surprisingly hearing sensitivity of fishes is well matched to their habitats. Fishes in noisy habitats, such as coastlines and swift rivers and streams, tend to have higher sound thresholds and narrower ranges for sound detection than fishes in calmer, quieter habitats such as small lakes and ponds with soft substrate bottoms (Schellart & Wubbels 1998). Sound waves may cause gas spaces in a fish, such as a **gas bladder**, to vibrate, thereby providing an opportunity to enhance sound detection. Fishes that are **hearing specialists** have mechanisms that transmit gas bladder vibrations to the inner ear for detection by the otolith organs, whereas fishes without such a connection, or that lack a gas bladder, are not as sensitive to sound and are referred to as hearing generalists (Yan 2003). Hearing specialists include the cods (Gadidae), which have a gas bladder close to the inner ear, and squirrelfish (Holocentridae) and herring and sardines (Clupeidae) in which anterior extensions from the gas bladder contact the inner ear (Akamatsu et al. 2003). African mormyrids (Mormyridae), also know for sensitive hearing, have separate otic gas bladders adjacent to the inner ear that assist with sound detection (Yan & Curtsinger 2000). And the saccule of the inner ear of gouramis (Anabantoidei) protrudes into the upper part of the air-filled suprabranchial chamber (used for air breathing), thereby significantly enhancing the fishes' hearing sensitivity (Yan 1998).

The largest group of hearing specialists is the **otophysan** fishes, which dominate the fresh waters of the world (over 60% of all freshwater species). They have particularly acute hearing and pitch discrimination due to the **Weberian ossicles**, a series of small bones derived from modified vertebrae that connect the anterior end of the gas bladder to the inner ear (Fig. 6.4). These conduct sound vibrations in

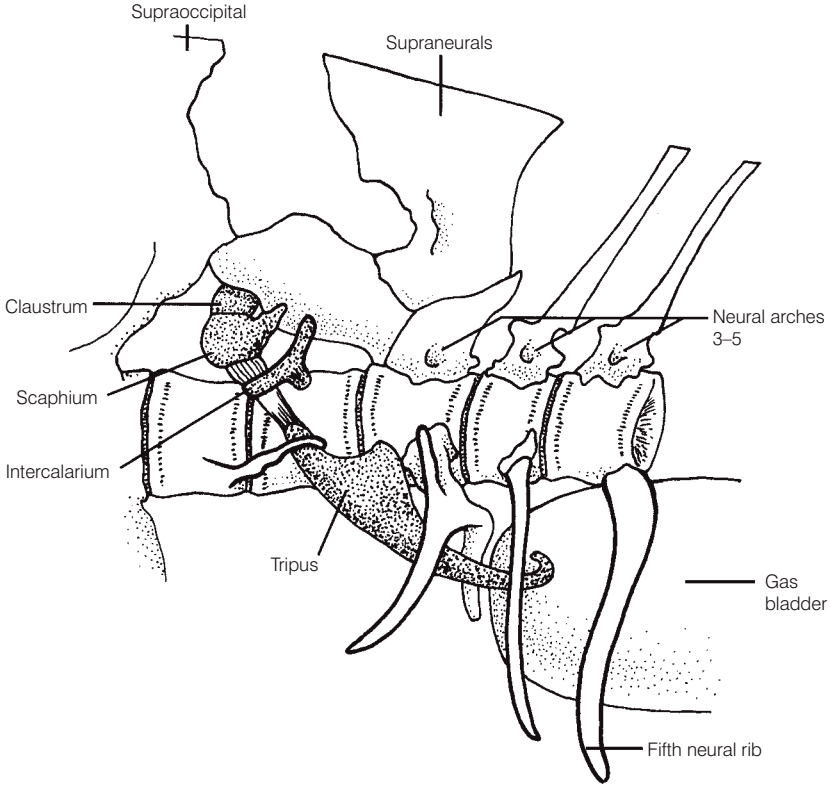


Figure 6.4
A lateral view of the left side of the anterior portion of the vertebral region of an otophysan fish (*Opsariichthys*, Cyprinidae). The Weberian ossicles (tripus, intercalarium, scaphium, claustrum) transmit sound vibrations from the gas bladder to the inner ear. The skull of the fish is to the left. Adapted from Fink and Fink (1981).

much the same manner as the middle ear ossicles of mammals. Because of the Weberian ossicles and gas bladder, the otophysans have the highest sensitivity and greatest frequency range of hearing among fishes. Interference with the Weberian ossicles of the otophysans, or deflation of the gas bladder of any of the hearing specialist fishes, results in decreased hearing sensitivity (Yan et al. 2000).

Much less is known about hearing in elasmobranchs than in bony fishes. The basic structure of elasmobranch inner ears is very similar to that of bony fishes, except that sharks have a connection from a depression in the back of their skulls to ducts in the semicircular canals that contain the sensory area (Hueter et al. 2004). This connection, called the **fenstra ovalis**, is presumed to enhance hearing by directing sound to the sensory area (macula neglecta) of the inner ear. Shark hearing is most sensitive at low frequencies, including those below 10 Hz, which are undetectable by humans, but they may be no more sensitive than many other fishes that are hearing generalists. Sharks are most sensitive to pulsed sounds in this range, such as those emitted by the erratic swimming of an injured fish, and can localize such sounds at distances of up to 250 m (Myrberg 1978; Myrberg & Nelson 1991; see Chapter 12, Subclass Elasmobranchii, Sensory physiology).

Sources of underwater sound

Apparently, natural selection pressures have driven the evolution of various adaptations to enhance hearing among fishes. So it must be important for some fishes to hear well – but what do they hear that could be so important? One source of sounds is predators. Cetaceans, such as dolphins, emit sounds and use echolocation for orientation and to locate prey. Although most marine fishes studied thus far cannot detect sound frequencies above about 500 Hz, at least some clupeids can detect considerably higher frequencies. The ability of some clupeids to detect ultrasound has been attributed to the anterior extensions of the gas bladder that is characteristic of the group. However, not all clupeids can detect ultrasound, and Higgs et al. (2004) believe that modifications of the utricle seen in those clupeids that can detect ultrasound is responsible for this ability. The American Shad (*Alosa sapidissima*), Alewife (*A. pseudoharengus*), and Pacific Herring (*Clupea pallasii*) can detect ultrasonic signals (up to 180 kHz in American Shad), and may use this ability to avoid predatory cetaceans trying to locate them using ultrasound (Plachta & Popper 2003). Another clupeid, the Spotlined Sardine (*Sardinops melanostictus*), can detect sounds of 1 kHz (Akamatsu et al. 2003).

Another source of underwater sounds are fishes themselves – many of which create sounds for inter- and intraspecific communication. Fishes can produce sounds using several different mechanisms. Some catfishes (Siluriformes), toadfishes (Batrachoididae), cods (Gadidae), and sea robins (Triglidae) use muscles to create sound from the gas bladder (see Ladich & Yan 1998). Some catfishes rub together bones of the pectoral girdle, whereas some cichlids and gouramis (Anabantoidei) create sound by grinding together their pharyngeal teeth. The croaking gouramis (*Trichopsis*) create pulsed sounds by strumming tendons over elevations of fin rays by rapidly beating their pectoral fins. The close proximity of the anabantoid sonic organs to the suprabranchial chamber, which is used for air breathing, suggests that this air-filled chamber may enhance the resonance of the sound produced. The close relationship between the frequencies of vocalization and maximum hearing sensitivity also suggests that these features coevolved (Ladich & Yan 1998).

Fishes detect ambient sounds from their environment, and alter their behavior accordingly. Biological sound, such as that produced by other fishes and invertebrates, attracts larval reef fishes to preferentially settle in areas with sounds that would indicate a suitable habitat (Montgomery et al. 2001b). Ambient noise may also impact the evolution of hearing and sound production for communication. Males of two species of freshwater gobies (Gobiidae) that inhabit swift, rocky streams respond to and produce courtship sounds at frequencies within a "quiet window" of ambient noise around 100 Hz (Lugli et al. 2003). The hearing of these fishes is most sensitive within this range, suggesting that ambient sound may be a selective force in the evolution of hearing and noise production.

The sensitivity of fishes, especially hearing specialists, to sound makes them potentially vulnerable to human-generated underwater noise. McCauley et al. (2003) showed that high-intensity, low-frequency sound produced by air guns used in marine petroleum exploration can cause severe damage to the hair cells of fish inner epithelia. And even less intense sound can result in loss of hearing sensitivity in the otophysan Fathead Minnow (*Pimephales notatus*), although the less sensitive hearing generalist Bluegill (*Lepomis macrochirus*) was not significantly affected (Scholik & Yan 2002). Prolonged exposure of Goldfish (*Carrasius auratus*) to loud sound resulted in hearing loss in this otophysan species (Smith et al. 2004).

Electroreception

Electroreception probably evolved over 500 million years ago and has apparently been lost and secondarily evolved in several different groups of aquatic vertebrates, including most groups of non-teleost fishes and several orders of teleosts (Collin & Whitehead 2004; Gibbs & Northcutt 2004). The receptor cells responsible for detecting electricity are derived from the hair cells of the acousticolateralis system, which is responsible for mechanoreception (von der Emde 1998; Collin & Whitehead 2004). In a study of lateral line development in larval sturgeon (Acipenseridae), Gibbs and Northcutt (2004) suggested that the electrore-

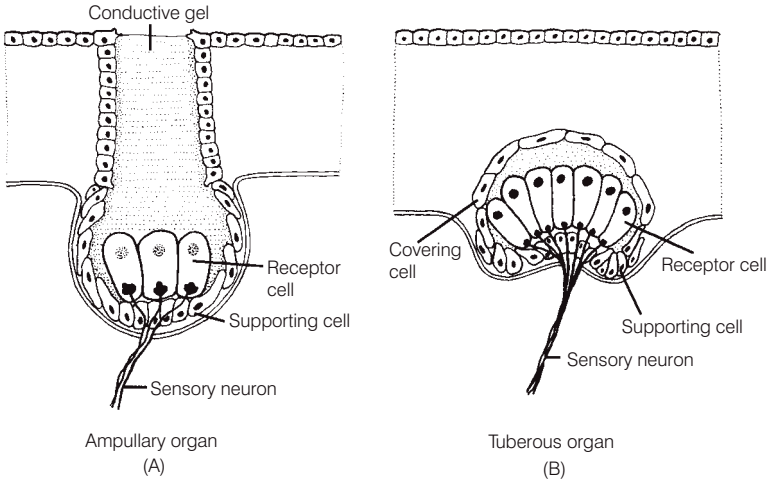


Figure 6.5

Schematic diagram of the structure of ampullary (A) and tuberous (B) electroreceptive organs. Both organs are surrounded by layers of flattened cells that join tightly to one another. This helps prevent current from bypassing the organs. Tight junctions between the receptor cells and supporting cells help focus incoming electric current through the base of the receptor cells, where they synapse with sensory neurons. Supporting cells in ampullary organs produce a highly conductive gel that fills the canal linking the sensory cells to the surrounding water. Adapted from Heiligenberg (1993), drawing courtesy of H. A. Vischer.

ceptive organs arise from the same embryonic precursors as the neuromasts of the lateral line. There are two general types of electroreceptor organs in fishes. **Ampullary receptors** are located in recesses in the skin that are connected to the surface by a canal filled with a conductive gel (Fig. 6.5A). They are sensitive to electric fields of low frequency (<0.1 to 25 Hz) and are found in many groups of fishes. **Tuberous receptors** are located in depressions of the epidermis, are covered with loosely packed epithelial cells (Fig. 6.5B), and detect higher frequency electric fields (50 Hz to > 2 kHz). They are found in fishes that use electric organs to produce their own electric fields, and are most sensitive to the frequencies produced by the fish's own electric organ.

Electroreceptors

Ampullary receptors

Ampullary receptors are much more widespread among fishes, and have been identified in lampreys (Petromyzontiformes), sharks and their relatives (Chondrichthyes), lungfishes (Ceratodontiformes), reedfishes (Polypteriformes), coelacanths (Coelacanthiformes), sturgeons and paddlefishes (Chondrostei), and several orders of more advanced bony fishes including the Osteoglossiformes, Gymnotiformes, and Siluriformes (Collin & Whitehead 2004). These receptors typically are located in small pockets in the skin at the end of a canal filled with an electroconductive gel made primarily of mucopolysaccharides and water. They are particularly abundant among elasmobranchs, where they were first identified as the ampullae of Lorenzini. Ampullary receptors are responsible for passive electroreception – the detection of electric fields originating from sources outside the fish receiving the signal.

Ampullary receptors respond to low-frequency electrical stimuli, including those that are a result of the physical environment and those of biological origin, such as muscle contractions or electric potential differences across epithelial membranes (von der Emde 1998). The sensory cells are modified hair cells whose release of neurotransmitter is modulated by the difference in membrane potentials between the apical and basal membrane (Collin & Whitehead 2004). The neurons to the brain constantly generate nerve signals (action potentials) and the rate of signals increases or decreases depending on external electric fields – so the system is extremely sensitive to any electrical changes outside the fish (von der Emde 1998). The rate of nerve signals may also change with temperature, leading to speculation that the ampullary receptors may also function as thermal receptors (Hueter et al. 2004).

Most fishes known to have ampullary receptors are marine – many are elasmobranchs, a primarily marine group. The higher ionic concentration of salt water makes it a very good conductor of electricity, and the conductive gel in the canal allows the voltage current to easily reach the receptor cells across the rather thick, less-conductive skin. Although fresh water does not conduct electricity as well as salt water does, elasmobranchs found in fresh water, such as the euryhaline Bull Shark (*Carcharhinus leucas*), also have functional ampullary receptors. Ampullary receptors also are known among exclusively freshwater fishes, although they tend to have fewer receptor cells than marine species have, and the receptor cells are closer to the surface of the skin, making the canals shorter. Freshwater fishes with ampullary receptors include sturgeons (Acipenseridae), some of which are also marine or anadromous, and the exclusively freshwater Eel-tailed Catfish (*Plotosus tandanu*) of Australia, and Paddlefish (*Polyodon spathula*) and Brown Bullhead (*Ameiurus nebulosus*) of North America (Collin & Whitehead 2004).

One of the main uses of ampullary receptors is for prey detection. Ampullae often are concentrated around the head, and in some fishes they are especially abundant around the snout and mouth (Collin & Whitehead 2004). Sharks have many ampullae concentrated in the head,

especially on the ventral side of the snout, and the broad head of the Scalloped Hammerhead Shark (*Sphyrna lewini*) may allow it to sample a wider area than sharks with narrower snouts (Kajiura & Holland 2002). Kalmijn (1971) showed that sharks could detect and would attack living prey or electrodes emitting mild electrical signals, but would ignore dead prey or live prey or electrodes that were covered by a barrier that prevented the conduction of electric fields. A similar experiment with Australian Lungfish (*Neoceratodus forsteri*) showed that they also use electroreception to detect prey (Watt et al. 1999).

Whereas sharks tend to have ampullary organs concentrated around the head, skates and rays also have them on the pectoral fins as well. The density of ampullary receptor pores on the ventral surface of skates that feed on benthic prey is higher than the density on the ventral surface of skates that feed on more mobile prey, further supporting the role of electroreception in prey detection (Collin & Whitehead 2004). Skates that live in deeper water have more and larger ampullae than those that live in shallower areas, even within the same species, perhaps making the deeper fish more sensitive to bioelectricity and permitting them to detect prey from a greater distance (Raschi & Adams 1988). The Eel-tailed Catfish has ampullary receptors on much of the body, but they are most abundant on the head (Whitehead et al. 2003). The electrosensory prey detection capability of the Paddlefish of the Mississippi River drainage of North America is among the best of all freshwater fishes studied thus far. The elongated and flattened rostrum of this fish contains many ampullary receptors, and acts as an antenna permitting juvenile Paddlefish to detect individual zooplankters from as far away as 9 cm (Wilkens et al. 2002; Wilkens & Hofman 2007). This is particularly helpful because Paddlefish often live in areas with murky water and poor visibility. As the fish gets larger and its gill rakers develop it becomes a nonselective filter feeder, so detecting individual zooplankters may not be as critical. However, larger fish begin filter feeding when live plankton are nearby, suggesting that the electrosensory capability may still help the fish detect and respond to the presence of zooplankton (see Fig. 13.16).

Another use of passive electroreception is the detection of potential predators. Embryonic Clearnose Skates (*Raja eglanteria*) use their tails to move water through the egg case for respiration, but the muscular activity also generates electrical signals which could be detected by nearby predators. When the skates detect weak electrical stimuli from another source, the tail movements stop (Sisneros et al. 1998). Similarly, newly hatched Small-spotted Catshark (*Scyliorhinus canicula*) temporarily cease the ventilatory activity of their gills when they detect electrical stimuli that might represent a nearby predator (Peters & Evers 1985).

Ampullary receptors may also be important in social interactions, such as the recognition and location of conspecifics for mating. Male Round Stingray (*Urobatus halleri*) can locate females buried in the sand based on the weak voltages produced by the female's respiratory muscles (Collin & Whitehead 2004). Peters et al. (2002) speculate that the variability of the bioelectric field created by basic physiological processes of the Brown Bullhead could provide a means of communication with conspecifics.

There has been considerable speculation regarding the role that electroreception may play in compass orientation among sharks. Kalmijn (1982, 1984, 2003) proposed that ampullary receptors may permit some sharks to detect electric fields that are the result of movement of the fish, or water masses such as ocean currents, across the earth's magnetic field – thereby providing navigational cues for compass orientation. Paulin (1995), however, hypothesized that a shark turning its head while swimming could alter electrosensory inputs created by the fish's movement enough that this, combined with sensory input from the semicircular canals, provides sufficient information for the fish to determine its direction. Klimley (1993) suggested that the shark's electrosensory organs, or some other yet-to-be-identified sensory system, may allow the shark to track the geomagnetic patterns created by the mineral content of the ocean floor.

The sensitivity of ampullary receptors, and therefore their specific purpose, may change during the life of a fish. For example, the response properties of the ampullary receptors of the Atlantic Stingray (*Dasyatis sabina*) changes from being able to detect signals typical of large predators while the fish is young to being better able to detect prey and locate mates when the fish is older (Sisneros & Tricas 2002). A somewhat similar ontogenetic shift in sensitivity occurs in the Clearnose Skate (*Raja eglanteria*), an electrogenic species that utilizes electrical communication for social and mating interactions (Sisneros et al. 1998). The density of ampullary receptors may also change as the age and the need for keen electroreceptive capability changes. Juvenile Scalloped Hammerhead Shark feed in turbid water with poor visibility, and have a very high density of ampullary pores on their heads. As the fish grows, the head broadens and the pores become more widely spaced – but the fish also moves into more open water where visibility is better (Collin & Whitehead 2004). Similar trends of decreasing ampullary pore density with increasing age are also seen in the Bonnethead (*Sphyrna tiburo*) and Sandbar Shark (*Carcharhinus plumbeus*).

Tuberous receptors

Tuberous receptors are responsible for active electrolocation – the detection of an electric field produced by the fish's own electric organs. Therefore, they are only found in those teleosts that generate an electric organ discharge (EOD), such as the mormyrids, gymnarchids, and mochokid catfishes of Africa and the gymnotoids of South America. Active electrolocation is limited to freshwater fishes, perhaps

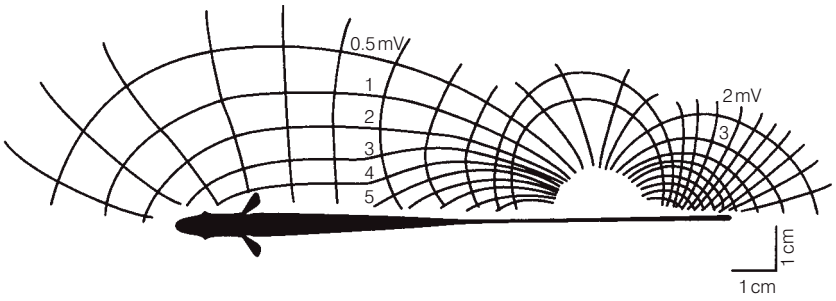


Figure 6.6
Dorsal view of an *Eigenmannia* and its electric field. From Scheich and Bullock (1974).

because sea water is such a good conductor that maintaining a functional sensory field is too difficult.

Tuberous receptors are located in depressions of the epidermis and are covered with loosely packed epithelial cells, allowing electric current to flow between the cells (see Fig. 6.5B). There are at least eight different types of tuberous organs in different species, but they fall into two main categories – those that encode timing of the EOD, and those that encode stimulus amplitude (von der Emde 1998). The fish's EOD frequency causes the tuberous receptor cells and their sensory neurons to generate a rather constant background rate of nerve impulses. A fish can detect objects moving into its electric field (Fig. 6.6) when those objects cause a change in the field and alter the rate of impulses received by the brain, such as when the fish encounters an object with different conductance than the surrounding water. This probably allows the fish to detect the size and distance of the object, and may also permit discrimination between living and nonliving objects because their different electrical properties would create different distortions of the electric field.

Active electroreception is used in a variety of ways. Many electric fishes are primarily nocturnal and use their electrosensory capabilities to locate hiding places during the day and to explore their environment at night (von der Ende 1998; Graff et al. 2004). Active electroreception also can be used to locate prey and assist with navigation and orientation, especially because the fish are most active during periods of low or no light. But the most studied use of active electroreception is in communication.

Electrical communication

Most fishes that produce electricity use it for communication. Signals are species specific and certain aspects of the EOD, such as amplitude, frequency, and pulse length, can be modified to exchange information about species, sex, size, maturation state, location, distance, and probably individual identification (von der Emde 1998; Collin & Whitehead 2004).

Agonistic interactions involving frequency shifts play an important role in dominance interactions in many electric fishes. South American gymnotiform knifefishes have individual characteristic waveforms to their EODs. In *Gymnotus carapo* (Gymnotidae), rapid increases and decreases in frequency indicate threat, whereas submissive individuals cease discharging (Black-Cleworth 1970). Within this species, individuals with higher EOD frequencies are consistently dominant. Male *Eigenmannia virescens* (Sternopygidae) will mouth fight until a dominance hierarchy is established, the ultimate dominant male assuming the lowest discharge frequency. Females compete for spawning territories, and dominant females have the highest frequency (Hopkins 1972, 1974a, 1974b). In the genus *Sternopygus* (Sternopygidae), mature males discharge at about an octave below the discharge of mature females, which is 120–240 Hz (Feng 1991). The Brown Ghost Knifefish (*Apteronotus leptorhynchus*) also demonstrates a variety of EODs that convey different meanings, including gender and social status (Zakon et al. 2002).

The diverse mormyriform elephantfishes (Mormyridae) of Africa use EODs for orientation, territorial interactions, species recognition, individual recognition, courtship, and to communicate social status (Carlson 2002; Terleph & Møller 2003). Mormyrids receive information based both on the waveform of the EOD and on intervals between discharges. Variations in discharge interval of fractions of a millisecond are detectable by the fish. EODs are again both species and sex specific among different life history stages. Males typically have a two to three times longer pulse duration than females. Interactions include cessation and frequency modulation of EODs ("bursts", "buzzes", and "rasps"), echoing, and dueting. Males alternate their outputs with other males, whereas females synchronize their outputs with investigating males. A male can determine the sex of a conspecific by "listening" to the response to his electric pulses. In direct analogy to gymnotiform behavior, the mormyriform *Gymnarchus niloticus* ceases discharging just prior to an attack on a conspecific, uses bursts of discharge pulses when aggressive, and modulates its frequency by 1–30 Hz as a submissive gesture (Møller 1980; Hopkins 1986; Bleckmann 1993).

Agonistic interactions include interference with a conspecific's electroreception. In *Gymnotus carapo*, dominant fish often shift their discharges to coincide with the short interval when a subordinate would be analyzing its own

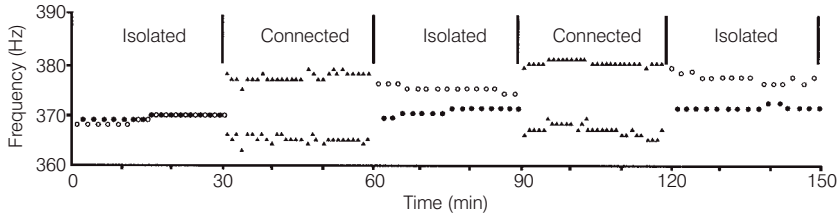


Figure 6.7
The jamming avoidance response (JAR) of two *Eigenmannia* kept in separate aquarium tanks. When electrically isolated, both fish converge on frequencies of about 370 Hz. When the tanks are connected electrically the fish shift and maintain an approximately 10 Hz difference in the frequencies of their EODs. From Scheich and Bullock (1974), originally in Bullock et al. (1972).

output, which could impair the subordinate's ability to electrolocate. Such interference is overcome in gymnotiforms such as *Eigenmannia* by a **jamming avoidance response** (JAR), in which fish shift their EOD frequencies when they get near one another, thereby preventing interference with one another's ability to electrolocate. Fish in a social group maintain a 10–15 Hz difference with their neighbors so that each individual has a "personal" discharge frequency (see Feng 1991). When several *Eigenmannia* were kept in separate tanks and all the tanks were connected by electrical wires, the fish shifted their frequencies to an average separation of 7 Hz (Fig. 6.7). The Brown Ghost Knifefish also demonstrates a JAR (Zakon et al. 2002), and, in several other species, fish in a social group have non-overlapping frequencies (Bullock et al. 1972; Hagedorn 1986).

This discussion of electrical communication would be incomplete without some consideration of the source of the electrical signals – the **electric organs**. The electric-generating cells of electric organs are referred to as **electrocytes**, and often are disklike modified muscle cells, called **electroplaques**. When stimulated, ion flux across the cell membranes creates a small electric current, and because the cells are arranged in a column and discharge simultaneously, they produce an additive effect. A sizeable stack of cells can produce a considerable current – like many small batteries connected in series (Feng 1991). Although electrocytes of most electric fishes are modified muscle cells, South American electric fishes of the family Apteronotidae utilize modified neurons (Zupanc 2002).

The generation and detection of weak electric fields is particularly well developed in several groups of freshwater tropical fishes living in murky waters with poor visibility, such as the Gymnotiformes of South America and the Mormyridae of Africa. The EOD of some species are brief pulses released at irregular intervals, whereas other species continuously produce oscillating, high-frequency waves of electricity (Zakon et al. 2002). The resulting electric field surrounds the fish (see Fig. 6.6) and any changes in the field are detected by the fish's tuberous organs. Bending the body would distort the electric field, so these fishes typically rely on their extensive dorsal or anal fins for propulsion so that they can maintain a straight body posture.

The production of weak electric fields, as demonstrated in the gymnotids and mormyrids, requires considerable coordination by the central nervous system. In the South American gymnotid *Apteronotus*, the electric organs are controlled by pacemaker cells in the medulla, which are regulated by input from two clusters of neurons elsewhere in the brain (Zakon et al. 2002). The location and function of the pacemaker neurons of the African mormyrids is somewhat similar – a remarkable coincidence considering the two groups are believed to have evolved their EOD capabilities independently (Carlson 2002).

The African mochokid catfishes also are believed to produce and detect weak electric fields for object detection or communication (Hagedorn et al. 1990). The electric organ is located dorsally on these catfishes and has apparently evolved from one of the muscles associated with sound production, which occurs by stridulation of the pectoral spines.

Electrical attack and defense

Although most electric fishes generate only mild electric fields for communication and sensory purposes, others can generate currents strong enough to stun prey or ward off predators. The electric organs of an electric ray *Torpedo* (Torpedinidae) have about 45 columns of electrocytes (700 per column). The columns are oriented dorsoventrally and the current is released dorsally because the dorsal surface of the organ and the overlying skin have lower resistance than the surrounding tissues. *Torpedo* can generate a discharge of 20–50 volts and several amps in sea water (Feng 1991), and stun prey 15 cm away (see Chapter 12, Subclass Elasmobranchii). The Electric Eel *Electrophorus* (Electrophoridae), not a true eel but a close relative of the South American knifefishes, can generate pulses of 400 volts, or 1 amp (see Feng 1991) with its several electric organs, the largest of which consists of about 1000 electrocytes. These organs are embedded in the fish's lateral musculature. The two electric organs of the electric catfishes (Malapteruridae) are located on either side of the body and each contains several million electrocytes. These organs generate a current of about 300 volts. Other fishes that emit strong electric currents include the stargazers (*Astroscopus*, Uranoscopidae), in which electroplaques are derived from ocular muscles.

Vision

Water is a variable visual environment, in part because the quality of light changes with depth. As depth increases, light becomes dimmer due to absorption, and the color of

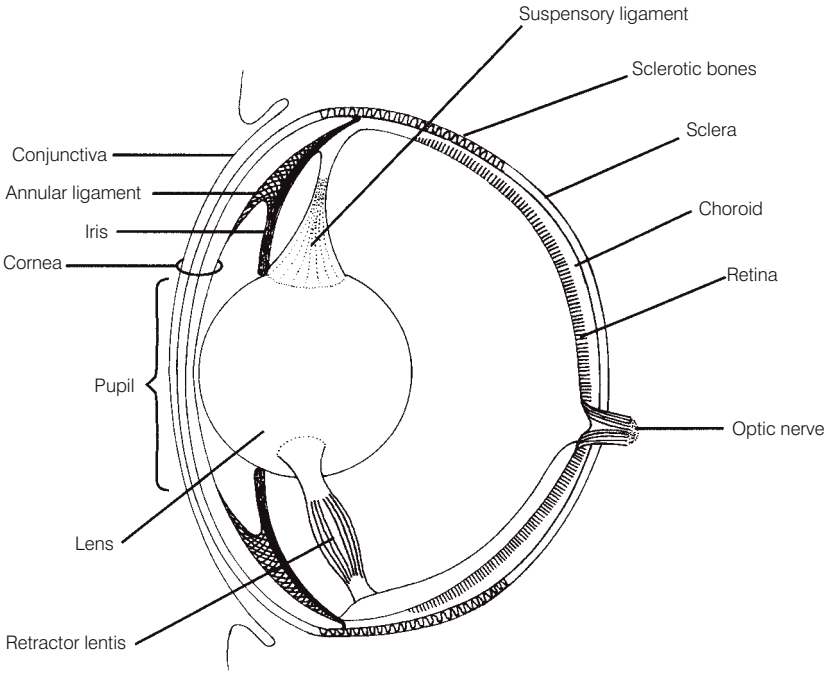


Figure 6.8
Cross-sectional view of the eye of a teleost. From Hildebrand (1988).

light changes because absorption is not equal for all wavelengths. Light on the red-orange end of the spectrum (>550 nm) is readily absorbed by water and therefore does not penetrate far. Moderate wavelengths, such as yellow and green, travel farther, and deep blue to violet light penetrates farthest into deep water. Ultraviolet light, however, does not penetrate far. It is not surprising, therefore, that over 500 million years of natural selection has produced numerous morphological and physiological adaptations suited to capturing and detecting light that is characteristic of the habitat in which a species lives.

The eyes of fishes are similar to those of other vertebrates, including those of humans (Fig. 6.8). Light first passes through a thin, transparent **cornea** and enters the eye through the **pupil**. The diameter of the pupil is fixed in teleosts and lampreys, but elasmobranchs have a muscular iris which controls its size and thereby regulates the amount of light entering the eye. The pupils of most deep water sharks are circular, whereas most other sharks have slitlike pupils; most skates and rays have pupils that are crescent-shaped (Hueter et al. 2004).

Light next passes through the **lens**, which is denser and more spherical than the convex lens of terrestrial vertebrates (Hawryshyn 1998), although the lenses of some elasmobranchs are somewhat elliptical. After light passes through the lens, it travels through the liquid-filled center of the eye before encountering the several layers of the **retina**, which contains the photosensory cells. Fishes focus on objects at different distances by moving the lens, thereby adjusting the distance between the lens and the retina.

Light passes through three layers of nerve cells before striking the photoreceptor cells in the retina's outermost layer. Fishes may have two general types of sensory cells in the retina, rods and cones. **Rods** are quite sensitive to low light levels and provide low resolution. Crepuscular species (those that are active at dawn and dusk) have high rod : cone ratios, and many nocturnal and deepsea fishes have only rods. In other fishes, photomechanical movement of melanin in the retina exposes the rods in dim light and shields them in bright light (Hawryshyn 1998).

Many fishes also have **cones**, which are less sensitive than rods and therefore require brighter light. Cones provide greater resolution, and cone : rod ratios are highest in diurnal fishes, which rely more on vision. There are several types of cones, each with a different photoreceptive glycoprotein (opsin) that responds to different wavelengths of light. Fishes may have only two or three of these types of cones, depending on the light quality in the fish's habitat (see Guthrie & Muntz 1993; Hueter et al. 2004). Porphyropsins are sensitive to yellow-red light, which has longer wavelengths and attenuates relatively quickly in water. Therefore, porphyropsins tend to be more common in fishes living in shallow areas or closer to the surface. Rhodopsins are more sensitive to shorter wavelength, blue-green light which penetrates further into the water, and are therefore common in fishes inhabiting somewhat deeper areas. Most elasmobranchs, for example, have rhodopsins, but porphyropsins are rare in this group. Chrysopsins are most sensitive to deep blue light, which penetrates furthest into the water due to its short wavelength, and these are found in deepsea fishes.

Some fishes also have photoreceptors sensitive to ultraviolet (UV) light, which does not penetrate far into water. Therefore, UV-sensitive fishes tend to inhabit relatively

shallow areas. Sensitivity to violet and UV light is common among coral reef fishes, and may be especially useful for close-range communication because UV light attenuates rapidly in water. Two-bar Damselfish (*Dascyllus reticulatus*) have a UV-reflective patch on their dorsal fin that is used as an alarm signal to conspecifics, but is not noticed by predatory fishes because they cannot detect UV light (Losey 2003). Male damselfish of another species, *Pomacentrus amboinenesis*, have UV-reflective patterns on their faces, which are important in aggressive territorial interactions, but are not visible to nearby predators (Siebeck 2004). Some freshwater fishes also use UV communication for attracting mates. Male Panuco Swordtail (*Xiphophorus nigrensis*) have UV-reflective markings that attract females but that are not visible to the species' main predator *Astyanax mexicanus* (Cummings et al. 2003). UV vision can be useful for prey capture as well. Juvenile Rainbow Trout (*Oncorhynchus mykiss*) rely on UV vision to see their zooplankton prey (*Daphnia*), which appear transparent to humans (see Warrant & Locket 2004). As the trout mature, they lose their UV sensitivity as photoreceptors in the retina change (Hawryshyn 1998), but their diet also changes.

Photoreceptors are not evenly distributed on the retina, and may occur in distinct patches or bands with higher densities. This has been noted in some elasmobranchs (Hueter et al. 2004), but it is not yet fully understood how this may affect a fish's vision. The pattern of photoreceptors in the retina of the Striped Marlin (*Tetrapturus audax*) suggests that the region of the retina receiving light from above or in front of the fish provides greater acuity and color recognition, whereas the region of the retina receiving light from below is better suited for detecting dim, upwelling blue light (Fritsches et al. 2003). This arrangement provides sharp color vision in brighter surface waters, and also permits the detection of dimly lit objects below the fish. The pattern of photoreceptors of the European Smelt (*Osmerus eperlanus*) also seems suited for sharp prey detection in front of the fish, and maximum sensitivity to dim light, and perhaps predators, coming from below (Reckel et al. 2003). The retinal structure of the burrowing, deep water Rufus Snake Eel (*Ophichthus rufus*) suggests three regions of high visual acuity that could help with locating food and burrows (Bozzano 2003).

Fishes may show ontogenetic shifts in photoreceptors that correlate with changes in habitat at different life stages. We mentioned earlier the loss of UV-sensitive cones in Rainbow Trout as they grow and shift diet. In another example, juvenile Lemon Sharks (*Negaprion brevirostris*) have porphyropsins, which are beneficial in shallow, turbid, inshore habitats, but as the fish get older the pigments change to rhodopsins, which are more useful as the fish move to the deeper, clearer open ocean (see Hueter et al. 2004). Similar porphyropsin–rhodopsin shifts occur in other fishes, including diadromous lampreys, salmon, and eels, which change pigments as part of the endocrine-induced physiological changes needed to move from shallow freshwater habitats into the much deeper open sea (see Hawryshyn 1998). Yellowfin Tuna (*Thunnus albacares*) also may show changes in expression of visual pigments as they grow from planktivorous larvae to larger piscivores (Loew et al. 2002).

Not only can fishes detect a wide range of light wavelengths, including UV, but some fishes, such as anchovies (Engraulidae), cyprinids, salmonids (Salmonidae), and cichlids (Cichlidae), can detect polarized light. This probably enhances the contrast of objects viewed underwater, permitting a better view of predators, prey, and potential mates, as well as providing directional information for migrating fishes. The ability to detect polarization may be most useful at dawn and dusk, when the percent polarization of light is highest (Hawryshyn 1992, 1998).

The **choroid** is a highly vascularized region between the protective sclera and the photoreceptive retina. It may contain a **tapetum lucidum**, a layer of reflective guanine crystals that probably enhances visual sensitivity under low light conditions by reflecting light not absorbed by the retina back into the eye. The tapetum causes the reflective shine in the eyes of sharks and many nocturnal fishes. Tapeta lucida are found in the Australian Lungfish (*Neoceratodus*), bichirs (*Polypterus*), most elasmobranchs, the Holocephali, coelacanths, sturgeons, and some teleosts (Bone & Moore 2008). In some sharks, such as those that are active near the surface during the day, the tapetum can be covered by dark pigment when light is abundant, and only uncovered when needed under low light conditions (Hueter et al. 2004). The tapeta of deepsea sharks remain reflective all of the time.

The retina has among the highest oxygen demand of any tissue in the body, and in most fishes a **choroid gland** maintains high oxygen levels in the retina. This U-shaped structure surrounds the optic nerve where it exits the eye. Blood flowing to and from the choroid gland travels through a rete mirabile (a countercurrent mechanism similar to that of the gas bladder; see Chapter 5, Buoyancy regulation), maintaining high oxygen levels in the gland and assuring the retina of a plentiful oxygen supply. The choroid gland receives oxygenated blood from the pseudobranch, a gill-like structure on the inside surface of the operculum. Removal of the pseudobranch in trout (*Salmo*) results in decreased oxygen near the retina and a progressive loss of visual pigment (Ballintijn et al. 1977). Antarctic fish with a choroid rete have more oxygen in the eye and a better optomotor response than a related species that lacks a choroid rete (Herbert et al. 2003).

The outer layer of the eye (the **sclera**) is reinforced to protect the eye's delicate internal structures. The sclera of agnathans is fibrous and firm, chondrichthyans have cartilaginous plates in their sclera, and teleosts frequently possess sclerotic bones. These are well developed in the mackerels and tunas (Scombridae) and particularly in the

billfishes (Istiophoridae and Xiphiidae), which have a bony stalk extending part way back along the path of the optic nerve to the brain.

Visual adaptations for special habitats

Fishes that live at the water's surface, or that occasionally find themselves totally out of the water, must be able to see in the air. The eyes of mudskippers (Periopthalmidae) are well adapted for aerial vision. A strongly curved cornea and slightly flattened lens permit focusing out of water (Brett 1957). This structural adaptation, along with the location of the eyes on retractable stalks on the top of the head, allows these fishes to forage on tidal flats and exposed mangrove roots of the swamps in which they live. The eyes of the surface-dwelling South American "four-eyed fishes" (*Anableps*, Anablepidae), are adapted to permit simultaneous vision above and below the water (see Brett 1957). Each eye has two pupils (one above and one below the surface of the water), an oblong lens, and a retina that is divided into dorsal and ventral sections. Light entering from above the water's surface enters the upper pupil, travels through the short axis of the oblong lens, and focuses on the ventral retina. Conversely, light from below the surface enters the lower pupil, travels the long axis of the lens, and is focused on the dorsal retina.

The deep sea is an optically challenging environment – the only light is either dim blue light from above or point sources of bioluminescence. Deepsea fishes demonstrate a variety of adaptations that help to optimize vision in these vast areas with little light. The mesopelagic zone (approximately 150–1000 m) has light filtering down from the surface, which diminishes with depth, as well as sources of bioluminescence, so we see great variation in eye designs in fishes of this zone. Adaptations include changes in the size, shape, and orientation of the eyes, as well as changes in visual pigments, in order to maximize the capture and detection of the wavelengths of light reaching these depths (see Chapter 18, The deep sea).

Even faint deep blue light from the surface does not reach the bathypelagic zone (>1000 m), where the only light is from bioluminescence. In this zone, small eyes seem to be the answer for a couple of reasons. Small eyes are well suited for detecting point sources of light that are nearby, and therefore within range of bathypelagic fishes, which are weak swimmers due to their watery muscles. In addition, eyes are energetically quite expensive to maintain, and meals in the bathypelagic zone are few and far between – so small eyes are less of a drain on the fish's overall energy budget.

Some fishes lack functional eyes as a result of degenerative evolution in perpetually dark habitats. The lack of eyes in hagfishes (Myxinidae) is likely a degenerative condition, like the loss of functional eyes among some populations of cave-dwelling fishes (Hawryshyn 1998; see also Chapter 18). Although some cave fishes lack a cornea, lens, and iris, they still may possess the genes that code for the opsins needed to detect light (Parry et al. 2003).

Chemoreception

The aquatic environment is filled with a wide variety of chemical signals because so many chemicals dissolve in water. Therefore, fishes can learn a great deal about their environment through chemoreception, which often is used for finding and identifying food, locating habitat, detecting and avoiding predators, and communicating with conspecifics. The sense of smell (**olfaction**) helps fishes detect a broad range of chemical stimuli, whereas the sense of taste (**gustation**) is primarily focused on food recognition (Sorensen & Caprio 1998).

Smell

The organs of smell in fishes are contained within olfactory chambers (Sorensen & Caprio 1998). Jawed fishes have paired olfactory chambers, each of which has an incurrent and excurrent nostril. Cilia within the chambers move water into and out of the nostrils, which usually are small pits separated by a flap of skin, but may be tubular in some fishes such as the Bowfin (Amiidae) and eels (Anguillidae). Hagfishes and lampreys have only a single naris and a median olfactory sac nostril. In hagfishes a nasohypophyseal duct connects with the pharynx so that hagfishes can smell water as it moves to the gills. In lampreys, however, the lone medial nostril leads to an olfactory chamber in a dead-end nasopharyngeal pouch. In teleosts the olfactory chambers also are dead-end sacs that do not lead to the pharynx, except in a few cases such as stargazers (Uranoscopidae). The nares of elasmobranchs are located ventrally on the snout and also are not connected to the pharynx. Chimaeras (Holocephali) and lungfishes (Ceratodontiformes) have paired nares that connect to the oral cavity.

Each olfactory sac is lined with a highly folded **olfactory epithelium**, often arranged in rosettes (Fig. 6.9). Molecules of odorants bind to receptor proteins on membranes of the receptor cells in the sensory epithelium. The receptors cells then send nerve impulses to the brain (Hara 1993). Structure of the rosettes and olfactory sacs is related to the olfactory sensitivity of a fish. The more extensive the lamellar folding, the greater the surface area available for sensory cells and the more sensitive the sense of smell. Freshwater eels (*Anguilla*) are known for their extremely keen sense of smell and have from 69 to 93 folds in each rosette. Perch (*Perca*), with less sensitive olfactory capabilities, have 13–18 folds in each rosette.

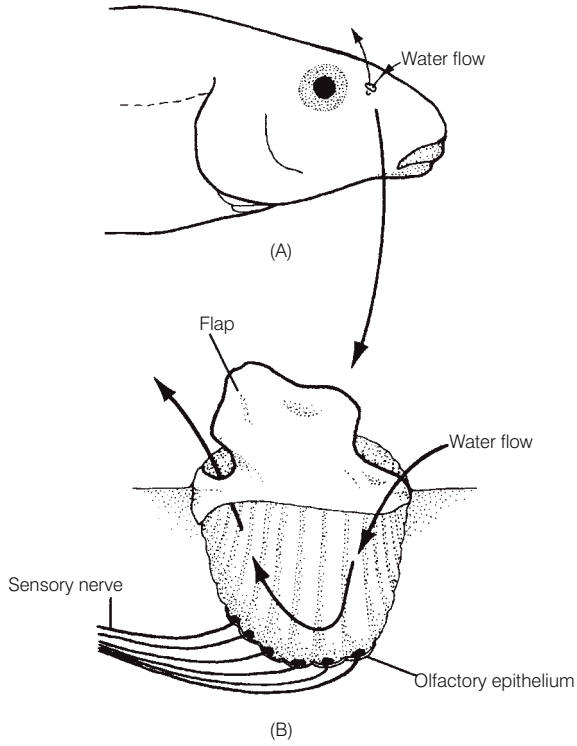


Figure 6.9
(A) External view of the nares of a fish. (B) The obvious flap of skin directs water across the sensory epithelium. Adapted from Lagler et al. (1977).

Fishes are extremely sensitive to certain types of chemicals. Amino acids, particularly those of fairly simple structure and with certain attached groups, are detectable by many fishes at concentrations of around 10^{-10} mol/L (see Hara 1993). Other compounds that are detectable by some fishes at very low concentrations include bile acids (10^{-9} mol/L), salmon gonadotropin-releasing hormone (10^{-15} mol/L), and some sex steroids (10^{-12} mol/L). This ability to detect such small concentrations of certain chemicals makes olfaction valuable in homing in salmon (Stewart et al. 2004; see Chapter 23, Mechanisms of migration), and in habitat location for some other fishes.

Sea Lamprey (*Petromyzon marinus*) also are anadromous, and although they do not return to their home streams, they rely on olfaction to identify a suitable spawning stream. A chemical signal released by juveniles (ammocoetes) provides a signal to adults that the stream apparently provides a suitable spawning and nursery habitat, and sexually mature males release another pheromone that attracts mature females (Wagner et al. 2006). This knowledge is being used to try to control Sea Lamprey, which parasitize larger fish, by diverting them during their spawning migration (see Chapter 13, Petromyzontiforms).

Juvenile eels in New Zealand may use odor to locate suitable habitats as they migrate upstream after hatching at sea. Glass eels of both the Longfin Eel (*Anguilla dieffenbachii*) and Shortfin Eel (*A. australis*) preferred water from their river of capture over well water, and the Shortfin Eels preferred water from lowland streams, where they tend to occur, over water from the mainstream of a river (McCleave & Jellyman 2002).

Olfactory cues also can be used to locate mates, and some fishes exhibit different olfactory sensitivities between sexes. In deepsea ceratioid anglerfishes, males have enlarged olfactory organs, olfactory nerves, and olfactory lobes in the brain, whereas these features are much smaller among females. In these species, females, which are much larger, are thought to release species-specific pheromones that the smaller, more mobile males use to locate them. Males then attach themselves to the females and spend the rest of their lives as parasitic sperm factories (see Chapter 18, The deep sea). Gilthead Seabream (*Sparus aurata*) are sensitive to the excreted body fluids of sexually mature conspecifics (Hubbard et al. 2003), and male Brown Trout (*Salmo trutta*) and Lake Whitefish (*Coregonus clupeaformis*) both show courtship behavior when exposed to a prostaglandin released by females ready to spawn (Laberge & Hara 2003).

Olfaction may also be used to detect and avoid predators. Juvenile Lemon Sharks (*Negaprion brevirostris*) react to the odor of organic compounds produced by American crocodiles (*Crocodylus acutus*) that prey on small sharks where they co-occur (Hueter et al. 2004). Many fishes respond to chemical alarm cues released from injured conspecifics, or other prey species with which they occur (Brown 2003). The alarm substance, or a metabolite of it, also is present in the feces of predatory species and would therefore also be present in the water nearby. This allows potential prey to inspect predators and assess their potential threat (see Chapter 20, Shoaling and search).

Chemical contaminants can interfere with olfaction and thereby disrupt important interspecific communication. For example, cadmium accumulates on the olfactory epithelium of Rainbow Trout (*Oncorhynchus mykiss*) and affects fish social behavior, including blocking their ability to detect alarm substance (Scott et al. 2003; Sloman et al. 2003).

Taste

The sense of taste is used primarily for food recognition. The chemosensory cells responsible for taste are located in and around the mouth, including barbels and lips, and may also be found on the fins and trunk (Sorensen & Caprio 1998). Taste receptor cells are often clustered into taste buds, which can contain 30–100 sensory cells, or they may occur individually on parts of some fishes. These solitary chemosensory cells can be numerous, with up to 4000 per mm^2 in some minnows (Cyprinidae). Sensory neurons synapse with the sensory cells at their basal surface, and when stimulus molecules bind to receptors on the sensory cells, neurotransmitters are released that affect the generation of action potentials by the sensory neuron that carries

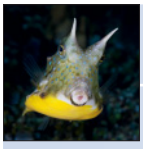
the signals to the gustatory centers of the brain (Sorensen & Caprio 1998). Toxins, amino acids, and bile salts can stimulate taste receptors at sensitivity thresholds similar to those of olfactory receptors (see Hara 1993).

Magnetic reception

As mentioned earlier, some fishes, such as elasmobranchs, may have such a sensitive electroreceptive ability that they can detect the weak electric fields they create as they move through the earth's magnetic field. This ability would provide these fishes with an indirect way of sensing the earth's magnetic field and give them directional information with respect to compass headings. Round Stingrays (*Urobatis halleri*) in the lab learned to orient in induced magnetic fields; the rays switched the location in which they searched for food when the electric field around them was artificially reversed, suggesting that geomagnetic cues might be used in daily activities (Kalmijn 1978).

Some fishes, however, may be able to detect magnetic fields directly. Several species of salmon and trout, eels, Yellowfin Tuna, and sharks and rays can detect magnetic fields (see Formicki et al. 2004), and magnetite has been extracted from the heads of Yellowfin Tuna, Chinook Salmon (*Oncorhynchus tshawytscha*), and Chum Salmon (*O. keta*) (Walker et al. 1984; Kirschvink et al. 1985; Ogura et al. 1992). The Japanese Eel (*Anguilla japonica*) can be conditioned to respond to magnetic fields that are similar in magnitude to that of the earth (Nishi et al. 2004), and larval Brown Trout (*Salmo trutta*) also responded to magnetic fields (Formicki et al. 2004). The ability to discriminate among different field strengths and inclinations and to orient to the directional polarity of the earth's magnetic field would aid in magnetic compass orientation and navigation.

The mechanism for direct sensing of magnetic fields remains a mystery. Walker et al. (1997) found crystalline material that they believed to be magnetite within the folds of the olfactory epithelium of Rainbow Trout, and nerve tracts run from these cells to the brain. These observations led Walker et al. to propose that Rainbow Trout have magnetoreceptive cells in their olfactory capsule. Others, however, have proposed that magnetoreception may be related to the other mechanoreceptive sensory systems such as the inner ear and the lateral line system. Harada et al. (2001) studied the chemical composition of the otoliths of several birds and fishes and found significant levels of iron in the lagena of some species. They speculated that, although the two largest otolith organs, the saccule and utricle, responded to movement, the small size and higher iron content of the lagenal otoliths makes this a potential site for geomagnetic sensing. More research is needed to locate the organs of magnetoreception in fishes. Among the challenges is that magnetic fields can pass through animal tissues, so magnetoreception could take place anywhere in the body. Therefore, receptor cells and their neurons would not have to be concentrated in a particular location – they could be widely dispersed throughout the body. In addition, magnetite particles would be extremely rare and small, making them difficult to identify.



Summary

SUMMARY

1. Sensory systems convert stimuli from a fish's environment into biological signals (nerve impulses) that can be integrated, interpreted, and acted upon.
2. Fishes can detect and respond to noxious stimuli, but we do not know enough about the mental processing of these stimuli or the functioning of fish brains to conclude whether or not fishes can experience something similar to what humans would describe as "pain".
3. Disturbances in the water are sensed by neuromasts, clusters of sensory hair cells and supporting cells covered by a gelatinous cupula. Neuromasts may be free-standing in a fish's skin or located in canals beneath the scales along the trunk (the lateral line) or in the dermal bones of the head. Small pores allow vibrations from the surrounding water to enter these canals.
4. Equilibrium, balance, and hearing are mechanoreceptive senses primarily located in various chambers of a fish's inner ear. The relative movement of fluid (endolymph) or solid deposits (otoliths) stimulates sensory hair cells, which generate signals that are subsequently carried to the brain by sensory nerves. Hearing in some fishes is enhanced by the transmission of vibrations from the gas bladder to the inner ear via anterior extensions of the gas bladder or a chain of small bones known as the Weberian ossicles.

5 Two general types of receptors are used by fishes to detect electricity in their environment. Ampullary receptors can detect the weak electricity generated by living prey organisms. Some teleosts possess specialized organs capable of generating an electric field which is subsequently received by tuberous receptors. These fishes utilize this sensory system to gather information about their environment and to communicate with conspecifics.

6 Fish eyes are structurally quite similar to those of terrestrial vertebrates, except that the lens is more spherical. The retinas of fishes contain rods, for vision in dim light, and cones, for color vision and vision in bright light. Different cones respond to light of different wavelengths of the spectrum visible to humans, and some fishes have cones capable of detecting ultraviolet light. Some fishes also can detect polarized light, thereby enhancing underwater vision and perhaps providing directional cues for migration.

7 Fishes rely a great deal on their chemical senses, smell and taste. The organs of smell are located in blind nasal sacs and are open to the surrounding water via nostrils. Some fishes can detect very low concentrations of odorant molecules, on the order of 10^{-15} to 10^{-10} mol/L. Taste receptors are located in the mouth and pharynx, and some fishes have taste buds on their gill rakers, gill arches, and externally on barbels, fins, or elsewhere on the body.

8 Some fishes can detect magnetic fields, thus providing valuable orientation information during migration. Sensitive electroreceptors may enable some fishes to detect the electricity generated by their own movement through the earth's magnetic field, hence providing an indirect means of magnetic reception. Other fishes, however, have demonstrated direct magnetic sensory abilities, and biologically produced magnetic particles have been found in regions of their skull believed to be the site of this sense.

Supplementary reading

SUPPLEMENTARY READING

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Chapter 7

Homeostasis

Chapter contents

CHAPTER CONTENTS

In this chapter we explore those processes that maintain internal equilibrium, or homeostasis, thereby allowing other physiological systems to function properly. Specifically, we will investigate: (i) the roles of the endocrine system and the autonomic nervous system in controlling various physiological responses; (ii) the importance of body temperature and thermal relationships between fishes and their environments; (iii) the mechanisms involved in maintaining water, solute, and pH balance; (iv) how fish immune systems defend the body against invasion; and (v) how various forms of physiological stress can compromise a fish's ability to maintain an internal steady state.

Coordination and control of regulation

The nervous and endocrine systems maintain communication among the various tissues in the body and regulate many physiological functions. Neural circuitry and the speed of action potentials make the nervous system comparatively direct and fast-acting, whereas the endocrine system is better suited for long-term regulation of physiological processes because its tissues release chemical signals (**hormones**) into the blood. These hormones travel throughout the body, but only affect those cells with the proper molecular receptors.

The nervous and endocrine systems overlap considerably – particularly in the control of various endocrine tissues by the brain. As endocrinological research on fishes and other animals advances, it has often proven difficult to distinguish separate roles for these two regulatory systems.

The endocrine system

Ongoing research has rapidly expanded knowledge of the endocrine systems of fishes, and it is not surprising that there is great diversity in the hormones and their functions among various groups of fishes. Therefore, it is not possible given the space available to provide a complete synopsis of fish endocrine tissues, their hormones, and their effects. Instead, we will provide a brief summary of some of the hormones important to homeostasis, but will not address the many other physiological functions of hormones in fishes.

Many endocrine functions are ultimately controlled by the hypothalamus of the brain regulating the many functions of the pituitary which, in turn, helps regulate many other endocrine tissues in the body. The pituitary has two main functional regions. The **posterior pituitary**, or **neurohypophysis**, is continuous with the hypothalamus and consists primarily of the axons and terminals of neurons that originate in the hypothalamus. The **anterior pituitary**, or **adenophypophysis**, lies in contact with the posterior pituitary, and in the actinopterygians the tissues fuse. The hypothalamus controls the anterior pituitary by releasing hormones delivered via blood vessels in some fishes, such as chondrichthyans, or by direct innervation as seen in some actinopterygians. Some fishes also have an intermediate lobe of the anterior pituitary, and elasmobranches have a ventral lobe below the anterior pituitary (Takei & Loretz 2006).

The posterior pituitary is primarily the storage and release site of chemical messengers of the hypothalamus. Neuroendocrine cells (neurons that function as endocrine cells) begin in the hypothalamus and extend into the neurohypophysis where they release their chemicals, some of which are hormones that are released into blood vessels and trigger effects elsewhere in the body. **Vasopressin** (also called arginine vasotocin), for example, plays an important role in osmoregulation (Takei & Loretz 2006). Other chemicals released by the posterior pituitary regulate the function of cells of the adjacent anterior pituitary and intermediate lobe, and are sometimes referred to as releasing factors or releasing hormones. Some of these diffuse to the intended target cells in immediately adjacent sections of the pituitary, whereas others travel the short distance to their target cells via blood vessels.

The anterior pituitary, largely under the control of the hypothalamus, manufactures and releases hormones that control many physiological functions elsewhere in the body, including many other endocrine tissues. For example, the anterior pituitary releases **adrenocorticotropic hormone** (ACTH), which influences the production and release of cortisol from the interrenal tissue, and **thyroid-stimulating hormone** (TSH), which stimulates the thyroid gland to release thyroxin, gonadotropins (which stimulate the gonads), and **growth hormone** (GH) which affects various tissues throughout the body (Takei & Loretz 2006).

Fishes are the only jawed vertebrates known to possess a caudal neurosecretory system. Located at the caudal end of the spinal cord, this region of neuroendocrine cells, the **urophysis**, is most highly developed in the ray-finned fishes and produces **urotensins** that help control smooth muscle contraction, osmoregulation, and the release of pituitary hormones (Takei & Loretz 2006).

The thyroid tissue of most fishes is scattered as small clusters of cells in the connective tissue of the throat region, as opposed to the rather discrete gland found in tetrapods. When stimulated by TSH from the anterior pituitary, these cells produce **thyroxin**, which plays an important role in growth, development, and metabolism in many fishes. Thyroxin is quite important in development, including the sometimes extreme morphological and physiological changes associated with metamorphosis – such as the transformation of flounder from larvae with an eye on each side of the head to flatfish with both eyes on one side of the head. It also initiates seaward migratory behavior and the accompanying osmoregulatory adaptations of juvenile salmonids during their seaward spawning migration (Takei & Loretz 2006; see Chapter 10, Complex transitions: smoltification in salmon, metamorphosis in flatfish).

Maintaining proper calcium balance, including regulating calcium uptake at the gills, involves several hormones, including **stanniocalcin** from the corpuscles of Stannius embedded in the kidney, **calcitonin** produced by the ultimobranchial bodies in the back of the pharynx, and **prolactin** and **somatolactin** from the anterior pituitary (Takei & Loretz 2006).

The interrenal tissues of fishes are homologous with the distinct adrenal glands of the tetrapods, but are somewhat scattered in their location. The interrenal consists of two different types of cells, each of which produces different hormones. The chromaffin cells are located in the wall of the posterior cardinal vein in the pronephros of agnathans, along the dorsal side of the kidney in elasmobranchs, and in the anterior, or head, kidney of teleosts. Chromaffin cells produce and release the catecholamines **epinephrine** (adrenaline) and **norepinephrine** (noradrenaline) (Takei & Loretz 2006). The catecholamines maintain or enhance the delivery of oxygen to body tissues by increasing gill ventilation rates and blood flow, and increasing oxygen transport capability by increasing the release of red blood cells from the spleen and increasing the intracellular pH of red blood cells (Hazon & Balment 1998). This increased blood flow to the gills may lead to increased ion exchange, which may explain why stressed fishes can experience significant osmoregulatory imbalances (discussed later in this chapter).

The second group of interrenal cells is that of the steroid-producing cells, located primarily in the pronephric or head kidney region. These manufacture and release corticosteroids, including **cortisol**, which is important in energy metabolism and maintaining electrolyte and water balance (Takei & Loretz 2006). Many other hormones also are involved in osmoregulation. For example, prolactin from the anterior pituitary, along with cortisol, is important in freshwater adaptation. Seawater adaptation involves cortisol, GH from the anterior pituitary, vasopressin from the posterior pituitary, urotensins from the urophysis, atrial natriuretic peptide from the heart, and probably others (Takei & Loretz 2006).

Glucose metabolism is influenced by **insulin**, **glucagon**, and **somatostatin** from cells within the pancreas. Insulin enhances the transport of glucose out of the blood, promotes glucose uptake by liver and muscle cells, and stimulates the incorporation of amino acids into tissue proteins. Glucagon and related glucagon-like proteins seem to function in opposition to insulin, promoting the breakdown of glycogen and lipids in the liver and increasing blood glucose levels. Somatostatin also helps elevate blood glucose levels by promoting metabolism of glycogen and lipids, and by inhibiting the release of insulin (Takei & Loretz 2006).

Melatonin, produced by the pineal gland (near the top of the brain) and the retina of the eye, is secreted during the dark phase of daily light–dark cycles and helps regulate fish responses to daily and annual cycles of daylight. This hormone influences many physiological processes and behaviors through its role in the maintenance of circadian activity cycles (see Chapter 23, Circadian rhythms), daily changes in temperature preference, and changes in growth and coloration associated with changes in photoperiod and temperature (Takei & Loretz 2006).

Box 7.1

Endocrine disrupting compounds

Endocrine disrupting compounds (EDCs) include a growing list of industrial chemicals, pharmaceuticals, and natural and synthetic hormones found in industrial effluent, agricultural and municipal runoff, and waste water from municipal sewage treatment facilities. The list includes, but is not limited to, pesticides (e.g., aldrin, atrazine, chlordane, DDT, mirex, toxaphene), phthalates (found in cosmetics, plasticizers, adhesives, insecticides, printing inks, safety glass), and organohalogens (e.g., furans, polychlorinated biphenyls, dioxins). These chemicals make their way into surface waters, accumulate in fishes, and, because of their structural similarity with fish hormones, can interfere with hormonally controlled physiological processes, even if present only in very small concentrations in the water.

The effects of these chemicals can include altering levels of sex hormones, interfering with intracellular hormone receptors, altering secondary sex characteristics, altering gonad size and condition, creating intersex individuals (gonads contain both testicular and ovarian tissue), altering age or size of maturity, and affecting hatching success or incubation time. Some of the specific effects that have been noticed include the masculinization of female mosquitofish (Poeciliidae) exposed to effluent from pulp and paper mills (Bortone & Davis 1994) (Fig. 7.1), noticeable changes in levels of androgens, estradiol, and vitellogenin in carp (Cyprinidae) found in some contaminated areas, and altered reproductive behavior in Goldfish (Cyprinidae) and guppies (Poeciliidae; see Greeley 2002). The introduction of 17α-ethynylestradiol (EE2), a synthetic estrogen used in birth control pills and often found in wastewater effluent, to an experimental lake in Ontario interfered with the sexual development of Fathead Minnow (Cyprinidae), including inducing the development of intersex males, and resulted in the collapse of the population within 2 years (Kidd et al. 2007). Exposure to wastewater treatment effluent with EE2 for just 21 days altered the sexual development of Fathead Minnow in laboratory studies (Filby et al. 2007). The occurrence of intersex Roach (Cyprinidae) in rivers in the United Kingdom correlated with predicted levels of estrogenic compounds from sewage effluent (Jobling et al. 2006). Intersex Smallmouth Bass (Centrarchidae) were reported to have been found in the Potomac River (Fahrenthold 2004), and intersex Smallmouth Bass and Largemouth Bass were found in the Colorado River and its tributaries (Hinck et al. 2007). It seems that we only need to look in order to find additional examples of the effects of endocrine disruption in fishes and a wide variety of other animals, including some suggestions of effects on humans (see, for example, the April 2006 supplement 1 of volume 114 of the journal *Environmental Health Perspectives*).

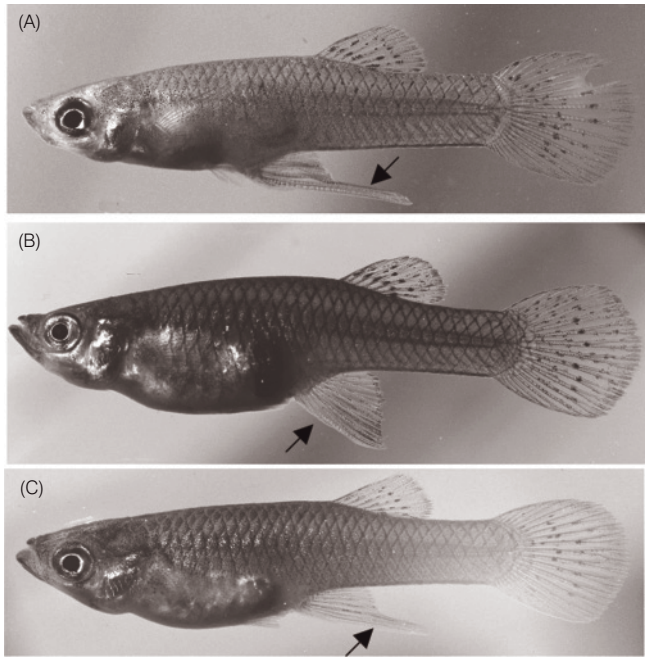


Figure 7.1

(A) The anal fin of a normal male *Gambusia* is elongated to form the gonopodium (arrowed), an intromittent organ used to inseminate females. (B) In normal females, the anal fin is fan-shaped. (C) A masculinized female exposed to pulp mill effluent, in which the anal fin has developed into a gonopodium.

As briefly summarized in the preceding paragraphs, the endocrine system regulates most physiological systems associated with maintaining homeostasis. Hormones also can have a large impact on other aspects of fish biology, including sexual development and reproductive behavior, which ultimately impact the stability of fish populations and aquatic communities. This is one reason that there has been a growing concern over human-generated **endocrine disrupting compounds** and their effects on development and fish population stability (Box 7.1).

The autonomic nervous system

Involuntary physiological functions, such as control of internal organ function, are at least in part controlled by the autonomic nervous system or **ANS**. Neural signals from the central nervous system (brain and spinal cord) travel to ganglia of the ANS that are located either along the spinal cord or near or within the target organs. Signals then travel from these ganglia to the target tissues. The ANS is poorly developed in agnathans, better developed in elasmobranchs, and well developed in the bony fishes (Donald 2006). The ANS often works together with the endocrine system to control involuntary physiological functions such as heart rate, blood pressure, blood flow through the gills, and many functions of the gastrointestinal system that are important to digestion and nutrition. The ANS also controls gas bladder volume, and therefore fish buoyancy, by regulating the absorption and secretion of gases and blood flow to various parts of the gas bladder (see Chapter 5, Buoyancy regulation, for a discussion of gas bladder function). The dispersion and aggregation of pigment in melanophores is also partly controlled by the ANS, along with melanophore-stimulating hormone from the anterior pituitary.

Temperature relationships

The view that many people have of fishes as "cold-blooded" is not accurate. Most fishes are about the same temperature as the surrounding water, which may be cold or warm depending on the habitat. That temperature can change, but usually any change is slow due to the thermal stability of water. Animals that rely primarily on external heat sources are referred to as **ectotherms**, and include most invertebrates, fishes, amphibians, and reptiles. Animals that generate their own heat and generally maintain stable body temperatures, such as birds and mammals, are **endotherms**.

Most fishes are ectothermic because they lack any mechanism for heat production and retention. In addition, when blood flows through the gills it becomes the same temperature as the surrounding water due to the thin gill membranes, before then flowing to the rest of the fish's body. There are, however, interesting exceptions of heat production or conservation in some fishes, a condition often referred to as either **heterothermy** or **regional endothermy**.

Coping with temperature fluctuation

Most fishes are ectothermic, so their body temperature reflects that of the surrounding environment. Fishes that experience changing environmental temperatures, such as those characteristic of diel or seasonal changes, have several cellular and subcellular mechanisms for adapting to the new set of conditions. Many physiological adjustments are the result of switching on or off genes that are responsible for the manufacture of particular proteins. For example, acute heat stress initiates the synthesis of stress proteins, also known as **heat shock proteins** or **HSPs**, which maintain the structural integrity of proteins that otherwise would become denatured at higher temperatures, thereby allowing them to function biochemically.

To compensate for the decreased rate of biochemical reactions at low temperatures, fishes may increase the concentration of intracellular enzymes by altering the rate of enzyme synthesis, degradation, or both. Increased cytochrome c concentration in Green Sunfish (Centrarchidae) that were moved from 25 to 5°C is due to a greater reduction in the degradation rate than in the rate of synthesis (Sidell 1977).

In some fishes alternative enzymes (termed **isozymes**) may be produced to catalyze the same reaction more efficiently at different temperatures. Isozymes are regulated by switching on or off the different genes that control their production. Rainbow Trout (Salmonidae) acclimated to 2 versus 18°C exhibit different forms of acetylcholinesterase, an enzyme important to proper nerve function because it breaks down the neurotransmitter acetylcholine (Hochachka & Somero 1984). The ability of Longjaw Mudsuckers (Gobiidae) to tolerate rather wide ranges of temperature is probably due to the fish's ability to regulate the ratio of isozymes of cytosolic malate dehydrogenase, an important enzyme in the Kreb's cycle (Lin & Somero 1995).

Polyploid species have extra sets of chromosomes (see Chapter 17, Polyploidization and evolution), and may have a better capacity to cope with a wide range of temperatures; perhaps the multiple copies of genes provide more opportunities for evolution to bring about changes in alleles that may prove to be beneficial. For example, among cyprinids, Goldfish and Common Carp are both polyploid and can tolerate a wide range of temperatures, and the polyploid Barbel can acclimate better to different temperatures than can the diploid Tinfoil Barb (O'Steen & Bennett 2003).

Laboratory acclimation studies, in which a single variable such as temperature is altered while other factors are

controlled and remain constant, can be helpful in understanding how fishes respond to a change in a single variable. However, in their natural habitats, fishes usually acclimatize to simultaneous changes in several variables, such as temperature, photoperiod, and perhaps reproductive condition as seasons change. The absence of natural seasonal cues, such as changing photoperiod, may cause an artificially acclimated fish to respond somewhat differently than one that has been naturally acclimatized. For example, laboratory acclimated fishes typically have higher metabolic rates at higher temperatures (see Chapter 5, Metabolic rate), yet seasonal reproductive cycles cause naturally acclimatized sunfish (Centrarchidae) to have higher metabolic rates in spring than in summer (Roberts 1964; Burns 1975). Other studies also have shown seasonal changes in metabolic rate that were independent of temperature in trout (Salmonidae; Dickson & Kramer 1971), two minnows (Cyprinidae; Facey & Grossman 1990), sunfish (Evans 1984), and sculpin (Cottidae; Facey & Grossman 1990).

Some fishes exhibit **allozymes**, alternative forms of the same enzyme that are controlled by different alleles of the same gene. Different populations of the species may exhibit higher or lower frequencies of the appropriate alleles depending on their geographic location. Livers of Mummichog (Cyprinodontidae) along the east coast of the United States exhibit two allozymes of lactate dehydrogenase, an important enzyme in carbohydrate metabolism. In Maine, the frequency of the allele for the form more effective at colder temperatures is nearly 100%, and the frequency decreases progressively in populations further to the south (Place & Powers 1979). In Florida, the alternative allele, which codes for the form more effective at higher temperatures, has a frequency approaching 100%.

Acclimation to cold temperatures includes modifications at the cellular and tissue level as well. Fishes, as well as other organisms, can alter the ratio of saturated and unsaturated fatty acids in their cell membranes to maintain uniformity in membrane consistency (Crockett & Londraville 2006). The proportion of unsaturated fatty acids, which are more fluid at colder temperatures (e.g., compare vegetable oil and butter at low temperature), increases in those species that are active during winter. Some fishes also decrease cholesterol levels in cell membranes to increase fluidity at lower temperatures. Fishes that live in very cold habitats, such as polar seas (see Chapter 18, Polar regions), often show cellular-level metabolic adaptations such as enzymes that function well at low temperatures and more mitochondria in their swimming muscles (Crockett & Londraville 2006). Therefore, they can function better at lower temperatures than would a nonpolar fish acclimated to very low temperature.

Decreased muscle performance at low temperatures can be compensated for at several levels of muscle function. Acclimation of Striped Bass (Moronidae) to low temperatures results in a substantial increase in the percent of red muscle cell volume occupied by mitochondria (Eggington & Sidell 1989), and an overall increase in the proportion of the trunk musculature occupied by red fibers (Jones & Sidell 1982); both of these adaptations would increase the aerobic capability of the fish. Muscle fibers of Goldfish (Cyprinidae) show an increased area of sarcoplasmic reticulum at lower temperatures (Penney & Goldspink 1980), which would make available more calcium ions to help activate more proteins needed for contraction.

At colder temperatures fishes may utilize more muscle fibers to swim at a particular speed than they use at warmer temperatures (Sidell & Moerland 1989). Because lower temperatures require the recruitment of more muscle fibers to sustain a given speed than is necessary at higher temperatures, maximum sustainable swimming velocities are lower at low temperatures (Rome 1990).

Temperature changes may affect ion exchange at the gills in a few different ways (Crockett & Londraville 2006). Higher temperatures typically increase molecular activity, causing increases in diffusion rates. Changes in membrane fluidity due to changes in the saturation of fatty acids or concentration of cholesterol, as discussed earlier, can also affect membrane permeability – less fluid membranes tend to be more permeable. Freshwater fishes often show increased activity of Na-K adenonsine triphosphatase (ATPase) at lower temperatures, whereas marine fishes show increased Na-K ATPase activity at higher temperatures. Both trends suggest increased metabolic activity to maintain osmotic balance as temperature changes.

Heterothermic fishes

Some large, active, pelagic marine fishes are heterothermic, using internally generated heat to maintain warm temperatures in the swimming muscles, gut, brain, or eyes (Dickson & Graham 2004). Heterothermic fishes include representatives of the tunas (Scombridae), swordfishes (Xiphiidae), marlins (Istiophoridae), sharks (Lamnidae, Alopiidae), and perhaps the Giant Manta and Sicklefin Devil Ray (Mobulidae). The heat utilized is generally the result of either swimming muscle activity, processes associated with digestion, or ocular muscles that have become modified into "heater organs" (see Box 4.1). In all cases the heat is retained by a rete – a modification of the circulatory system that forms a countercurrent exchange mechanism.

Heterothermic fishes that maintain elevated swimming muscle temperatures include some of the tunas, swordfish, and sharks. Their internal temperatures often are warmer than the surrounding water and remain fairly stable even as the fishes move from warm surface waters to colder deep water (Dickson & Graham 2004). Bluefin Tuna keep their muscle temperatures between 28 and 33°C while swimming through waters that range from 7 to 30°C (Carey & Lawson 1973). Yellowfin Tuna maintain muscle temperatures at about 3°C above ambient water, whereas Skipjack Tuna keep their muscles at about 4–7°C above ambient (Carey

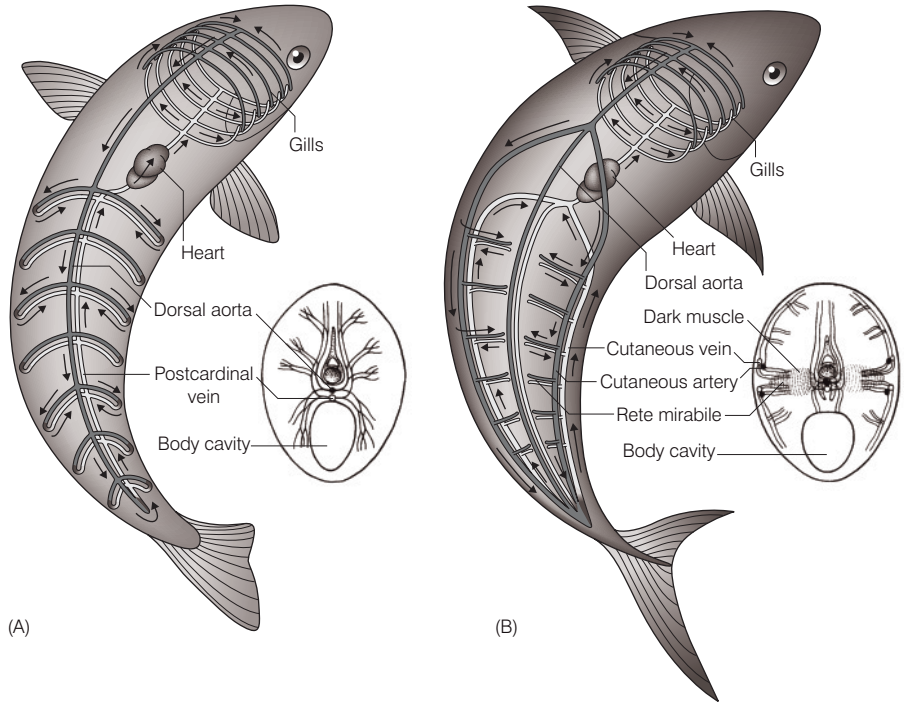


Figure 7.2

(A) The circulatory system of a "typical" fish sends blood from the gills down the core of the fish, making it impossible to maintain an elevated core temperature in cold water. Arrows indicate the direction of blood flow. (B) In the warm-bodied Bluefin Tuna (*Thunnus thynnus*), most of the blood from the gills is shunted toward cutaneous vessels near the body surface and is carried through a heat exchanging rete en route to the active swimming muscles, which stay warm through this heat conservation mechanism. After Carey (1973).

et al. 1971). These warm-bodied fishes conserve heat from muscular activity through adaptations of their circulatory systems. In a typical ectothermic fish, blood returns from the body to the heart and then travels to the gills for gas exchange (see Chapter 4, Cardiovascular system). The large surface area and thin membranes of the gills permit heat to escape to the environment, so that when the blood leaves the gills it is the same temperature as the surrounding water. In a typical fish this blood would then travel down the core of the fish via the dorsal aorta, keeping the core body temperature about the same as the surrounding water (Fig. 7.2A). In the large tunas, however, the cool blood leaving the gills is mostly diverted to large peripheral vessels that run along the outside of the fish's body (Fig. 7.2B). As arterial blood flows toward the large swimming muscles near the core of the body, it passes through a network of small blood vessels where it runs countercurrent to warm blood leaving these muscles. This type of arrangement of blood vessels is referred to as a **rete mirabile** ("wonderful net"), as discussed in Chapter 5 for the gas bladder. The oxygenated blood is warmed as it passes through the rete and travels toward the swimming muscles. In this way the heat generated by the activity of the large swimming muscles is kept within the muscles themselves and is not transported via the blood to the gills where it would be lost to the surrounding water (Dickson & Graham 2004). Bigeye Tuna can regulate their body temperature by utilizing the heat exchange mechanism only in colder water when it is needed (Holland et al. 1992).

In most fishes, the red muscle tissue responsible for sustained swimming is located laterally and just below the skin, where it readily loses heat to the water. In the tunas, however, red muscle is located more centrally, along the spinal column. This arrangement of the swimming muscles contributes to the unique and very efficient swimming style observed in the tunas (termed "thunniform") in which the high, thin tail oscillates rapidly while the body remains rigid (see Chapter 8, Locomotory types). The evolution of thunniform swimming and the accompanying displacement of the red swimming muscles toward the body core put an insulating layer of less-vascularized white muscle between the heat-generating red muscle and the surrounding water (Block & Finnerty 1994). This muscle arrangement may have been a prerequisite for the development of the circulatory adaptations necessary to maintain elevated body temperatures (Block et al. 1993; Block & Finnerty 1994). Swordfish (Xiphiidae) also have their red swimming muscles more centrally located, and also possess an associated heat exchanger (Carey 1990).

Smaller tunas also have retia (plural for rete) for heat exchange, but they tend to be located more centrally, below the vertebral column (Stevens et al. 1974). Cool blood from the dorsal aorta is warmed as it passes through the rete and into the swimming muscles. It appears that this type of centrally located rete is found in smaller tunas that inhabit warmer oceans, whereas large tunas from colder regions have lateral retia, as shown in Fig. 7.2B. Large sharks of the family Lamnidae such as the White Shark, makos, and Porbeagle maintain elevated visceral and body core temperatures with a heat exchanging rete located anterior to the liver (Carey et al. 1981). Small retia also have been observed in the viscera and red muscle of two species of thresher sharks (Alopiidae; Block & Finnerty 1994), and Bernal and Sepulva (2005) reported elevated muscle temperature in the Thresher Shark. Some sharks and tunas, then, have found a way to take advantage of many of the

benefits of endothermy by conserving and recirculating heat that would have been lost to the environment, thereby avoiding the additional metabolic costs of specialized thermogenic tissues.

Another use of heterothermy in fishes is in warming parts of the central nervous system, especially the brain and eyes, which may enhance vision and neural processing in deeper, colder habitats, although this has yet to be tested (Block & Finnerty 1994). All endothermic fishes studied warm some part of their central nervous system, suggesting that this may have been a strong factor in the evolution of endothermy. This is accomplished by the generation of heat by special thermogenic tissues and by circulatory adaptations that use blood warmed in other parts of the body. In Swordfish (Xiphiidae) and marlins (Istiophoridae) the superior rectus eye muscle, and in the Butterfly Mackerel (Scombridae) the lateral rectus eye muscle, have lost the ability to contract and instead produce heat when stimulated by the nervous system. When these cells are stimulated calcium is released from the sarcoplasmic reticulum, which would trigger contraction in normal muscle cells. Instead, this calcium is rapidly transported back into the sarcoplasmic reticulum by ion pumps and the continuous release and pumping generates heat (see Dickson & Graham 2004). This thermogenic organ (the only vertebrate thermogenic tissue known other than mammalian "brown adipose tissue") seems to have developed for the particular purpose of generating heat for the brain and eyes. Eye muscles of other tunas and the lamnid sharks do not appear to be modified as heater organs (Block & Finnerty 1994), but retia near the eyes apparently help maintain elevated eye and brain temperatures. The lamnid sharks also have a large vein that drains warm blood from the core swimming muscles to the spinal cord, thereby warming the central nervous system (Wolf et al. 1988).

The diversity of heterothermic fishes, the different mechanisms employed, and the different locations of countercurrent exchange retia suggest that heterothermy evolved independently several times among fishes. This diversity also provides examples of convergent evolution of physiological strategies designed to retain heat. Countercurrent heat exchange is also found in other animals, including mammals, birds, and insects (Willmer et al. 2005).

Five primary factors have been proposed as driving forces in the evolution of heterothermy: (i) the expansion of thermal niches; (ii) the stabilization of temperatures of some important internal tissues; (iii) an enhanced ability to detect thermal gradients; (iv) increased metabolic rates and faster recovery from anaerobic activity; and (v) increased growth rates (Dickson & Graham 2004; Crockett & Londraville 2006). In addition, it has been hypothesized that higher brain and eye temperatures may enhance neural processing and vision, that elevated gut temperatures may increase efficiency of digestion, and that increased swimming muscle temperatures may increase burst or sustained swimming performance. However, as logical and appealing as these ideas are, there has been little evidence accumulated to test them empirically.

Dickson and Graham (2004) reviewed past studies and found some support for the niche expansion hypothesis – tunas and billfishes with more active red muscle mass closer to the body core and with a well-developed rete tended to undergo vertical migrations to deeper and colder water than related species with more peripherally located red muscle and a less developed rete. Heterothermy may have allowed some members of the tunas, a generally tropical group, to utilize colder ocean environments (Dickson & Graham 2004). However, non-heterothermic fishes also use these habitats, so even if heterothermy helps some fishes it clearly is not a requirement for success. Block et al. (2001) reported that internally implanted electronic tags showed that the Bluefin Tuna maintained a relatively constant internal temperature of about 25°C while traveling through seas ranging from 2.8 to 30.6°C, and speculated that the elevated muscle temperature may enhance swimming in cold water. Dickson and Graham's (2004) review did not find evidence that warmer swimming muscles improved swimming performance, but noted that the available studies had not adequately evaluated the largest fishes, which would have the warmest swimming muscles and therefore might gain the greatest advantage. Studies comparing heterothermic and similar-sized ectothermic scombrids have shown that the heterotherms have higher metabolic rates, and hence higher Energetic costs, but that the heterotherms also have higher optimal swimming speeds, which may be useful for long-distance migrations. More studies must be done to help us better understand the benefits of heterothermy in large pelagic fishes. The diversity of species exhibiting heterothermy and the multiple mechanisms that have evolved to permit it suggest that there must be some fairly strong evolutionary benefit.

Coping with temperature extremes

Extreme temperatures are dangerous to many living systems. Proteins, including the enzymes that catalyze critical biochemical reactions, are temperature sensitive. High temperatures may cause structural degradation (denaturation), resulting in partial or complete loss of function. Death can come quickly to a seriously overheated animal. Cold temperatures can slow critical biochemical reactions by reducing molecular movement and interaction.

Living in water generally protects fishes from extreme environmental temperatures. Nevertheless, even at moderately high temperatures, fishes encounter an additional problem associated with the aquatic environment – decreased oxygen availability due to limited gas solubility. When combined with elevated oxygen demand due to increased metabolic rate and a temperature-induced Bohr effect that interferes with hemoglobin function, high tem-

peratures result in a physiologically stressful situation, as discussed in Chapter 5 (Gas transport). Not surprisingly, few fishes tolerate high temperatures (see Chapter 18, Deserts and other seasonally arid habitats).

The physiological challenges of low temperature include compensating for the effects on cellular metabolism, nervous function, and cell membranes (Crockett & Londraville 2006). Probably the greatest potential danger at very low temperatures is intracellular formation of ice crystals which can puncture cell membranes and organelles, leading to cell death. Intracellular ice formation also causes extreme osmotic stress because as water freezes, solutes remain dissolved in a decreasing volume of cytoplasm, causing osmotic concentration to increase.

Freshwater fishes generally are protected from dangerously cold temperatures because fresh water freezes at 0°C but is densest at 4°C. Ice, therefore, forms on the surface of a lake or pond. Ions and other solutes depress the freezing point of the intracellular fluid of most fishes to around –0.7°C and freshwater fishes below the ice will not experience temperatures cold enough to freeze their body fluids. Freshwater fishes, therefore, seldom need special physiological mechanisms to cope with potentially freezing conditions.

Marine fishes at high latitudes, however, are faced with different circumstances (see Chapter 18, Polar regions). Sea water freezes at about –1.86°C, which is below the freezing point of the body fluids of most fishes. A marine fish could, therefore, find itself in a situation where the temperature of its environment is lower than the fish's freezing point – a potentially dangerous situation. Although some intertidal invertebrates and terrestrial vertebrates can survive freezing, fishes, instead, prevent ice formation through several different mechanisms.

One tactic involves a physical property of crystal formation. Crystals will not grow unless a "seed" crystal exists to which other molecules can adhere. Under controlled laboratory conditions, Mummichog (*Fundulus heteroclitus*) were cooled to about –3°C, well below their normal freezing point, without ice formation (Scholander et al. 1957), but when touched with ice crystals the fish froze nearly instantaneously. This phenomenon of supercooling, also called undercooling, apparently is used by some marine fishes in very cold environments (Fletcher et al. 2001; DeVries & Cheng 2005). The potential danger of contacting ice crystals is less of a problem for fishes that live in deep water, where they are unlikely to encounter ice.

Many polar fishes do come in direct contact with ice, however, and still do not freeze, indicating that they have developed physiological mechanisms to prevent internal ice formation (DeVries & Cheng 2005; see Chapter 18, Adaptations and constraints of Antarctic fishes). This protection generally involves the production of some type of biological antifreeze, a process which is controlled by genes that are activated seasonally (Fletcher et. al. 2001). Antifreeze compounds, usually proteins or glycoproteins, can bring the freezing point of some Antarctic fishes, particularly the notothenioid ice fishes, down well below the freezing point of sea water (Fletcher et al. 2001; DeVreis & Cheng 2005). These antifreeze compounds are produced in the liver and distributed throughout the body, and they also are produced in tissues likely to contact ice, such as the skin, gills, and gut. Several different protein or glycoprotein antifreezes have been identified among cold water fishes, and all function by adhering to small ice crystals as they begin to form thereby preventing growth of the seed crystal.

The freezing point of body fluids also can be lowered by increasing the concentration of osmolytes (ions and other solutes) – the higher the concentration, the lower the freezing point. Notothenioids do this and achieve a slight (tenths of a degree) lowering of the freezing point. Other fishes rely strongly on increasing osmolytes to lower their freezing points in sea water. Rainbow Smelt (Osmeridae) use a combination of ice prevention tactics. They have an antifreeze in their blood to help prevent ice crystal growth. At very low temperatures, however, this antifreeze apparently is not enough protection, so the Rainbow Smelt produce glycerol to increase the osmotic concentration of the blood and intracellular fluids, thereby further decreasing the freezing point (Raymond 1992). At temperatures near the freezing point of sea water, the glycerol concentration is so high that the smelt are nearly isosmotic to the ocean. This increase in glycerol concentration is more apparent in the colder winter months and may account for the reported sweeter flavor of these fish during that time of year.

Other fishes that live in areas that have warmer and colder seasons, such as Atlantic Cod (Gadidae), Shorthorn Sculpin (Cottidae), and Winter Flounder (Pleuronectidae), also exhibit increased levels of biological antifreezes during winter (Fletcher et al. 2001). Because glycerol and protein or glycoprotein antifreezes are metabolically costly to produce, it makes sense to manufacture them only when needed; photoperiod seems to be the seasonal cue to increase or decrease antifreeze production (Fletcher et al. 2001). Rainbow Smelt along the east coast of North America seem to rely mainly on the colligative properties of the glycerol to decrease the freezing point of their blood – they begin increasing levels of glycerol and antifreeze protein in their blood in fall, when water temperatures decline to about 5°C (Lewis et al. 2004).

Species most likely to encounter ice have more copies of the genes that code for antifreeze production than fish that encounter less ice (Fletcher et al. 2001). Some have speculated that even within a species, higher latitude populations may be better equipped to deal with colder temperatures. However, although Atlantic Cod (Gadidae) from the northern tip of Newfoundland produced significantly more antifreeze glycoprotein than those from further south (Goddard et al. 1999), Purchase et al. (2001) showed that young cod raised from eggs and sperm from spawning

adults captured in the Gulf of Maine (42°N, 70°W) were capable of producing as much antifreeze glycoprotein as young raised from spawning adults captured in the Grand Banks (46°N, 55°W) when both groups were exposed to equally low temperatures.

Very similar antifreeze compounds may occur in unrelated species, demonstrating convergent evolution at the genetic and biochemical level. For example, northern cods (superorder Paracanthopterygii, family Gadidae) and Antarctic nototheniids (superorder Acanthopterygii, family Nototheniidae) have very similar antifreeze glycoproteins, but the genes responsible for producing them do not appear to be related. In another example, herring (subdivision Clupeomorpha, family Clupeidae), smelt (subdivision Euteleostei, superorder Protacanthopterygii, family Osmeridae,) and sea ravens (subdivision Euteleostei, superorder Acanthopterygii, family Cottidae) all have the same antifreeze protein. This is a different antifreeze, however, than is found in two sculpins, which are in the same family as the sea ravens. And each of these two sculpins (family Cottidae) have different antifreezes, suggesting that antifreeze compounds have evolved independently and perhaps somewhat recently in the Cottidae (Fletcher et al. 2001).

Antarctic fishes of the suborder Notothenioidei must maintain year-round protection from freezing because their environment rarely gets above –1.5°C, even in summer. In most fishes molecules as small as glycoprotein antifreezes would be lost in the urine. The fish would then need to produce more, at considerable energetic cost. The urine of notothenioids, however, does not contain these antifreezes because the kidneys of these fishes lack glomeruli, the small clusters of capillaries through which blood normally is filtered (DeVries & Cheng 2005; kidney function, including aglomerular kidneys, is discussed later in this chapter).

Freeze protection strategies may not completely prevent ice formation within fishes. Small crystals of ice have been found in tissues that contact the surrounding water, such as the gills, skin, and gut. Ice also has been found in the spleen of some Antarctic fishes, perhaps carried there by macrophages that ingest small ice particles as part of the fish's immune response (DeVries & Cheng 2005).

Thermal preference

The strong effect of temperature on biochemical and physiological processes drives fishes to select environmental temperatures at which they can function efficiently (Coutant 1987). Because different physiological processes may have different optimal temperatures, the temperature selected by a fish often represents a compromise, or "integrated optimum" (Kelsch & Neill 1990). Fishes probably select temperatures that maximize the amount of energy available for activity, or metabolic scope (the difference between standard and maximum metabolic rates) (Fry 1971; Kelsch & Neill 1990; see also Chapter 5, Metabolic rate). Of course, habitat selection in the wild involves a compromise between temperature requirements and other important factors, such as dissolved oxygen levels, food availability, current velocity, substrate type, and avoidance of predators and competitors (see Coutant 1987). Temperature is, however, a very strong determinant of habitat choice by some fishes. Temperature-sensitive radio transmitters surgically implanted in the body of trout revealed that when the water temperature of a New York stream exceeded 20°C, the fish selected cooler microhabitats within the river, such as tributary confluences and areas of groundwater discharge. The body temperature of Brook Trout was up to 4°C below river temperature, whereas Rainbow Trout had body temperatures up to 2.3°C below river temperature (Baird & Krueger 2003).

Numerous laboratory investigations have shown most fishes select temperatures close to those to which they have become accustomed (see Kelsch & Neill 1990). There are a few exceptions, however. Chum Salmon (Salmonidae) and Blue Tilapia (Cichlidae) show very narrow and constant temperature preferences regardless of acclimation temperature, and guppies (Poeciliidae) show a slight decline in preferred temperature with increased acclimation temperature (see Kelsch & Neill 1990). The physiological ability to adapt to different temperatures to the point of shifting temperature preference may reflect the climate in which a species evolved (Kelsch & Neill 1990). Species that evolved in areas with substantial seasonal changes in temperature, such as the Bluegill (Centrarchidae) of temperate North America, need the biochemical and physiological ability to shift temperature optima. More tropical species, such as guppies and tilapia, and coldwater fishes, such as salmonids, probably have not had to respond to selective pressures that would favor individuals that can make these kinds of adjustments.

Temperature preferences can change as fishes grow, leading to different life stages of a given species utilizing different thermal niches. For example, juvenile Striped Bass (Moronidae) prefer temperatures around 25°C, whereas large adults will select cooler temperatures, around 20°C (Coutant 1985). This ontogenetic shift in temperature preference has important implications for the success of efforts to introduce this highly prized sport fish into various reservoirs and estuaries. A body of water that is ideal for the success and growth of young fish may be thermally unsuitable for large adults, which may congregate in small areas of slightly cooler water (often 18–20°C) such as near underground spring inputs or in the hypolimnetic waters of stratified lakes and reservoirs (see Chapter 25, Temperature, oxygen, and water flow). Extreme crowding can lead to increased susceptibility to disease and overfishing. It also can lead to locally depleted food supplies and subsequent poor growth and reduced fecundity. The thermal preference may be so strong that starving fish will not leave cooler deep waters to feed on abundant prey in warmer surface waters (Coutant 1985).

Strong thermal preferences probably are the result of natural selection resulting in fishes selecting habitats that offer them the best chances for growth and reproduction. This physiological constraint on habitat selection can become a liability, however, particularly in the face of human alterations of aquatic environments. In summer the deep, cooler hypolimnion of warm reservoirs can be attractive to large Striped Bass. As summer progresses, however, these deep waters can become low in oxygen, leading to fish mortality. Coutant (1985) discusses evidence for and implications of this temperature–oxygen habitat squeeze on Striped Bass populations in several diverse habitats, including freshwater and coastal systems. Potential impacts of global warming on temperature preferences are discussed in Chapters 25 and 26.

Power plant cooling systems often discharge heated water into lakes and rivers, thereby altering their thermal structure. This can cause fishes to congregate in areas that may not be ultimately beneficial. For example, if the plant shuts down for a few days during the winter, fish that had become acclimated to the warmer water are suddenly left stranded in a cold environment and can die. Hydroelectric dams often release deeper, cooler water from an upstream reservoir. Fishes that congregate in these cooler hypolimnetic waters may be more susceptible, therefore, to being drawn through the turbines and injured or killed. The release of cooler water through a hydroelectric dam also can attract downstream fishes to the tailrace water during the warm summer months. The concentration of fish can create an attractive sport fishery, but it also can lead to overfishing and subsequent depletion of brood stock. In some "pumpback" hydroelectric dams, large motors run turbines in reverse to push water back to the upstream side of the dam when power is not needed. When more electricity is needed, such as during periods of peak demand, this water is released again to generate electricity. The attraction of fishes to the foot of the dam during periods of power generation can set the stage for high fish mortality if those fishes are drawn through the turbines as water is pumped back to the upstream side of the dam (Helfman 2007).

The combination of cooler temperatures and high turbulence can cause water that is released from dams to become supersaturated with gases, especially nitrogen and oxygen. The blood of fishes living in these areas also can become supersaturated because of gas diffusion across the highly permeable gill membrane. When these fishes move to warmer, less turbulent areas, the gases come out of solution and form bubbles in the blood. This **gas bubble disease** (similar to "the bends" in humans) can cause blocked and ruptured blood vessels, resulting in disorientation and death.

Thermal preferences also may cause fishes to congregate in areas with high levels of toxic pollutants, as has been reported for Striped Bass in the San Francisco Bay-Delta area. Uptake and bioaccumulation of some of these contaminants has been correlated with poor growth, high parasite loads, and decreased reproductive potential (Coutant 1985).

The impact of temperature preferences on fish habitat selection is a good example of links among fish physiology, behavior, ecology, and conservation. The effect of temperature preferences on the success of introduced Striped Bass also demonstrates the importance of basic physiological and behavioral information, as well as a thorough understanding of the habitat, when considering ecosystem manipulation or species introductions.

Osmoregulation, excretion, ion and pH balance

One of the most important homeostatic functions of living organisms is proper regulation of the internal osmotic environment. Deviation from the normal range can jeopardize proper physiological function through water loss or gain, the changing of internal ionic concentrations, and shifts in ionic and osmotic gradients. Most fishes, like all other vertebrates, are **osmoregulators** – they regulate their internal osmotic environment within a fairly narrow range that is suitable for proper cellular function, even if the external osmotic environment fluctuates. Fishes that can tolerate only small changes in the solute concentration of their external environment are referred to as **stenohaline**, whereas those with the ability to osmoregulate over a wide range of environmental salinities are **euryhaline**.

Gills are an important osmoregulatory and excretory organ for fishes. Their large surface area, thin membranes, and highly specialized cell types make them well suited for this role. Nitrogen wastes are eliminated in the form of ammonia (NH_3) and its cation ammonium (NH_4^+), both of which are soluble in the surrounding water. Diffusion of these wastes across the gills does, however, require immersion in water. Fishes that can survive out of water for extended periods convert ammonia to urea, which is less toxic and can be stored until the fish returns to the water. For example, African lungfishes (Protopteridae) produce ammonia when in the water but switch to urea production while estivating in a mud cocoon through long dry periods (Yancey 2001; see Chapter 13, Subclass Dipnoi, Order Ceratodontiformes: the lungfishes). The amphibious mudskippers (*Boleopthalmus*, Gobiidae) increase mucus production by the skin and gills during terrestrial forays, and the mucus contains high levels of ammonia and urea (Evans et al. 1999). Other air-breathing fishes, including some that inhabit intertidal zones, may utilize several strategies to protect themselves against ammonia toxicity, including

Table 7.1

Percent of nitrogenous wastes eliminated as ammonia nitrogen and urea nitrogen through the gills and kidney of various fishes. From Wood (1993).

Fishes	Medium	Gill		Kidney		Reference
		Ammonia	Urea	Ammonia	Urea	
Agnatha						
Lamprey (*Lampetra*)[a]	FW	95	0	4	1	Read (1968)
Chondrichthes						
Dogfish (Squalus)[a]	SW	2	91	0	7	C. M. Wood & P. A. Wright (unpubl. data)
Sawfish (*Pristis*)[a]	FW	18	55	2	25	Smith & Smith (1931)
Bony fishes						
Carp (*Cyprinus*)[a]	FW	82	8	10	0	Smith (1929)
Goldfish (*Carassius*)[b]	FW	79	13	7	1	Smith (1929)
Catfish (*Heteropneustes*)[a]	FW	85	11	0	4	Saha et al. (1988)
Trout (*Oncorhynchus*)[a]	FW	86	11	1	2	Wood (1993)
Cichlid (*Oreochromis*)[b]	FW	61	25	0	14	Sayer & Davenport (1987)
Trout (*Oncorhynchus*)[a]	10% SW	56	32	10	2	Wright et al. (1992)
Mudskipper (*Periophthalmus*)[b]	25% SW	47	23	13	17	Morii et al. (1978)
Goby (*Boleophthalmus*)[b]	25% SW	61	14	11	14	Morii et al. (1978)
Poacher (*Agonus*)[b]	SW	41	9	43	7	Sayer & Davenport (1987)
Sculpin (*Taurulus*)[b]	SW	63	4	20	13	Sayer & Davenport (1987)
Wrasse (*Crenilabrus*)[b]	SW	67	2	28	3	Sayer & Davenport (1987)
Blenny (*Blennius*)[b]	SW	35	18	39	8	Sayer & Davenport (1987)

FW, freshwater; SW, sea water.

[a] Kidney excretion measured by urinary catheter. Therefore, any excretion via the skin or gut would be included in the "gill" component.

[b] Kidney excretion measured by placing the fish in a chamber with a watertight curtain separating the anterior (head and gills) and posterior sections. Therefore, any excretion via the skin or gut is mostly included in the "kidney" (posterior) component.

reducing amino acid catabolism to reduce ammonia production, converting ammonia to less toxic compounds such as glutamine or urea, excreting ammonia through the gut or skin, and increasing physiological tolerance to ammonia (Ip et al. 2004a).

The kidneys also play an important role in osmoregulation and excretion (Table 7.1). The basic process of urine formation in most fishes is similar to that of other vertebrates, but unlike most terrestrial vertebrates fishes cannot produce urine that is more concentrated than their blood. In the kidneys, blood pressure forces water and small ions across the walls of small capillary beds, called glomeruli, and into the surrounding Bowman's capsules, which are the beginning of the kidney tubules (nephrons). As the filtrate travels along the nephron, water and important solutes are removed and added back to the blood. Waste products, excess ions, and other molecules that were not contained in the initial filtrate are added to the urine for elimination from the body. Urine drains from the nephrons into collecting ducts, and then to the bladder where it may be held prior to being excreted. The urinary bladder may play an important role in salt and water balance by removing salts from the urine of freshwater fishes and removing water from and adding salts to the urine of saltwater fishes (Marshall & Grosell 2006).

Osmoregulation in different types of fishes

Agnathans

Hagfishes (Myxinidae; see Chapter 13, Myxiniforms), are **osmoconformers**, similar to many marine invertebrates. Their overall internal osmotic concentration is about the same as that of sea water (Table 7.2). Because they live in fairly stable osmotic conditions near the bottom in relatively deep water, they do not have to contend with internal osmotic instability. Although the overall internal osmotic concentration of hagfishes is the same as the ocean, there are differences in the concentrations of some individual ions. There is no difference, however, in the concentration of the two major ions, sodium and chloride, giving hagfishes the highest concentrations of these physiologically important ions among the vertebrates. Lampreys (Petromyzontidae), the other group of extant agnathans, are osmoregulators and appear to utilize osmoregulatory strategies very similar to those of teleosts (Evans 1993).

Elasmobranchs

To prevent osmotic stress in the hyperosmotic marine environment, marine elasmobranchs (see Chapter 12) convert

Table 7.2

Plasma ionic concentrations (in milliosmoles per liter) of sea water, fresh water, and various fishes. From Evans (1993).

	Na	Cl	K	Mg	Ca	SO_4	Urea	TMAO	Total
Sea water	439	513	9.3	50	9.6	26	0	0	1050
Hagfish (*Myxine*)	486	508	8.2	12	5.1	3	–	–	1035
Lamprey (*Petromyzon*)	156	159	32	7.0	3.5	–	–	–	333
Shark[a]	255	241	6.0	3.0	5	0.5	441	72	1118
Teleost (*Lophius*)	180	196	5.1	2.5	2.8	2.7	–	–	452
Euryhaline teleost (*Pleuronectes*)	142	168	3.4	–	3.3	–	–	–	297
Fresh water (soft)	0.25	0.23	0.005	0.04	0.07	0.05	–	–	1
Lamprey (*Lampetra*)	120	104	3.9	2.0	2.5	–	–	–	272
Stingray (*Potamotrygon*)	150	150	–	–	–	–	1.3	–	308
Teleost (*Cyprinus*)	130	125	2.9	1.2	2.1	–	–	–	274
Euryhaline teleost (*Pleuronectes*)	124	132	2.9	–	2.7	–	–	–	240

[a] Na, Cl, urea, and total data from *Scyliorhinus canicula*; other data from *Squalus acanthias.*

their nitrogen wastes into **urea** and retain high concentrations of it in their blood. This, in addition to **trimethylamine oxide (TMAO)**, which helps to stabilize proteins against the denaturing effect of urea, gives elasmobranch blood an osmotic concentration slightly higher than that of sea water (Table 7.1). Elasmobranch gills are not readily permeable to urea, and this is probably enhanced by the cells transporting urea back into the blood and thereby reducing the gradient between the cell and the surrounding water (Marshall & Grosell 2006). As a result of this urea retention, elasmobranchs are hyperosmotic to sea water and gain water by diffusion across their gills.

Elasmobranch gills have **mitochondria-rich cells**, which may help with acid–base balance but apparently play no significant role in sodium or chloride balance. Instead, marine elasmobranchs rid themselves of excess sodium and chloride by active secretion via the **rectal gland**, which lies just anterior to the cloaca. Secretory tubules of the gland are lined with salt-secreting cells that are similar structurally and biochemically to the mitochondria-rich cells of teleost gills. The rectal gland produces a solution that has about twice the NaCl concentration as the fish's extracellular fluids (Marshall & Grosell 2006), and this solution drains into ducts leading to the lower intestine and is eliminated with other wastes.

Over 40 species of elasmobranchs, representing four families, are either euryhaline or exclusively freshwater species. Those that are euryhaline tend to lose urea when they spend time in fresh water, and those that live exclusively in fresh water, such as the freshwater stingrays (Potamotrygonidae), do not produce much urea at all and rely on ammonia excretion to get rid of nitrogen wastes, as teleosts do (Marshall & Grosell 2006). The rectal glands of these fishes are also smaller and may become atrophied due to lack of use.

Marine elasmobranchs have glomerular kidneys, and their glomerular filtration rate is somewhat similar to those of freshwater fishes because the high urea content of the marine elasmobranchs causes them to gain water from their environment. The nephron is long, convoluted, and has several specialized segments – the proximal segment, intermediate segment, distal segment, and collecting duct. Divalent ions, such as magnesium and sulfate, are actively transported from the blood into the proximal segment (as in marine teleosts), and the close proximity of the looping segments suggests that a countercurrent mechanism may be at work, perhaps to recover urea and TMAO (Marshall & Grosell 2006). A facilitated transporter for urea has been identified in the latter segments of the nephron.

Sarcopterygians

The coelacanths (Coelacanthidae) are extant marine sarcopterygians that also maintain elevated levels of urea and TMAO in their blood to offset the high ionic concentration of the external environment (see Yancey 2001), as do the marine elasmobranchs. The African and South American lungfishes (Dipnoi) are freshwater sarcopterygians that can survive long periods of drought by estivating in mud burrows. During this estivation period they produce and retain high levels of urea, perhaps as a way of storing their nitrogen wastes in a form that is less toxic than ammonia and perhaps to help retain water. The phylogenetic distance between the sarcopterygians and the elasmobranchs, and the fact that both groups use urea as a nitrogenous waste and osmolyte, indicates an example of convergent evolution in the face of similar physiological challenges.

Freshwater teleosts

Freshwater teleosts are hyperosmotic to their environment (see Table 7.1) and therefore tend to gain water and lose solutes by diffusion across the thin membranes of the gills and pharynx (Fig. 7.3A). Solutes also are lost in the urine. If left unchecked, the fish's cells would swell and burst from

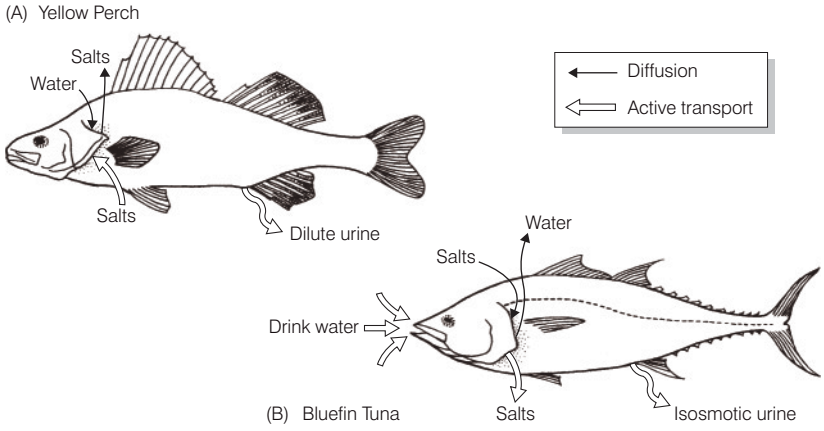


Figure 7.3

Maintaining osmotic balance in fresh versus sea water. (A) Freshwater bony fishes must produce a large volume of dilute urine to offset the passive uptake of water across their gills. They also must actively transport ions into the blood at the gills to compensate for the loss of these ions to the dilute freshwater environment. (B) Marine bony fishes passively lose water to their environment and gain salts by diffusion across their gills. They must, therefore, take in water through their food and by drinking sea water. Monovalent ions are actively transported out of the blood at the gills. Magnesium and sulfate ions, which are abundant in sea water, are excreted in the urine. Marine fishes conserve water by producing urine that is isosmotic to their blood.

the constant influx of water. To prevent this, freshwater fishes excrete a large volume of dilute urine and actively transport solutes back into their blood. Some of these solutes are recovered from urine as it is being formed in the kidney tubules. In addition, sodium and chloride ions are taken up from the surrounding water at the gills by specialized mitochondria-rich cells (often referred to as "**ionoregulatory cells**" or "**chloride cells**" in some literature). Although the specific biochemical mechanisms of this transport are not fully understood, it appears that sodium and chloride uptake are accomplished by different cells and that these processes may be linked with secretion of hydrogen ions and bicarbonate ions, respectively (Marshall & Grosell 2006). The basolateral membranes of these mitochondria-rich cells, which are essentially inward extensions of the extracellular environment, come very close to the apical surface of the cell which is in contact with the surrounding water (Fig. 7.4A). This allows the transport mechanisms on the membranes to establish gradients of either hydrogen ions or bicarbonate ions high enough so that they diffuse from the cell to the surrounding water, and either sodium or chloride ions enter the cell as part of an ion exchange to maintain electrochemical balance (Fig. 7.4B, C).

The exchange of hydrogen ions for sodium ions, or bicarbonate ions for chloride ions, is likely enhanced by the enzyme carbonic anhydrase which accelerates the conversion of water and carbon dioxide to hydrogen and bicarbonate ions. Tresguerres et al. (2006) propose that the exchange of chloride for bicarbonate may be achieved by the close linkage of carbonic anhydrase and ion exchangers on the apical and basolateral membranes, a mechanism which they call the "freshwater chloride-uptake metabolon". Sodium uptake is probably achieved by a protein that uses ATP to exchange incoming sodium ions for potassium ions (Marshall & Grosell 2006). Freshwater fishes also take up calcium at the gills by actively transporting calcium into the blood at the basolateral membrane, thereby decreasing the intracellular calcium concentration and encouraging diffusion of calcium into the cell from the surrounding water (Perry et al. 2003).

Kidneys also play a role in osmoregulation and ion balance. In freshwater teleosts, glomerular filtrate passes into the proximal tubule where water and solutes, including sodium, chloride, and glucose, are recovered into the blood. Additional sodium and chloride may be recovered in the distal tubules, collecting ducts, and bladder before the urine is released from the body (Marshall & Grosell 2006).

Marine teleosts

Marine teleosts face the opposite problem from that of freshwater teleosts. The high salt concentration of the ocean draws water out of the fish, and ions diffuse in across the permeable membranes (see Fig. 7.3B). To counteract potential dehydration, marine teleosts drink sea water and actively excrete excess salts. The mitochondria-rich cells of the gills actively transport chloride ions from the fish's extracellular fluid into the cell along the extensive basolateral membrane. This increases the chloride concentration in the cell and results in chloride diffusing out of the cell at its apical surface and into the surrounding sea water. The build up of these negatively charged chloride ions at the outside of the apical surface attracts positively charged sodium ions, which apparently pass through the gill epithelium between the mitochondria-rich cells and the adjacent accessory cells (see Fig. 7.4D). Larger multivalent ions, especially magnesium and sulfate, which are abundant in sea water, are not readily absorbed in the gut and therefore are excreted (Marshall & Grosell 2006).

Most marine teleosts have glomerular kidneys, so urine forms initially by glomerular filtration. Some polar fishes, however, lack glomeruli and rely exclusively on active transport of solutes from the blood into the nephron to form urine. This means of urine formation prevents the loss of important molecules, such as biological antifreezes (see above, on coping with extreme temperatures). Whether

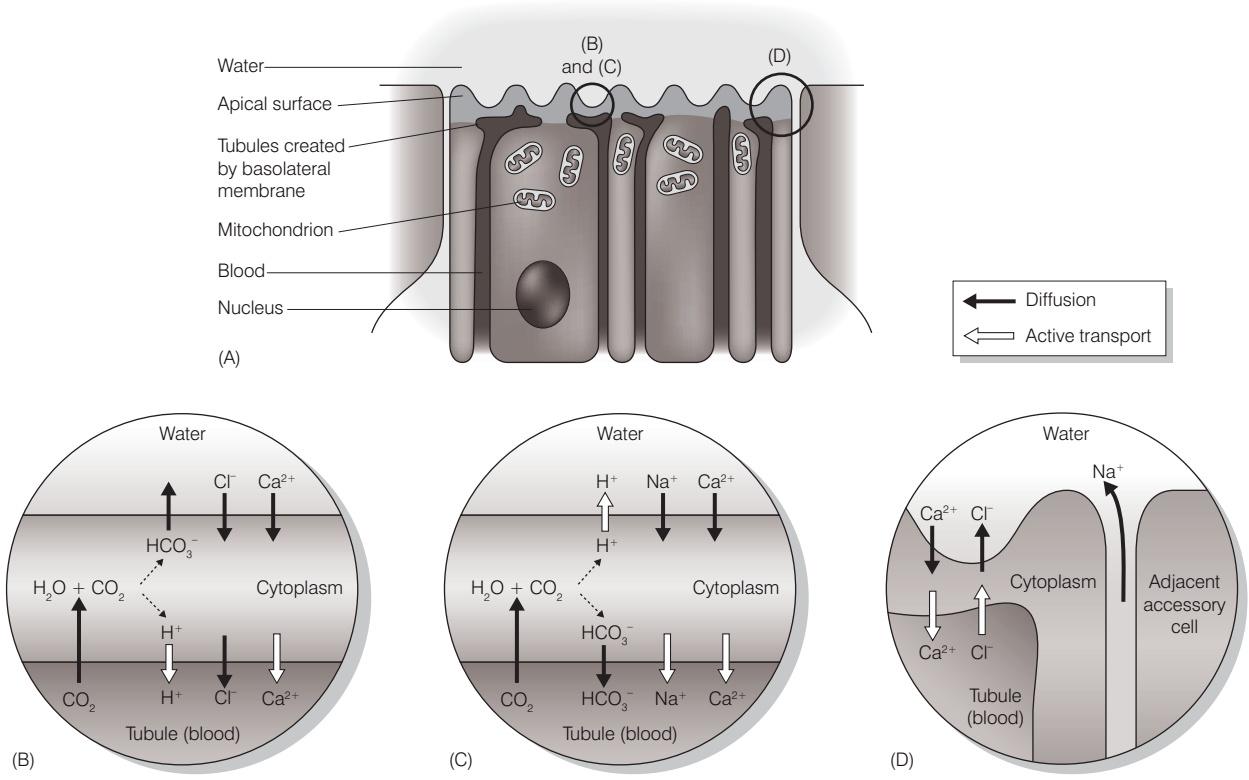


Figure 7.4

(A) In addition to the abundant mitochondria that provide the energy needed for high levels of active transport, mitochondria-rich (MR) cells have a highly infolded basolateral membrane that greatly increases surface area by creating a tubule system within the cell. This also brings the extracellular fluid within the tubules in close proximity to the apical surface of the cell, allowing the establishment of concentration gradients that assist with ion exchange. (B) The apical surface of some of the MR cells in the gills of freshwater fishes take up chloride ions from the surrounding water in exchange for the secretion of bicarbonate ions created by combining carbon dioxide with water. Proton pumps that transport hydrogen ions out of the cell and into the blood help to drive this process indirectly. (C) Other MR cells in freshwater fish gills take up sodium ions from the water by the excretion of hydrogen ions across the apical surface, removing sodium from the cell and transporting it into the blood at the basolateral surface. (D) Marine bony fishes actively transport chloride into the MR cells of the gills from the blood, creating a high intracellular concentration that results in the diffusion of the chloride across the apical surface and into the surrounding sea water. The outward flow of negatively charged chloride ions helps draw positively charged sodium ions out through the leaky membrane connecting the MR cell to an adjacent accessory cell. In B, C, and D the active transport of calcium ions out of the cell into the blood helps to draw in more calcium from the surrounding water. After Marshall and Grosell (2006) and Tresquerres et al. (2006).

glomerular or aglomerular, solutes such as sodium, chloride, magnesium, and sulfates, which are absorbed from the surrounding environment, are actively transported from the blood into the initial segment of the proximal tubule of the nephron to be eliminated in the urine. Marine teleosts also have a functionally distinct latter section of the proximal segment for the recovery of water, some sodium and chloride, and glucose. There is no distal tubule segment in marine teleosts, so the urine passes from the proximal tubule through the collecting duct and into the bladder where additional sodium and chloride can be recovered if needed. In addition, the bladder of marine teleosts is permeable to water, unlike that of freshwater teleosts, providing an additional opportunity for water recovery. This is why marine teleosts can produce urine that is isotonic with their blood, whereas freshwater teleosts can only produce dilute urine.

Diadromous teleosts

Teleosts that migrate between fresh and salt water, such as salmonids, must make appropriate adjustments in the mitochondria-rich cells of the gill epithelium to physiologically adapt to the dramatic change in osmoregulatory environment. For example, as Arctic Char migrate from the ocean into rivers, the membrane proteins of the gill epithelial cells responsible for sodium–potassium exchange increase in abundance, and so do the plasma sodium concentration and blood osmolarity (Bystriansky et al. 2007). This apparently is the result of increased activity of the genetic and molecular mechanisms responsible for creating these proteins, and also provides evidence that this sodium–potassium exchange plays an important role in sodium uptake in freshwater fishes. Bystriansky et al. (2007) also note that there are apparently two forms of this sodium–potassium exchange

protein, one that excretes excess sodium from saltwater fishes and another that assists with sodium uptake in freshwater fishes.

Control of osmoregulation and excretion

Like many homeostatic functions, osmoregulation is controlled mainly by hormones. Some of these hormones act quickly to help fishes cope with rapid changes in the osmotic concentration of their environment by controlling the activity of existing cell membrane transporters or channels. Others act slowly and for longer time periods by regulating the synthesis of proteins that create the channels and transporters, and may also play a role in restructuring osmoregulatory tissues (see Takei & Loretz 2006). **Prolactin** appears to play a large role in adaptation to fresh water by decreasing the permeability of gill, kidney, bladder, and intestinal membranes to water and stimulating the uptake of sodium and chloride by the mitochondria-rich cells of the gills. **Cortisol**, a stress hormone, apparently assists with sodium and chloride uptake by freshwater fishes, and C-type natriuretic peptides seem to help with sodium uptake and retention in hypoosmotic environments.

Cortisol also plays an important role in saltwater adaptation, apparently by increasing the size and number of mitochondria-rich cells responsible for reducing levels of sodium and chloride in the blood and modifying the lining of the intestine to increase water absorption (Takei & Loretz 2006). Blood levels of cortisol increase when euryhaline fishes are transferred to salt water. Growth hormone also increases the size and number of chloride-transporting mitochondria-rich cells and enhances the activity of the enzymes associated with sodium–potassium exchange. It also enhances the expression of genes responsible for the protein involved in ion transport across epithelial cell membranes. **Vasopressin** (from the posterior pituitary) and **urotensins** (from the urophysis) may also play a role in osmoregulation, but the evidence is not conclusive. **Atrial natriuretic peptide** and related hormones appear to help with short-term adaptation to high salinity environments by inhibiting swallowing of salt water and reducing the uptake of sodium by the intestine. And although the specific function of the guanylins is unknown, the genes responsible for their production become activated when eels are transferred to salt water, suggesting a role in the transition of anguillid eels from a freshwater or estuarine juvenile to an ocean-dwelling, spawning adult (Takei & Loretz 2006).

pH balance

Like all animals, fishes must maintain blood and tissue pH within certain limits because many enzymes that control critical biochemical processes are pH sensitive. Low or high pH can alter the configuration of these molecules, inhibiting their function. Blood pH is largely affected by metabolic byproducts such as carbon dioxide, which forms carbonic acid when in solution, and organic acids such as lactic acid from anaerobic metabolism. Terrestrial vertebrates primarily regulate pH through altering their respiration rate to regulate the amount of carbon dioxide in their blood. Fishes cannot, however, effectively lower blood pH by increasing ventilation, in part due to the high solubility of carbon dioxide in water, and therefore must regulate pH in other ways (Claiborne et al. 2002; Marshall & Grosell 2006). Fishes instead rely on epithelial transport of ions that affect pH, such as hydrogen ions and bicarbonate ions, and the primary responsibility for this seems to fall on mitochondria-rich cells that typically are found in the gills, but also may occur in the skin of some fishes (Marshall & Grosell 2006).

Carbon dioxide from cellular metabolism is mainly carried by the blood in the form of bicarbonate ions, and some is converted back to dissolved carbon dioxide at the gills where it can easily diffuse into the surrounding water. Some of the mitochondria-rich cells in the gill epithelium also seem to have the ability to exchange bicarbonate ions for chloride ions (see Fig. 7.4B). In addition, excess hydrogen ions are exchanged for sodium ions, also by some of the mitochondria-rich cells (see Fig. 7.4C). Protein transporters designed for sodium/hydrogen ion exchange have been found on the gills of elasmobranchs, teleosts, and an agnathan (Claiborne et al. 2002). In addition, proteins that use ATP to actively transport hydrogen ions into the surrounding water may be important to pH regulation in freshwater teleosts and indirectly responsible for sodium uptake (the secretion of the hydrogen ions results in a charge imbalance, resulting in sodium entering the cells via sodium channels). These transport proteins have been found in the gills of marine elasmobranchs and teleosts, but do not seem to be as important as they are in freshwater fishes. Claiborne et al. (2002) review numerous studies in which the genetic and molecular mechanisms of the mitochondria-rich cells control the activity and abundance of the protein transporters to allow fishes to maintain relatively stable blood pH. Perry et al. (2003) provide additional examples, particularly with respect to freshwater fishes, and also point out that kidneys play a role by regulating the amount of bicarbonate ion excreted in the urine.

The immune system

The immune system plays an important role in homeostasis by maintaining animal health in both innate and adaptive ways (Rice & Arkoosh 2002). Innate mechanisms are found in agnathan and gnathostome fishes, and consist of immune factors that block invasion by potential pathogens. For

example, the external layer of skin and scales is a physical barrier to infectious organisms. In addition, the sticky, viscous consistency of the mucus secreted by fish epithelial cells probably helps to trap microorganisms, and the mucus can contain antibodies and chemicals that destroy or inhibit bacteria (Bernstein et al. 1997). The volume of mucus secreted may increase in stressful situations, indicating a response on the fish's part to shield itself from potentially harmful chemicals, microorganisms, or other agents. Other parts of the innate response include inducible phagocytic cells that can attack and destroy potential pathogens, cytotoxic cells that destroy cells infected by viruses, and the complement system of proteins that attack the membrane of invading cells (Rice & Arkoosh 2002).

The adaptive response, in contrast, involves the detection of an invader and the creation of specialized response mechanisms to identify and destroy it. This response has not been seen in agnathans, but is present in the gnathostomes (Bernstein et al. 1997). The organs primarily responsible for this response are the kidney, thymus, spleen, and gut.

The adaptive response includes both **cellular** and **humoral** components (Rice & Arkoosh 2002). The cellular component of the adaptive response includes **cytotoxic T cells** that can destroy cells that have become infected by viruses or that show signs of becoming cancerous. The humoral response involves the detection of specific invading compounds (antigens) and the production of antibodies designed to bind to them. These antibodies tag the antigenic particles for destruction by other components of the immune system, such as **macrophages** that engulf and digest the tagged antigens, or **complement proteins** that destroy tagged cells by puncturing their membranes. Antibody structure of the Chondrichthyes is somewhat similar to that of the higher bony fishes and mammals. The structures of the genes responsible for antibodies are quite different, however, with those of the bony fishes somewhat intermediate between those of the Chondrichthyes and those of mammals (Bernstein et al. 1997).

In mounting an antibody response, the immune system also produces **memory cells** that remain in the blood stream for extended periods (Rice & Arkoosh 2002). Memory cells help the animal's immune system react quickly if it encounters the same antigen in the future. Consequently, subsequent exposures to an antigen are dealt with quickly and the antigens are destroyed much more quickly than was the case during the initial exposure to that same antigen. Vaccinations, which have become important in fish culture, take advantage of memory cell development. By exposing fish to a less virulent form of a pathogen, the fish's immune system can defeat this initial infection and will retain memory cells to help it respond quickly and more effectively to subsequent exposures to a potentially more virulent form of the pathogen.

Stress

In a broad context, **stress** can be considered as a biological response that drives physiological systems outside their normal range. Fishes typically respond to short-term, or acute, stress by mechanisms designed to maintain physiological function by compensating for the stress for a while, and then when the stress passes the fish can return to its previous physiological state. If the stress is chronic (persists for a long period of time), however, it may result in a readjustment of physiological set-points and the establishment of a new baseline condition. This is sometimes referred to as **allostasis**, because rather than returning to its previous physiological state (homeostasis), the organism instead establishes a new baseline condition. This would include changes in gene expression that result in long-term alterations of proteins needed to maintain function under the new conditions (Iwama et al. 2006).

Physiological responses to stress typically occur in three phases (Barton et al. 2002; Iwama et al. 2006). The **primary response** is mainly the immediate release of epinephrine, followed by the release of **cortisol** in teleosts or **1α-hydroxycorticosterone** in elasmobranchs. Epinephrine release and the physiological responses that it initiates can occur in seconds, but do not persist for long. The release of cortisol and the reaction to it, however, begin more slowly and are sustained for a longer period of time. Together, these hormones activate biochemical pathways that lead to the secondary phase of the stress response, which is marked by elevated levels of blood glucose to support an increased metabolism. In addition to elevated blood glucose, the **secondary response** also is characterized by increased respiration rate, increased blood flow to the gills, and increased gill permeability (Barton et al. 2002). These increases help the fish to take in more oxygen to support elevated metabolism, but also increase the diffusion of water and ions across the gill epithelium, creating more osmoregulatory stress and demanding more active transport, and therefore energy, for the fish to maintain its osmotic balance.

Another part of the secondary response occurs at the cellular level – the induction of **stress proteins**. These are often called heat shock proteins (HSPs) because they were initially described as a response to elevated temperatures. However, they are now recognized as a general cellular-level response to many types of stress, including temperature, various types of pollution, handling, hypoxia, and pathogens. There are three general categories of stress proteins, based on their molecular weight, and they seem to help maintain the function of other proteins that are critical to cellular biochemical processes by protecting the shape of, helping repair, or helping control degradation of these other proteins. For example, the stress protein identified as HSP-90 apparently is important in protecting the function

of the cellular receptor for cortisol, which would help sustain the ability of the cell to respond to this important stress hormone (Iwama et al. 2006). Because stress proteins are a general response to many types of stress, they can be used as an indicator of a fish's exposure to a stressor, such as unfavorable environmental conditions.

If stress persists, the primary and secondary responses may lead to **tertiary responses** at the whole-animal or population level (Barton et al. 2002; Iwama et al. 2006). Persistent elevated levels of the stress hormones, especially cortisol, can negatively affect fish growth, condition factor (length^3/mass), reproduction, and behavior such as swimming stamina because energy that would have been available for these functions has been diverted to dealing with stress (see Chapter 5, Bioenergetic models).

Several factors can influence a fish's response to stress. These include sex, because the sex hormones themselves can affect the stress response, and the developmental stage of the individual, because juveniles and adults often will respond differently. A fish's nutritional state or whether it is affected by an existing stressor also can impact its response to subsequent stress (Barton et al. 2002). Responses to stress can also be seen at all levels of biological organization (Adams 2002; Hodson 2002). Short-term exposure to stressors can lead to changes at the subcellular level as a fish tries to compensate physiologically, but these effects may not have implications at higher levels of organization, such as the overall health of the organism or the status of the population.

Chronic stress can affect fish immune systems, in part because sustained elevated levels of cortisol can suppress immune function and thereby diminish disease resistance and ultimately survival. Experimentally induced stress designed to resemble the stress of capture significantly impacted the immune responses of Sablefish (*Anoplopoma fimbria*), so that those released as unwanted bycatch might have diminished capabilities to resist natural pathogens (Lupes et al. 2006). And Chinook Salmon smolts exposed to elevated levels of ammonia for 96 h had lowered counts of lymphocytes, which could lead to increased susceptibility to disease (Ackerman et al. 2006). Environmental contaminants may also negatively affect fish immune systems by compromising the protective barriers of skin and mucus, affecting organs that filter pathogens from the blood, and interfering with intercellular signaling. For example, juvenile salmon from Puget Sound, known for its elevated levels of various pollutants, were more susceptible to pathogens because their immune responses were suppressed, and English Sole may also be affected (see Rice & Arkoosh 2002).

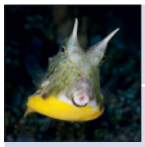
Chronic stress also may affect reproduction, and therefore population and community structure. A range of chemical contaminants have been identified as endocrine disrupting compounds (EDCs) because they interfere with some aspects of the hormonal signaling system that regulate the gonads and secondary sex characteristics (Greeley 2002). As more potential EDCs are identified in our surface waters, concern increases over the potential impacts on aquatic life, including fish populations (see Box 7.1).

Indicators of stress

Because chronic stress is not immediately lethal, it often goes undetected until its effects influence fish populations and community structure. Interest in the early detection of stress in fishes has led to increased study of **biomarkers**, which are cellular and subcellular indicators of environmental stress (Adams 2002). The principle behind the study of biomarkers is that stress can be detected at the subcellular and cellular level before it affects organismal or population health. Biomarkers, as well as biological indicators of stress at higher levels of biological organization, have been an active area of research.

Environmental stressors can result in the alteration of DNA and interfere with the molecular activity of some hormones (Hodson 2002; Filby et al. 2007). Exposure to many chemicals can result in increased levels of liver enzymes responsible for their detoxification and metabolism, and also the induction of stress proteins (discussed earlier). Therefore, levels of these biochemicals can be indicators of exposure to stress. Chronic stress can result in a variety of changes in cellular and tissue morphology in various organs, and biomarkers at this histopathological level are seen as good indicators because they show integrated, cumulative effects of physiological stress (Myers & Fournie 2002). Various biomarkers in the liver, spleen, skin, and musculoskeletal system seem to be the best supported by research thus far. The liver is the primary organ of contaminant detoxification, so it frequently shows signs of a fish dealing with environmental contaminants. The spleen also shows signs of environmental stress because of its important role in fish immune systems, as indicated by the presence of **macrophage aggregates**, also called melanomacrophage centers. These have been shown to be good biomarkers of multiple environmental stressors and also can be indicators of past exposure because they remain once they have formed and accumulate with age. Several studies have supported the use of splenic macrophage aggregates as indicators of environmental stress (Wolke et al. 1985; Blazer et al. 1987; Macchi et al. 1992; Blazer et al. 1994), and they may be able to show decreased stress in fish in areas that have undergone environmental improvement (Facey et al. 2005).

Through these and other biomarkers and bioindicators, it is becoming possible to detect stress from a variety of agents, thereby permitting early detection of potential impacts on fish physiology, health, growth, reproductive success, and community structure.



Summary

SUMMARY

1. Most long-term regulation of physiological processes in fishes is accomplished by the endocrine system. Many endocrine tissues are controlled by the pituitary, which is controlled by the hypothalamus of the brain. Physiological functions controlled by the endocrine system include osmoregulation, growth, metabolism, color changes, development and metamorphosis, and stress responses. Some environmental contaminants can disrupt hormonally regulated physiological functions, such as sexual differentiation, because their structure mimics that of naturally occurring hormones.
2. Involuntary physiological functions, such as heart rate, blood pressure, blood flow to the gills and gas bladder, and the contraction of the smooth muscles of the gut, are controlled by the autonomic nervous system.
3. Most fishes have body temperatures close to that of the water around them because of heat exchange at the gills. Some large pelagic predators, such as tunas and lamnid sharks, can maintain elevated body temperatures by conserving the heat generated in the active swimming muscles through countercurrent heat exchange. Billfishes use heat from special thermogenic tissue behind the eye to keep their eyes and brain warm while swimming in deep, cool water.
4. Seasonal changes in water temperature affect fish metabolism. Fishes can compensate for some change by altering the concentration or form of certain enzymes to maintain essential biochemical processes in cold conditions.
5. High water temperatures diminish the availability of oxygen in the water and can destroy physiologically important proteins such as hemoglobin and many enzymes. Hence, few fishes can survive warm water temperatures. The temperature of sea water in polar regions drops below the freezing point of the blood of most fishes. To avoid freezing, many polar fishes rely on supercooling or biological antifreeze compounds.
6. The large surface area of the highly permeable gill membrane allows for considerable exchange of water and ions between a fish's blood and the surrounding water. To maintain a fairly stable internal osmotic condition, freshwater bony fishes produce dilute urine and take up ions through mitochondria-rich cells in the gills. Saltwater bony fishes must drink sea water to replace water lost by diffusion, and they also must eliminate excess ions through their kidneys and the mitochondria-rich cells of the gill epithelium. Elasmobranchs gain water by diffusion due to high levels of urea and TMAO in their blood.
7. Osmoregulation in fishes is controlled by several hormones, including urotensins, cortisol, prolactin, and the catecholamines (epinephrine and norepinephrine).
8. Most fishes eliminate nitrogenous wastes at their gills in the form of ammonia or ammonium. Fishes also produce urea, which is excreted in the urine. Kidney structure in fishes does not permit the concentration of urine to exceed the concentration of the blood plasma.
9. A fish's immune system acts to prevent the entry of pathogens, or to destroy them if they do enter the body. The proper functioning of this system can be compromised by stress, such as that caused by handling or environmental factors including certain contaminants.
10. Stress from environmental factors also can result in a thicker mucus layer on a fish's gills, thereby inhibiting gas exchange, and cause a variety of other physiological impacts that can affect long-term energy balance and fish health.

Supplementary reading

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Chapter 8

Functional morphology of locomotion and feeding

Chapter contents

CHAPTER CONTENTS

> Structure without function is a corpse and function without structure is a ghost.
>
> Vogel and Wainwright (1969, p. 93)

Structure and function are inseparable. In the preceding five chapters, we have characterized the anatomy of fishes and described the function of various physiological systems. Such anatomical and physiological descriptions only make evolutionary sense when we understand their function, and function has not been ignored in the preceding introductory material. But structure–function relationships deserve more in-depth exploration. The study of how parts operate and how environmental selection pressures have influenced their construction and operation is variously referred to as functional morphology, physiological ecology, ecomorphology, and ecological physiology. These closely interrelated topics draw heavily on many disciplines besides anatomy and physiology, including physics, biomechanics, biochemistry, ultrastructure, structural engineering, developmental biology, population ecology, behavior, paleontology, and of course evolution. Our goals in this chapter are to further explore the anatomical and physiological challenges that arise from living in water, and to bring together and expand upon the subject matter introduced in the preceding chapters. We will focus on two general tasks in this chapter – locomotion and feeding – for examples of the intimacy and intricacy of structure and function; additional discussions that emphasize functional morphology can be found in several other chapters (e.g., Chapters 9, 18–20). We can only literally skim the surface of this fascinating, interdisciplinary topic and we strongly encourage interested readers to pursue the additional and more detailed information available in the cited references and suggested readings at the end of the chapter.

Locomotion: movement and shape

> . . . the gap between the swimming fish and the scientists is closing, but the fish is still well ahead.
>
> Lindsey (1978, p. 8)

Body shape and locomotory behavior in fishes are determined by the extreme density of water. Locomotory adaptations in terrestrial and flying animals strongly reflect a need to overcome gravity. Body and appendage shape in fishes in contrast reflects little influence of gravity because gas bladders or lipid-containing structures make most fishes neutrally buoyant (see Chapter 5, Buoyancy regulation). Fish locomotion is more constrained by the density of water and the drag exerted by it (Videler 1993).

Water is about 800 times more dense and 50 times more viscous than air. Locomotion through this dense, viscous medium is energetically expensive, a problem exacerbated by the 95% reduction in oxygen-carrying capacity of water as compared to air (see Chapter 5, Water as a respiratory environment). The chief cause of added energetic cost is

drag, which has two components, **viscous or frictional drag** involving friction between the fish's body and the surrounding water, and **inertial or pressure drag** caused by pressure differences that result from displacement of water as the fish moves through it. Viscous drag is not affected greatly by speed but more by the smoothness of a surface and by the amount of surface area, which is linked to body and fin shape; production of mucus reduces viscous drag. Inertial drag increases with speed and is therefore also intimately linked to body shape. Most fast-swimming fishes have a classic streamlined shape that minimizes both inertial and viscous drag. A streamlined body is round in cross-section and has a maximum width equal to 25% of its length. The width : length ratio is 0.26 in some pelagic sharks, 0.24 in swordfish, and 0.28 in tunas. The thickest portion of a streamlined body occurs about two-fifths of the way back from the anterior end, another rule followed by large pelagic predators. Interestingly, these same streamlined fishes are also slightly negatively buoyant and hence sink if they cease swimming. They often have winglike pectoral fins that are extended laterally at a positive attack angle, thus generating lift (except sharks, see below). They minimize drag by retracting paired and median fins into depressions or even grooves in the body surface; a sailfish houses its greatly expanded dorsal fin "sail" in a groove on its dorsal surface during fast swimming (Hertel 1966; Hildebrand 1982; Pough et al. 2001).

Most fishes swim by contracting a series of muscles on one side of the body and relaxing muscles on the other. The muscle blocks, called **myomeres**, attach to collagenous septa which in turn attach to the backbone and skin (Fig. 8.1). Depending on the swimming form involved (see below), contractions may progress from the head to the tail or occur on one side and then the other. The result of the contractions is that the fish's body segments push back on the water. Given Newton's Third Law of Motion concerning equal and opposite forces, this pushing back produces an opposite reactive force which thrusts the fish forward. Forward thrust results from combined forces pushing forward and laterally; the lateral component is cancelled by a rigid head and by median fins and in some cases by a deep body that resists lateral displacement.

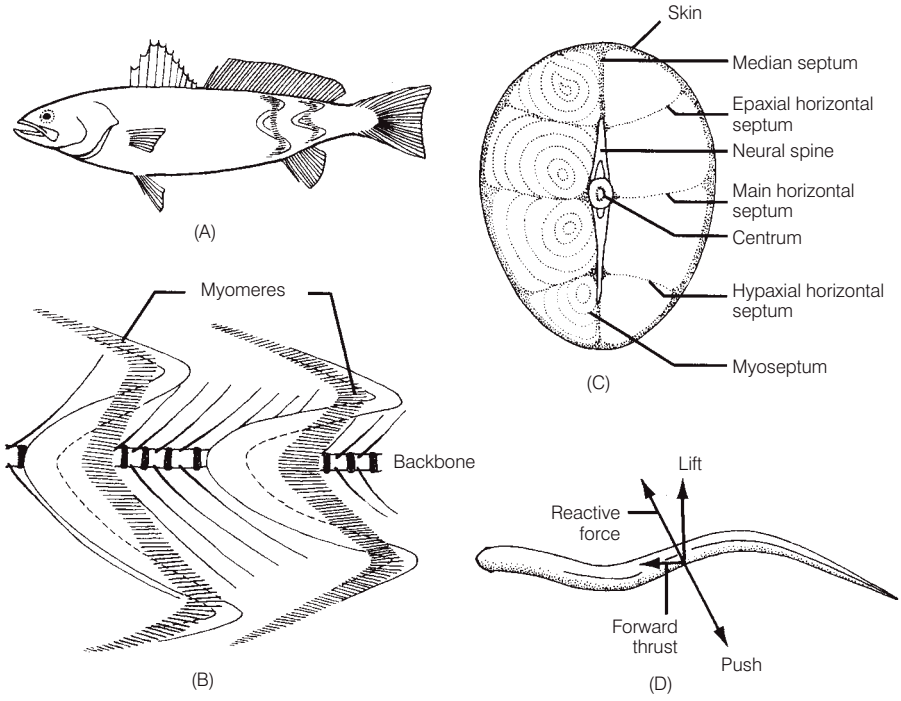


Figure 8.1

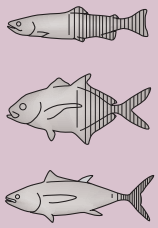
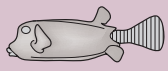
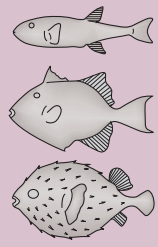
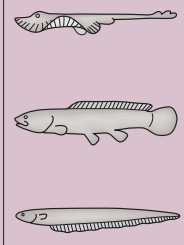
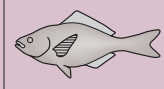
The anatomy of swimming in teleosts. (A) Lateral view of a Spotted Sea Trout, *Cynoscion nebulosus*, with the skin dissected away to show the location of two myomeres on the left side. (B) The same myomeres as they appear relative to the backbone in a sea trout. The hatched region is the part of the myomere located closest to the skin, the dashed line shows the interior portion of the myomere where it attaches to the vertebral column. The anterior and posterior surface of each myomere is covered by a myoseptum made of collagen fiber in a gel matrix, shown as a slightly thickened line. (C) Cross-section of a generalized teleost near the tail, showing the distribution of the various septa and their relationship to the backbone. Myosepta join to form median and horizontal septa. (D) How contractions produce swimming in a generalized fish (an eel is shown here). Progressive, tailward passage of a wave of contractions from the head to the tail **push** back on the water, generating **forward thrust** as one component of the **reactive force**. Sideways slippage (**lift**) is overcome by the inertia of the large surface area presented by the fish's head and body. After Wainwright (1983) and Pough et al. (1989).

Locomotory types

A general classification of swimming modes or types among fishes has been developed, building on the work of Breder (1926), Gray (1968), Lindsey (1978), and Webb (1984; Webb & Blake 1985). The chief characteristics of the different types are how much of and which parts of the body are involved in propulsion and whether the body or the fins undulate or oscillate. **Undulation** involves sinusoidal waves passing down the body or a fin or fins; **oscillation** involves a structure that moves back and forth (Table 8.1). About one dozen general types are recognized: anguilliform,

Table 8.1

Form, function, and locomotion in fishes. About 12 generalized types of swimming are recognized among fishes. The body part or fin providing propulsion is indicated by cross-hatching; the density of shading denotes relative contribution to propulsion. These locomotory patterns correlate strongly with body shape, habitat, feeding ecology, and social behavior. Convergence among unrelated fishes in terms of body morphology, swimming, and ecology demonstrates the evolutionary interplay of form and function. See Lindsey (1978), Beamish (1978), Webb and Blake (1985), and Pough et al. (2001) for details. Line drawings from Lindsey (1978); used with permission.

	Swimming type					
	Via trunk and tail			Via fins		
		Via tail				
	Anguilliform	Subcarangiform[a] Carangiform Thunniform	Ostraciiform	Tetraodontiform Balistiform Diodontiform[b]	Rajiform[b] Amiiform Gymnotiform	Labriform[c]
						
Representative taxa	Eels, some sharks, many larvae	Salmon, jacks, mako shark, tuna	Boxfish, mormyrs, torpedo ray	Triggerfish, ocean sunfish, porcupinefish	Rays, Bowfin, knifefishes	Wrasses, surfperch
Propulsive force	Most of body	Posterior half of body	Caudal region	Median fin(s)	Pectorals, median fins	Pectoral fins
Propulsive form	Undulation	Undulation	Oscillation	Oscillation[d]	Undulation	Oscillation
Wavelength	0.5 to >1 wavelength	<1 (usually <0.5) wavelength			>>1 wavelength	
Maximum speed bl/s	Slow-moderate 2	Very fast – moderate 10–20	Slow?	Slow?	Slow to moderate 0.5	Slow 4
Body shape: lateral view cross-section	Elongate Round	Fusiform Round	Variable	Variable Often deep	Elongate Often flat	Variable
Caudal fin aspect ratio	Small Medium to low	Medium to large Low to high	Large Low	Small to medium Low	Variable Low	Large Low
Habitat	Benthic or suprabenthic	Pelagic, wc, schooling	Variable	wc	Suprabenthic	structure associated

bl/s, body lengths per second attainable; wc, up in water column.

[a] In subcarangiform types (salmons, cods) the posterior half of the body is used, carangiform swimmers (jacks, herrings) use the posterior third, and thunniform or modified carangiform swimmers (tunas, mako sharks) use mostly the caudal peduncle and tail (see text).

[b] Rajiforms (skates, rays) swim with undulating pectoral fins, amiiforms (Bowfin) undulate the dorsal fin, and gymnotiform swimmers (South American knifefishes, featherfins) undulate the anal fin.

[c] Labriform swimmers use the pectorals for slow swimming, but use the subcarangiform or carangiform mode for fast swimming.

[d] Balistiform and diodontiform swimming is intermediate between oscillation and undulation; porcupinefishes also use their pectoral fins.

subcarangiform, carangiform, modified carangiform (= thunniform), ostraciiform, tetraodontiform, balistiform, rajiform, amiiform, gymnotiform, and labriform; some of these are additionally subdivided. The names apply to the basic swimming mode of particular orders and families, although unrelated taxa may display the same mode, and many fish use different modes at different velocities.

The first four types involve sinusoidal undulations of the body. **Anguilliform** swimming, seen in most eels, dogfishes, other elongate sharks, and many larvae occurs in fishes with very flexible bodies that are bent into at least one-half of a sine wave when photographed from the dorsal view (Table 8.1). All but the head contributes to the propulsive force (Muller et al. 2001). As a wave proceeds posteriorly it increases in amplitude. The speed (frequency) of the wave remains constant as it passes down the body and always exceeds the speed of forward movement of the fish because of drag and because of energy lost to reactive forces that are not directed forward (see above). To swim faster, faster waves must be produced. Anguilliform swimmers are comparatively slow because of their relatively long bodies and involvement of anterior regions in propulsion; the same segments that push back on the water also waste energy by pushing laterally and also create drag because water pushes on these bent sections as the fish moves forward. Anguilliform swimming has its compensating advantages, including a greater ability to move through dense vegetation and sediments and to swim backwards (D'Aout & Aerts 1999). Anguilliform swimming in larval fishes, including such species as herrings that use carangiform swimming as adults, probably occurs because the skeleton of early larvae is unossified and the fish is exceedingly flexible and anatomically constrained from employing other modes (see Chapter 9, Larval behavior and physiology).

To get around the self-braking inherent during anguilliform swimming, faster swimming fishes involve only posterior segments of the body in wave generation, using ligaments to transfer force from anterior body musculature to the caudal region. The progression of types from **subcarangiform** (trout, cod) through **carangiform** (jacks, herrings) to **modified carangiform** or **thunniform** (mackerel sharks, billfishes, tunas) entails increasing involvement of the tail and decreasing involvement of the anterior body in swimming. One major advance in the carangiform and thunniform swimmers is the existence of a functional hinge that connects the tail to the caudal peduncle. This hinged coupling allows the fish to maintain its tail at an ideal attack angle of 10–20° through much of the power stroke. In anguilliform and subcarangiform swimmers, this angle changes constantly as the tail sweeps back and forth, producing less thrust at low angles and creating more drag at greater angles.

Thunniform swimmers also typically have a tail that originates from a narrow peduncle (= **narrow necking**) that is often dorsoventrally depressed and may even have lateral keels that streamline it during side-to-side motion. Narrow necking creates an overall more streamlined shape to the body and also reduces viscous drag and lateral resistance in a region of the body where they tend to be highest. The tail itself is stiff and sickle-shaped, being very narrow while quite tall. A tail with such a large height : width ratio, referred to as a **high aspect ratio** tail, experiences minimal drag and is ideal for sustained swimming: the shape reduces viscous drag by reducing surface area and reduces inertial drag by having pointed tips which produce minimal vortices at their tips. The efficiency of the system is increased by tendons that run around joints in the peduncle region and insert on the tail, the joints serving as pulleys that increase the pulling power of the muscle–tendon network. The thunniform mode of propulsion, involving a streamlined shape, narrow necked and keeled peduncle, and high aspect ratio tail, has evolved convergently in several fast-swimming, pelagic predators, including mackerel sharks, tunas, and billfishes, as well as porpoises and dolphins and the extinct reptilian ichthyosaurs. The fish and mammalian groups at least are also endothermic to some degree (Lighthill 1969; Lindsey 1978; Pough et al. 2001). Higher speed, sustained swimming in the mackerel sharks and tunas is also made possible by the large masses of red muscle along the fish's sides (see Chapter 4, White muscle versus red muscle). Location of the red muscle close to the fish's spine allows the body to remain fairly rigid and also permits the retention of heat generated by muscle contraction. Hence thunniform swimming and endothermy are tightly linked.

Low aspect ratio, broad, flexible tails, such as those found in subcarangiform minnows, salmons, pikes, cods, and barracudas are better suited for rapid acceleration from a dead start and can also aid during hovering by passing undulations down their posterior edge. Intrinsic muscles associated with the tail in low aspect ratio species help control its shape. Rainbow Trout are able to increase the depth and hence produce a higher aspect ratio tail during high-speed swimming. **Fast start** predators, such as gars, pikes, and barracudas, hover in the water column and then dart rapidly at prey. These unrelated fishes have converged on a body shape that concentrates the propulsive elements in the posterior portion of the body: the dorsal and anal fins are large and placed far to the posterior, the caudal peduncle is deep, and the tail has a relatively high aspect ratio. Maximum thrust from a high-amplitude wave concentrated in the tail region allows for rapid acceleration from a standing start (see Fig. 19.1).

Ostraciiform swimming, as seen in boxfishes and torpedo rays, is extreme in that only the tail is moved back and forth while the body is held rigid; the side-to-side movement of the tail is more an oscillation than an undulation. In the weakly electric elephantfishes, body muscles pull on tendons that run back around bones in the caudal peduncle region and insert on the tail, causing the fish to swim with jerky

tail beats. Such an arrangement is thunniform in anatomy but more ostraciiform in function. Weakly electric fishes, such as the elephantfishes and South American knifefishes mentioned below, often have devices for keeping their bodies straight while swimming. This relative inflexibility probably minimizes distortion of the electric field they create around themselves (see Chapter 6, Electroreception).

Ostraciid boxfishes carry this type of swimming to its extreme, having a rigid dermal covering that extends back to the peduncle area. Although a rigid, boxlike body propelled by a caudal fin seems an ungainly, even unlikely, means of getting around a coral reef, these active swimmers are elegantly constructed for dealing with water that flows past their bodies as they move or encounter currents. The flat surfaces and angular shelves and projections of the boxlike carapace generate vortices that counteract pitching and yawing that result from water flow, without active correction by fins, tail, or gas bladder. In fact, all of the "unfish-like" morphological features of the boxfish's box contribute to hydrodynamic stability (Bartol et al. 2005) (Fig. 8.2).

The last five swimming types employ median and paired fins rather than body–tail couplings. **Tetraodontiform** and **balistiform** swimmers (triggerfishes, ocean sunfishes) flap their dorsal and anal fins synchronously; their narrow-based, long, pointed fins function like wings and generate lift (forward thrust) continuously, not just during half of each oscillation. **Rajiform** swimmers hover and move slowly via multiple undulations that pass backwards or forwards along the pectoral fins of skates and rays; in **amiiform** swimmers, undulations pass along the dorsal fin (Bowfin, African osteoglossomorph *Gymnarchus*, seahorses), whereas in **gymnotiform** swimming, undulations pass along the anal fin (South American and African knifefishes or featherfins). Rajiform and related swimming modes are slow but allow for precise hovering, maneuvering, and backing. The frequency with which waves pass along a fin can be very high, reaching 70 Hz in the dorsal fin of seahorses. **Labriform** swimmers (chimaeras, surfperches, wrasses, parrotfishes, surgeonfishes) row their pectoral fins, pushing back with the broad blade, then feathering it in the recovery phase. As some negative lift is generated during the recovery phase, these fish often give the impression of bouncing slightly as they move through the water. If rapid acceleration or sustained fast swimming is needed, labriform swimmers, as well as many other fin-based locomotors, shift to carangiform locomotion.

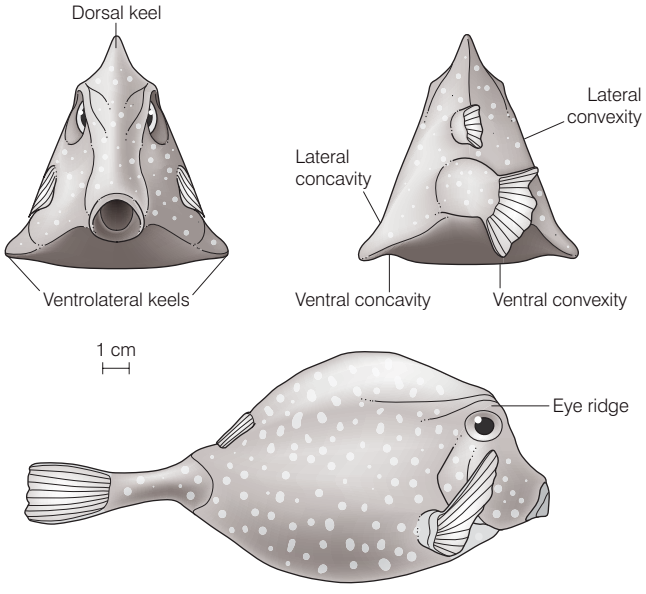


Figure 8.2
Anterior, posterior, and lateral views of a Smooth Trunkfish *Lactophrys triqueter*, showing its unusual body shape and protrusions, all which aid in hydrodynamics. After Bartol et al. (2003).

Three final aspects of locomotory types deserve mention. First, the distinctiveness of the different locomotory types suggests that they are specializations, and specialization for one function usually produces compromises in other functions. Fishes that specialize in efficient slow swimming or precise maneuvering usually employ undulating or oscillating median fins. The long fin bases necessary for such propulsion (e.g., Bowfin, knifefishes, pipefishes, cutlassfishes) require a long body, which evolves at a cost in high-speed, steady swimming. Low-speed maneuverability can also be achieved with a highly compressed (laterally flattened), short body that facilitates pivoting, as found in many fishes that live in geometrically complex environments such as coral reefs or vegetation beds (e.g., freshwater sunfishes, angelfishes, butterflyfishes, cichlids, surfperches, rabbitfishes; see Drucker & Lauder 2001). These fishes typically have expanded median and paired fins that are distributed around the center of mass of the body and can act independently to achieve precise, transient thrusts, a useful ability when feeding on attached algae or on invertebrates that are hiding in cracks and crevices. But a short, compressed body means reduced muscle mass and poor streamlining, whereas large fins increase drag. Again, such fishes achieve maneuverability but sacrifice rapid starts and sustained cruising. Relatively poor fast-start performance may be compensated for by deep bodies and stiff spines, which make these fishes difficult to swallow (see Chapter 20, Discouraging capture and handling); they also typically live close to shelter. At the other extreme, thunniform swimmers have streamlined bodies, large anterior muscle masses, and stiff pectoral and caudal fins that are extremely hydrodynamic foils. They trade-off exceptional cruising ability against an inability to maneuver at slow speeds. Although specialists among body types can be identified, optimal design for one trait – sustained cruising, rapid acceleration, or maneuverability – tends to reduce ability in the other traits. Because most fishes must cruise to get from place to place, must accelerate and maneuver to eat and avoid being

eaten, "the majority of fishes are locomotor generalists rather than locomotor specialists" (Webb 1984, p. 82).

Second, this generalist strategy means that few fishes use only one swimming mode. Many fishes switch between modes depending on whether fast or slow swimming or hovering is needed. In addition, most fishes have median fins that can be erected or depressed, adding a dynamic quality to their locomotion. A Largemouth Bass can erect its first dorsal and anal fins to gain thrust during a fast-start attack, then depress these fins while chasing a prey fish to reduce drag, then erect them to aid in rapid maneuvering. Most groups, with the exception of the thunniform swimmers, are capable of hovering in midwater by sculling with their pectoral fins or by passing waves vertically along the caudal fin. When hovering, some forward thrust is generated by water exhaled from the opercles; this force is countered by pectoral sculling. The fin movement involved in hovering may be difficult to detect, both by human observers and potential prey, because fishes that use these techniques often possess transparent pectoral fins.

Third, not all fishes fit neatly into one of these categories, and many additional categories can and have been erected to accommodate variations among taxa (see Lindsey 1978, Webb & Blake 1985, Videler 1993, and Blake 2004 for more complete and alternative categorizations, and see below on sharks).

Specialized locomotion

Among the more interesting variations on locomotory type are fishes that have abandoned swimming for other means of getting around. A number of species walk along the bottom of the sea or leave the water and move about on land; these fishes have bodies that depart from a streamlined shape. Searobins (Triglidae) move lightly across sand bottoms using modified pectoral rays that extend out from the fin webs. They give the appearance of someone tiptoeing on many moving fingers; dactylopterid flying gurnards similarly tiptoe but use modified pelvic rays instead. Antennarioid frogfishes and batfishes pull themselves along the bottom by moving their modified pectoral and pelvic fins; their forward motion is aided by jet propulsion of water out their backward-facing, constricted opercles (Pietsch & Grobecker 1987). Australian handfishes (Brachionichthyidae), which get their common name because their pectoral fins are modified into an armlike appendage with an elbow and fingers, also use pectoral and pelvic fins to walk (Bruce et al. 1998).

Fishes are not restricted to spending all their time in water, and some actually move about on land (Sayer 2005). Terrestrial locomotion is accomplished in a variety of ways. Climbing perches use paired fins and spiny gill covers to ratchet themselves along, whereas snakeheads row with their pectoral fins. So-called "walking catfishes" move across land by lateral body flexion combined with pivoting on their stout, erect pectoral spines. Mudskippers swing their pectoral fins forward while supporting their body on the pelvic fins. They then push forward with their pectoral fins, like a person on crutches. Rapid leaps of 30–40 cm are accomplished by coordinated pushing of the tail and pectoral fins. Their unique pectoral fins are roughly convergent with the forelimbs of tetrapods, including an upper arm consisting of a rigid platelike region and a fanlike forearm and plantar surface (Gray 1968). Some species with anguilliform movement (moray and anguillid eels) are able to move across wet land employing their normal locomotion, which is analogous to the "serpentiform" terrestrial and aquatic movements of most snakes (Chave & Randall 1971; Lindsey 1978; Ellerby et al. 2001).

Aerial locomotion grades from occasional jumping to gliding to actual flapping flight. Many fishes jump to catch airborne prey (trout, Largemouth Bass); meter-long arawanas (Osteoglossidae) can leap more than a body length upward and pluck insects and larger prey, including bats, from overhanging vegetation. Other fishes take advantage of the greater speeds achievable in air: needlefishes, mackerels, and tunas leave the water in a flat trajectory when chasing prey, and salmon leap clear of the water when moving through rapids or up waterfalls. Hooked fish jump and simultaneously shake their heads from side to side in an attempt to throw the hook; such oscillation is less constrained by drag in air than in water and therefore allows more rapid and forceful to-and-fro movement. Prey such as minnows, halfbeaks, silversides, mullets, and Bluefish jump when being chased.

Fishes capable of flight include gliders such as the exocoetid flyingfishes and pantodontid butterflyfishes, as well as gasteropelicid hatchetfishes, which purportedly vibrate their pectoral wings to generate additional lift (Davenport 1994; see Chapter 20, Evading pursuit). The anatomy of the marine flyingfishes is highly modified for flying. The body is almost rectangular in cross-section, the flattened ventral side of the rectangle providing a planning surface that may aid during take-off. The ventral lobe of the caudal fin is 10–15% larger in surface area than the dorsal lobe and is the only part of the body in contact with the water during taxiing. The pectoral fins are supported by enlarged pectoral girdles and musculature. The pectoral fins differ from normal teleost fins in the shape of and connections between the lepidotrichia, and the pectoral fin rays are thickened and stiffened, giving the leading, trailing, dorsal, and ventral surfaces more of a winglike than a finlike construction. In some flyingfishes, pelvic fins also contribute lift and are appropriately modified.

Some other atheriniform fishes such as needlefishes and halfbeaks also propel themselves above the water's surface by rapidly vibrating their tail, the lower lobe of which is the only part still in the water. Some halfbeaks have relatively large pectoral fins and engage in gliding flight. Gradations of pectoral fin length and lower caudal lobe strengthening

and lengthening among atheriniforms provide a good example of apparent steps in the evolution of a specialized trait, namely flying (Lindsey 1978; Davenport 1994).

Swimming in sharks: the alternative approach

Different fish lineages have evolved a variety of solutions to the challenges of locomotion in water. In the process, mutually exclusive specializations for cruising, rapid starts, or maneuverability have arisen (see above). The fossil record indicates that similar body morphologies and an apparent trend toward increasing concentration of activity in the tail region have appeared repeatedly during osteichthyan evolution (Webb 1982; see Chapter 11). These patterns and trends all capitalize on the substantial stresses that can be placed on a rigid, bony skeleton and the forces achievable by muscle masses attached directly or indirectly to bony structures. Elasmobranchs are, however, phylogenetically constrained by a relatively flexible and comparatively soft cartilaginous skeleton. Evolution of locomotion in chondrichthyans has, not surprisingly, taken a different albeit parallel path.

Most elasmobranches swim via undulations, either of the body (sharks) or of the pectoral fins (skates and rays). Most sharks swim using anguilliform locomotion, although the amplitude of each wave in the caudal region is greater in swimming sharks than in eels. This exaggerated sweep of the posterior region probably capitalizes on the increased thrust available from the large heterocercal tail of a shark. Exceptions to anguilliform swimming include the pelagic, predatory mackerel sharks, which have converged in body form and swimming type with tunas, dolphins, and ichthyosaurs (see above). Skates and rays also undulate, passing undulations posteriorly along the pectoral fins while the body is held relatively rigid. The exception in this group is the torpedo rays, which differ in that they have an expanded tail fin and swim via ostraciiform oscillations. In these strongly electrogenic rays, the pectoral region is unavailable for swimming because it is modified for generating electricity.

The mechanics of swimming in sharks are fascinating and somewhat controversial. Three topics have received the most attention, involving the functions of the median fins, skin, and tail during locomotion. Despite anguilliform movement, most sharks are active, cruising predators with relatively streamlined bodies. This would seem anomalous given the relatively low efficiency of the anguilliform mode and the apparent incompatibility of a fusiform body bent into long propulsive waves. However, sharks enhance the efficiency of their swimming mode in several ways.

Most sharks have two dorsal fins, the first usually larger than the second, separated by a considerable gap. The dorsal lobe of the pronounced heterocercal tail may be thought of as a third median fin in line with the dorsal fins, again separated from the second fin by a considerable gap. The distances between the three fins are apparently determined by the size of the fins, their shapes, and the waveform of swimming of the fish. Each fin tapers posteriorly, leaving behind it a wake as it moves through the water. This wake is displaced laterally by the sinusoidal waves passing down the fish, so the wake itself follows a sinusoidal path that moves posteriorly as the fish moves through the water. This wave is slightly out of phase with the fish's movements by a constant amount.

Calculations of the phase difference and wave nature of the wake suggest an ideal distance between fins that would maximize the thrust of the second dorsal fin and particularly of the tail. If timed correctly, the trailing fins can push against water coming toward them laterally from the leading fins. Such an interaction between flows would enhance the thrust produced by the trailing fin. Measurements of swimming motions and fin spacing in six species of sharks indicate just such an interaction (Webb & Keyes 1982; Webb 1984). Unlike bony fishes that use their median fins primarily for acceleration and braking but fold them while cruising to reduce drag, sharks use their median fins as additional, interacting thrusters. Sharks are not alone in this interaction among fins. Recent studies on bluegill sunfish indicate that the caudal fin also interacts with the vortices produced by the soft dorsal during steady swimming, thus providing additional thrust (Drucker & Lauder 2001).

The energy provided with each propulsive wave of muscular contraction is additionally aided by an interaction between the skin and the body musculature of a shark. The skin includes an inner sheath, the stratum compactum, made up of multiple layers of collagen fibers that are mechanically similar to tendons. The fibers form layers of alternately oriented sheets that run in helical paths around the shark's body, thus creating a cylinder reinforced with wound fibers, an exceptionally strong and incompressible – but readily bendable – structure (Motta 1977; Wainwright 1988b).

Inside the skin, hydrostatic pressure varies as a function of activity level. The faster the shark swims, the higher the internal hydrostatic pressure. Pressure during fast swimming is about 10 times what it is during slow swimming, ranging between 20 and 200 kPa (kilopascals: 1 Pa = 1 J/m^3 = 1 kg/m/s^2). Internal hydrostatic pressure develops from unknown sources, probably due to changes in the surface area of contracting muscles relative to skin area and to changes in blood pressure in blood sinuses that are surrounded by muscle. The shark's body is therefore a pressurized cylinder with an elastic covering.

During swimming, the higher the internal pressure, the stiffer the skin becomes, which increases the energy stored in the stretched skin. Body muscles attach via collagenous septa not just to the vertebral column but also to the inside of the skin (for this reason, it is exceptionally difficult to

remove the skin from the muscle of a shark). As the muscles on the right side of the body contract, muscles and skin on the left side are stretched. The stretched skin is very elastic, but stretched muscle is less so. As muscles on the right side relax, the energy stored in the skin on the left side is released, aiding muscles on the left side at a point when they can provide relatively little tension. Therefore, the skin may act in initiating the pull of the tail across the midline and increase the power output at the beginning of the propulsive stroke.

The faster the shark swims, the greater the elastic recoil from the stretched skin. Muscles attach to the relatively narrow vertebral column of calcified cartilage but also attach to the much larger surface area of stiff, elastic skin that encompasses the shark from head to tail and in essence forms a large, cylindrical, external tendon. The helically arranged fibers of the dermis extend onto the caudal peduncle and caudal fin, adding rigidity to both and perhaps storing elastic energy during each swimming stroke (Lingham-Soliar 2005). Muscles pulling on the skin provide propulsive energy that probably exceeds the thrust derived from muscles attached to the vertebral column (Wainwright et al. 1978; Wainwright 1983).

Most of the power in shark swimming comes from the tail, but this tail is not symmetrical as it is in most bony fishes. The heterocercal tail, with its expanded upper lobe, would seem to provide a lifting force to the posterior end of the body during horizontal locomotion. This lift should cause the body to rotate around its center of mass, plunging the anterior end in a perpetual dive (Fig. 8.3). One long-held explanation is that the flat underside of the head and the broad stiff pectoral fins create lift at the anterior end to counteract the downward force. However, it seems inefficient for the tail and the pectoral fins to function against each other, the tail propelling and the pectoral fins continually braking the shark's progress. Given the 400-million-year success of elasmobranchs and the widespread occurrence of heterocercal tails in many previously speciose lineages of both bony and cartilaginous fishes, it is hard to imagine that heterocercal tails are inherently inefficient. This apparent dilemma has prompted an ongoing search for mechanisms that promote relatively straightforward propulsion.

The search has turned into something of a debate. The classic model, as described above, proposes that the tail pushes back and down, creating a reactive force that causes rotation around the center of mass that is countered by head shape and pectoral fins. An alternative explanation, based on interpretations of photographs and selective amputation of fin parts of tails held in a test apparatus (Simons 1970; Thomson 1976, 1990), suggests that forward thrust is generated through the center of mass by differential movements of the upper and lower lobes of the tail (Fig. 8.3B). The classic model appears to be the most accurate description and is supported by video analysis (such as digital particle image velocimetry) and dye-tracer studies

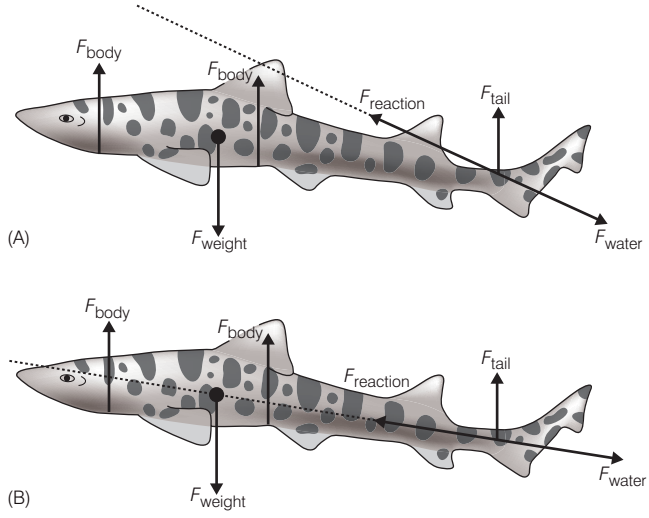


Figure 8.3

The two competing models that explain how horizontal locomotion is accomplished in sharks. (A) The modified classic model interprets the shape of the heterocercal tail as generating a downward and backwards thrust (F_{water}), lifting the tail up (F_{tail}); these produce a resultant force ($F_{reaction}$) that moves the body upwards and forwards. The flattened ventral profile of anterior body regions also provides lift (F_{body}). $F_{reaction}$ plus F_{body} counter the shark's tendency to sink because of its negative buoyancy (F_{weight}). The result is horizontal swimming. (B) In the alternative Thomson model, the upper and lower lobes of the tail provide counteracting forces that drive the fish directly ahead. The most recent research supports the modified classic model. However, the alternative model appears to explain locomotion dynamics in sturgeons, which also have heterocercal tails but which – unlike sharks – vary the flexibility and shape of dorsal and ventral tail lobes (Liao & Lauder 2000). After Wilga and Lauder (2002).

using free-swimming animals (Ferry & Lauder 1996). The classic model has been modified because shape and body angle, not pectoral lift, generate lift forces that are added to the lift exerted by the tail (Wilga & Lauder 2002). These forces are equal and opposite to the weight of the shark in the water. Braking by the pectoral fins is unnecessary.

The answer to how sharks climb, dive, and turn – rather than pivoting around their center of balance or rising in the water column – probably lies in their ability to continually adjust the relative angle of attack of their pectoral fins rather than altering thrust direction resulting from tail movement (Wilga & Lauder 2002). Maneuverability in bony fishes usually involves deep, compressed bodies and the use of median and pectoral fins; to accelerate, bony fishes increase the frequency of their tail beats. Sharks, with their streamlined bodies and relatively rigid fins, have taken a different evolutionary path to achieve maneuverability that may involve tail fin dynamics and paired fin adjustments. Sharks change speed by altering tail beat frequency, but they also vary tail beat amplitude and the length of the propulsive wave passing down their body (Webb & Keyes 1982). Sharks have taken the relatively inefficient anguilli-

form swimming mode imposed by their flexible bodies, and combined elastic skin, rigid but carefully spaced median fins, and a heterocercal tail that produces a constant direction of thrust to achieve an efficient compromise between cruising, acceleration, and maneuverability. The actual mechanics of swimming in sharks and bony fishes is still a matter of debate and research, but our growing understanding underscores the intricacies and importance of locomotory adaptations in fishes.

Feeding: biting, sucking, chewing, and swallowing

Adaptations concerned with feeding clearly involve structures used in food acquisition and processing, such as jaw bones and muscles, teeth, gill rakers, and the digestive system. Less obvious, but also important, are morphological adaptations in eye placement and function, body shape, locomotory patterns, pigmentation, and lures. The functional morphology of feeding deserves detailed exploration because of its intimate linkage to all aspects of fish evolution and biology.

For many fishes, a simple glance at jaw morphology, dentition type, and body shape allows accurate prediction of what a fish eats and how it catches its prey. Small fishes with fairly streamlined and compressed bodies, forked tails, limited dentition, and protrusible mouths that form a circle when open are in all likelihood zooplanktivores. This generalization holds for fishes as diverse as osteoglossiform mooneyes, clupeomorph herrings, ostariophysine minnows, and representative acanthopterygian groupers (e.g., *Anthias*), snappers (*Caesio*), bonnetmouths (*Inermia*), damselfishes (*Chromis*), and wrasses (*Clepticus*). Large, elongate fishes with long jaws studded with sharp teeth for holding prey, and with broad tails adjoined by large dorsal and anal fins set far back on a round body are piscivores that ambush their prey from midwater with a sudden lunge (see Chapter 19). An alternative piscivorous morphology includes a more robust, deeper body, with fins distributed around the body's outline, and a large mouth with small teeth for short chases and engulfing prey; this is the "bass" morphology of many acanthopterygian predators such as kelp basses, Striped Bass, seabasses, black basses, and Peacock Bass, all in different families.

Generalized body shapes in predators do not exclude highly successful specialists that have arrived at very different solutions to catching mobile prey. Examples include lie-in-wait and luring predators (goosefishes, frogfishes, scorpionfishes, stonefishes, flatheads, death-feigning cichlids), cursorial predators that run down their prey (needlefishes, Bluefish, jacks, mackerels, billfishes), electrogenic predators that shock prey into immobility (torpedo rays, electric eels), or fishes with either an elongate anterior or posterior region for slashing and incapacitating prey (thresher sharks, sawfishes, billfishes).

A strong correspondence between morphology and predictable foraging habits exists in most other trophic categories, including herbivores (browsers, grazers, phytoplanktivores), scavengers, mobile invertebrate feeders, sessile invertebrate feeders, and nocturnal planktivores, to name a few. Convergent solutions to similar selection pressures are a striking characteristic of the foraging biology of fishes (Keast & Webb 1966; Webb 1982).

Our emphasis here will be on the functional morphology of structures directly responsible for engulfing and processing food. Moderate detail is provided, but we can only superficially discuss the diversity in structure, action, and interconnection among the 30 moving bony elements and more than 50 muscles that make up the head region of most fishes.

Jaw protrusion: the great leap forward

Jaws evolved in fishes. The major difference between vertebrates and invertebrates is not so much the development of an ossified and constricted backbone; coelacanths, lungfishes, and sturgeons all lack distinct vertebral centra. The real advance that undoubtedly drove vertebrate evolution was the assembly of closable jaws used in feeding. The mechanics of jaw function and adaptive variation in jaw elements tell us a great deal about both how fishes feed and how fishes evolved.

As will be discussed in Chapter 11, one of the major advances made by, but not exclusive to, higher teleosts is the ability to protrude the upper jaw during feeding. Jaw protrusion makes possible the **pipette mouth** of the higher teleosts. Pipetting creates suction forces that can pull items from as far away as 25–50% of head length. Jaw protrusion also functions to overtake a prey item, extending the food-getting apparatus around the prey faster than the predator can move its entire body through the water. Attack velocity may thus be increased by up to 40%. As many as 15 different functions and advantages have been postulated for the protrusible jaw of teleosts. These advantages generally involve increased prey capture ability and efficiency but also suggest that antipredator surveillance and escape ability may be enhanced (Lauder & Liem 1981; Motta 1984; Ferry-Graham & Lauder 2001).

The elements involved in jaw protrusion include the bones of the jaw (premaxilla, maxilla, mandible), ligamentous connections of these bones to the skull and to each other (premaxilla to maxilla, ethmoid, and rostrum; maxilla to mandible, palatine, and suspensorium; mandible to suspensorium), and several muscles, notably the expaxials, levator operculi, hypaxials, adductor mandibulae, and levator arcus palatini (Fig. 8.4).

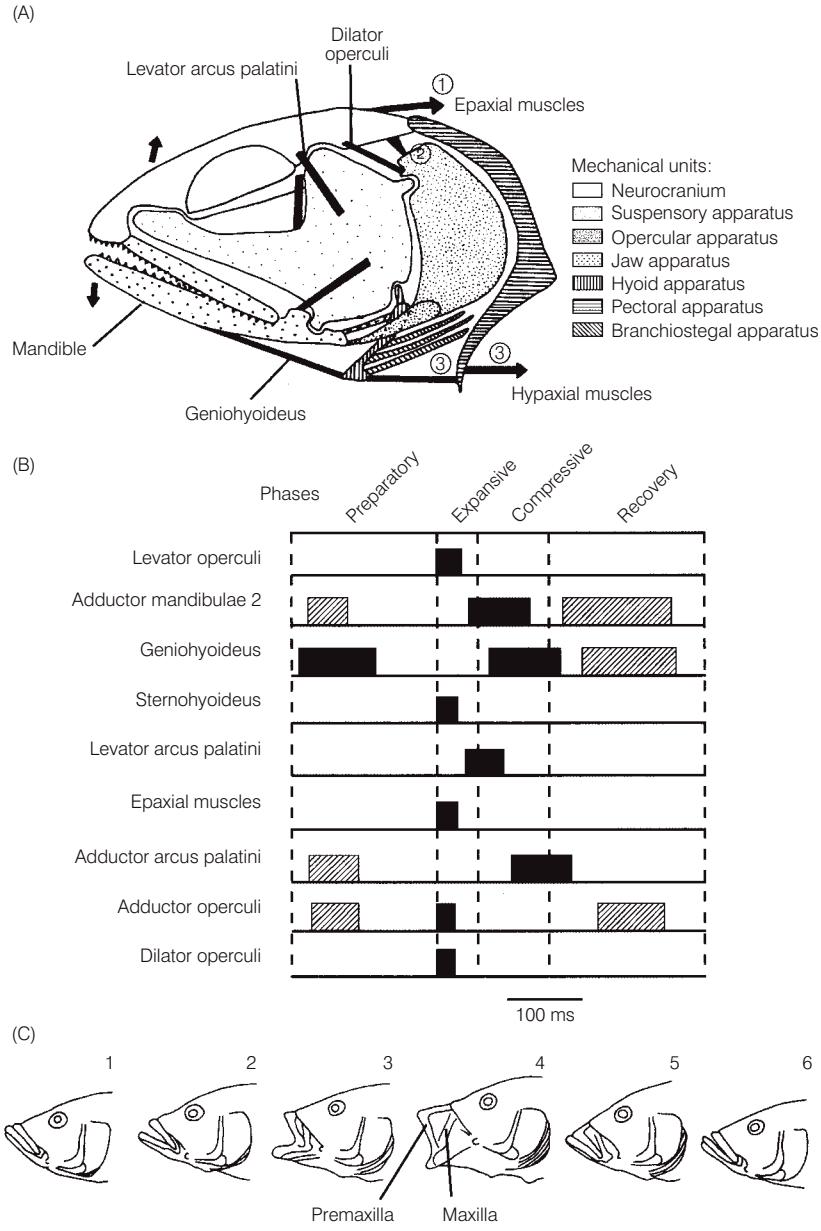


Figure 8.4

Opening, protrusion, and closing of the jaw in most percoids. (A) Jaw opening involves three major couplings of muscles, ligaments, and bones: 1, epaxial muscles that lift the cranium; 2, levator operculi muscles that move the opercular bones up and out and help depress the mandible; and 3, hypaxial muscles that depress the mandible via actions of the hyoid apparatus. (B) Electrical activity of different muscles groups as measured during four phases of jaw opening and closing. Blackened bars represent major muscle activity, cross-hatched bars indicate occasional activity. Abductors move bones outward, adductors move bones inward. (C) The sequence of events during the opening and closing of the jaw of a cichlid, *Serranochromis*: 1, preparatory; 2–4, expansion; 5–6, compression. (A, B) slightly adapted from Lauder (1985); (C) from Lauder (1985), after Liem (1978), used with permission.

During jaw protrusion, the entire jaw moves forward and slightly up or down. Protrusion in a generalized percomorph occurs as the cranium is lifted by the epaxial muscles and the lower jaw is depressed by muscles associated with the opercular and hyoid bone series. Movement of the mandible causes the maxillary to pivot forward, the suspensorium (the hinge joint that suspends the lower jaw from the cranium) contributing to maxillary rotation. The descending process of the premaxilla is connected to the lower edge of the maxilla, so the premaxilla is pushed forward, its ascending process sliding forward and down the rostrum. The jaw is closed through the actions of the adductor mandibulae muscle on the mandible, the levator arcus palatini on the suspensorium, and the geniohyoideus on the hyoid apparatus. Many variations on this simplified description exist, differing among taxa in terms of twisting of jaw bones, points of attachment and pivot between structures, inclusion of other small bony elements, and actions of muscles and ligaments on particular elements (Motta 1984).

Jaw protrusion creates rapid water flow that carries edible particles, both small and large, into the fish's mouth. Suction velocity increases from 0 m/s to as much as 12 m/s in as little as 0.02–0.03 s (Osse & Muller 1980; Ferry-Graham et al. 2003). Fishes that feed on such different prey as phytoplankton, zooplankton, macroinvertebrates, and other fishes utilize suction to capture prey; the larger the object, the more suction pressure must be pro-

duced to capture it. Suction feeding, also known as **inertial suction**, results from rapid expansion of the buccal (mouth) cavity, which creates negative pressure in the mouth relative to the pressure outside the mouth. Particles in the water mass ahead of the fish are carried into the mouth along with the water. The jaws then close, pushing the water out the gill covers but retaining the prey in the mouth. Gill rakers, jaw teeth, and teeth on various non-marginal jaw bones (palate, vomer, tongue) act to mechanically prevent escape from the opercular chamber.

Suction pressures vary during a feeding event in advanced percomophs, increasing and decreasing four times. The four phases of suction feeding are preparation, expansion, compression, and recovery (Lauder 1983a, 1985).

1. During **preparation**, as the fish approaches its prey, pressure in the buccal cavity increases as a result of inward squeezing of the suspensorium and lifting of the mouth floor.
2. The **expansion** phase is when maximal suction pressure develops; the mouth is opened to full gape via lower jaw depression, premaxillary protrusion, and expansion of suspensory, opercular, and mouth floor (hyoid) units. Expansion is the shortest phase during jaw activity, requiring only 5 ms in some anglerfishes. The negative pressures generated during expansion can reach –800 cmH_2O (0.7 atm) in the Bluegill Sunfish, approaching the physical limits imposed by fluid mechanics. Such rapidly achieved low pressure causes cavitation, which involves water vapor suddenly coming out of solution and forming small vapor-filled cavities (the bubbles produced behind an accelerating boat propeller result from cavitation) (Lauder 1983a). The popping noise made during feeding by Bluegill may result from the collapse of cavitation bubbles.
3. The **compression** phase occurs and pressure increases as the mouth is closed by reversing the movements of cranial bones, an activity that requires contraction of a different set of muscles (Fig. 8.4C). The opercular and branchiostegal valves at the back of the head open up after the jaws close, which allows water but not prey to flow out of the buccal and opercular cavities.
4. **Recovery** involves a return of bones, muscles, and water pressure to their pre-preparatory positions.

Modifications of this basic plan underscore some rather spectacular derivations that allow specialized feeding activities. In cichlids, the suspensorium and maxilla are mechanically decoupled. Jaw protrusion occurs as a result of movement of the suspensorium, independent of the maxilla. The consequence of this decoupling of suspensorium and maxilla is that the jaw can be protruded via four different pathways: lifting the neurocranium, abducting the suspensorium, lowering the mandible, or swinging the maxilla. Cichlids make use of different combinations of jaw elements and protrusion pathways to feed on different prey types or in different habitats (e.g., Waltzek & Wainwright 2003; Hulsey & De Leon 2005). High-speed motion picture analysis of jaw action indicates that some cichlids may use eight different feeding patterns in which they vary their gape, biting force, and amount of jaw protrusion depending on the prey type, location, and behavior. The cichlid jaw is the closest that fishes have come to a prehensile feeding tool. Cichlids show a diversity of foraging types unequaled in any other fish family (Goldschmidt 1996; see Chapter 15). It is likely that the derived trait of a decoupled suspensorium and the resulting trophic versatility have contributed greatly to their success (Liem 1978; Lauder 1981; Motta 1984; Liem & Wake 1985).

Fishes other than cichlids have reworked the basic elements of jaw protrusion and have evolved dramatic specializations that increase attack velocity or suction. As mentioned in Chapter 11, the Pikehead, *Luciocephalus pulcher*, shoots its jaw out, increasing its attack speed from 1.3 to 1.8 m/s. Little suction is generated during a strike. Extreme and rapid jaw protrusion in this species involves modified anterior vertebrae and massive epaxial muscles and tendons that run from the vertebrae to the posterior part of the cranium. Upward flexion of the head, made possible by a highly bendable neck, leads to extreme jaw protrusion. Other predators have converged on analogous neck-bending abilities to increase prey capture efficiency, including a characin and two cyprinids (Lauder & Liem 1981).

In most fishes, suction pressure is produced via expansion of the buccal cavity. A generalized perciform such as the Yellow Perch increases its mouth cavity volume by a factor of six, creating a negative pressure capable of supporting a water column about 15 cm high. The apparent record for volume increase is held by a small (30 cm long), bizarre, elongate midwater fish, *Stylophorus chordatus*. *Stylophorus*, among its other oddities, has a tubular mouth and a membranous pouch that stretches dorsally from its mouth to its braincase. During feeding, the fish throws its head back and thrusts its tubular mouth forward. The mouth becomes separated from the braincase by a distance of about 1 cm, the intervening space being filled by the now expanded membranous pouch. Mouth volume increases almost 40-fold, creating pressures three times greater than in the generalized perch. The fish engulfs copepods as water rushes in at a calculated velocity of 3.2 m/s, from as far away as 2 cm (Pietsch 1978).

Another extreme of jaw protrusion occurs in the tropical Sling-jaw Wrasse, *Epibulus insidiator* (Westneat & Wainwright 1989). Sling-jaws protrude their jaws up to 65% of their unextended head length, which is twice the extension found in any other fish (Fig. 8.5). This extreme protrusion is accomplished via a major reworking of many jaw elements. Several bones in the Sling-jaw's head have unique sizes and shapes, including the quadrate, interopercle, premaxilla, and mandible. Ligaments connecting these

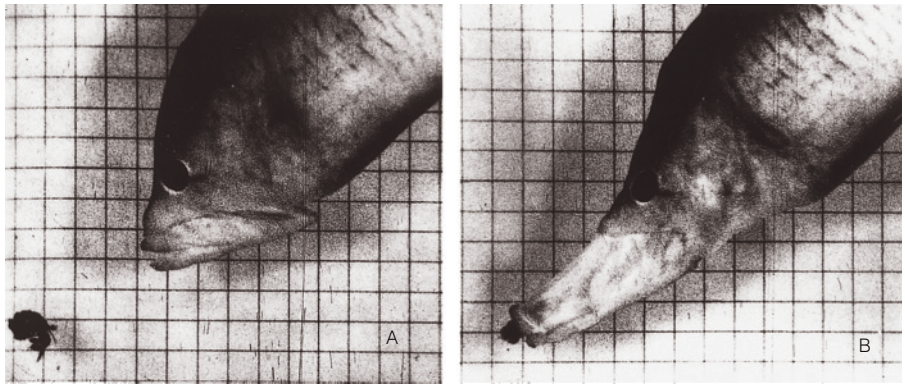


Figure 8.5

Extreme jaw protrusion in the Sling-jaw Wrasse, *Epibulus insidiator*. The Sling-jaw has novel bone shapes, extreme bone and ligament rotations, and has even invented a new ligament involved in jaw protrusion. (A) A 15 cm-long wrasse approaches its crustacean prey with its mouth in the retracted condition. Note that the posterior extension of the lower jaw, involving the articular and angular bones, extends as far back as the insertion of the pectoral fin. (B) During prey capture, the wrasse protrudes both its upper and lower jaws forward, extending them a distance equal to 65% of its head length. Jaw expansion creates suction forces that draw the prey into the mouth. Positions (A) and (B) are separated by about 0.03 s. From Westneat and Wainwright (1989), used with permission.

bones are unusually large, and a ligament found in no other fish links the vomer to the interopercle. The modified bones undergo extreme and in some cases unique rotations during jaw protrusion: the lower jaw actually moves forward during protrusion, a departure from the depression movement seen in all other fishes. The Sling-jaw shoots its mouth out at small fishes and crustaceans on coral reef surfaces, suctioning them into its mouth. It achieves a strike velocity of 2.3 m/s, but all of this speed is contributed by the jaw because the fish hovers almost still in the water while attacking prey. Extreme jaw protrusion in Sling-jaws involves the evolution of unique bones and ligaments, but the muscles of the jaw and skull have shapes, functions, and sequences of activity that differ little from generalized perciforms. Novel jaw function is therefore accomplished by drastic modification of some structures and the retention of primitive condition in others. The Sling-jaw exemplifies a widely made observation about the evolutionary process, that every species represents a mosaic of ancestral and derived traits.

Suction feeding has evolved repeatedly during fish evolution and occurs in many non-teleosts as well as in primitive and specialized teleosts that are unable to protrude their jaws. Elasmobranchs, including skates, rays, and such sharks as nurse and horn sharks, can generate suction forces as strong as –760 mmHg for feeding on buried mollusks or lobsters in reef crevices (Tanaka 1973; Motta & Wilga 1999, 2001). Lungfishes and Bowfin among non-teleosts, and anguillid eels, salmons, pickerels, and triggerfishes among teleosts do not protrude their jaws but use inertial suction for feeding; sturgeons have independently evolved jaw protrusion and suction feeding. Suction in the non-protruding species is often accomplished by rapid depression of the floor of the mouth. Triggerfishes and other tetraodontiform fishes such as boxfishes can reverse this flow and forcefully expel water from their mouths (Frazer et al. 1991). Alternate blowing and sucking is used to manipulate food items in the mouth during repositioning for biting. Blowing is also used for uncovering invertebrate prey buried in sand or for manipulating well-defended prey items. A Red Sea triggerfish, *Balistes fuscus*, feeds on long-spined sea urchins. The only spine-free region of the urchin is the oral disk around the mouth. Triggerfishes swim up to an urchin sitting on sand and blow a powerful jet of water at the urchin's base. The water stream lifts the urchin off the substrate and rolls it over, at which point the triggerfish bites through the now-exposed oral disk, killing the urchin (Fricke 1973). Triggerfishes also use blowing to uncover buried prey such as sanddollars. Blowing involves compression of the mouth via actions of muscles associated with the opercular, mandibular, and hyoid bones (Frazer et al. 1991; Turingan & Wainwright 1993).

Pharyngeal jaws

Depression of the mouth floor also creates water flow towards the throat, thereby helping push food items posteriorly. Here the prey encounter a second set of jaws, the **pharyngeal apparatus** (see Chapter 11, Division Teleostei). Pharyngeal jaws evolved from modified gill arches and their associated muscles and ligaments. The lower pharyngeal jaws are derived from the paired fifth ceratobranchial bones, whereas the upper jaws consist of dermal plates attached to the posterior epibranchial and pharyngobranchial bones. Both jaws bear teeth that vary depending on the food type of the fish (see below). Dentition not only varies functionally among species that eat different food types, but may develop differently among individuals of a

population as a function of the food types encountered by the growing fish. In the Cuatro Cienegas Cichlid of Mexico, *Cichlasoma minckleyi*, fish that feed on plants develop small pappiliform pharyngeal dentition, whereas those that feed on snails develop robust molariform dentition (Kornfield & Taylor 1983).

In their simplest action, pharyngeal jaws help rake prey into the esophagus. They may additionally reposition prey, immobilize it, or actually crush and disarticulate it. These actions involve at least five different sets of bones and muscles working in concert, including 10 different muscle groups and bones of the skull, hyoid region, lower jaw, pharynx, operculum, and pectoral girdle. The main action is the synchronous occlusion (coming together) of the upper and lower pharyngeal jaws. In cichlids, prey is crushed between the anterior teeth of both pharyngeal jaws, pushed posteriorly by posterior movement of both jaws, and then bitten by the teeth of the posterior region of the jaws (Lauder 1983a, 1983b, 1985).

Pharyngeal pads and their function as jaws influence feeding in another important manner. **Gape limitation**, the constraint on prey size imposed by mouth size (see Box 19.2), is in part determined by oral jaw dimensions: a fish can't eat anything it can't get into its mouth. But gape limitation is also influenced by pharyngeal gape. If a prey item is too large to pass through the pharyngeal jaws, it is also unavailable to the predator. Hence many predators can capture but not swallow a prey item because of pharyngeal gape limitation. In small-mouthed species, such as the Bluegill Sunfish, oral and pharyngeal gape differ only by 20–30%. But in piscivores that use oral protrusion for prey capture, such as the Largemouth Bass, oral jaws may be twice the size of the pharyngeal jaws, which means that usable prey size is considerably smaller than that which can be engulfed by the mouth. Posterior to the pharyngeal jaws is the throat, the width of which is determined by spacing between the cleithral bones of the pectoral girdles. Thus a predator can only eat prey that can pass through its oral jaws, pharyngeal jaws, and intercleithral space (Lawrence 1957; Wainwright & Richard 1995).

A crucial function of the pharyngeal apparatus in many species is therefore to crush prey to a size small enough to pass through the throat. Here prey morphology comes into play, because prey that is just small enough to fit between the pads may be too hard to crush and is thus unavailable to the predator. This interplay of structure, function, and the constraints created by the pharyngeal apparatus is shown nicely in Caribbean wrasses that feed on hard-bodied prey (Wainwright 1987, 1988a). Wrasses, along with other "pharyngognath" fishes such as parrotfishes and cichlids, have a highly modified pharyngeal apparatus that can crush hard-bodied prey. The size of the muscles that move the pharyngeal jaws differs among three species, the Clown Wrasse (*Halichoeres maculipinna*), Slippery Dick (*H. bivittatus*), and Yellowhead Wrasse (*H. garnoti*). In all three species, muscle mass and pharyngeal gape increase with

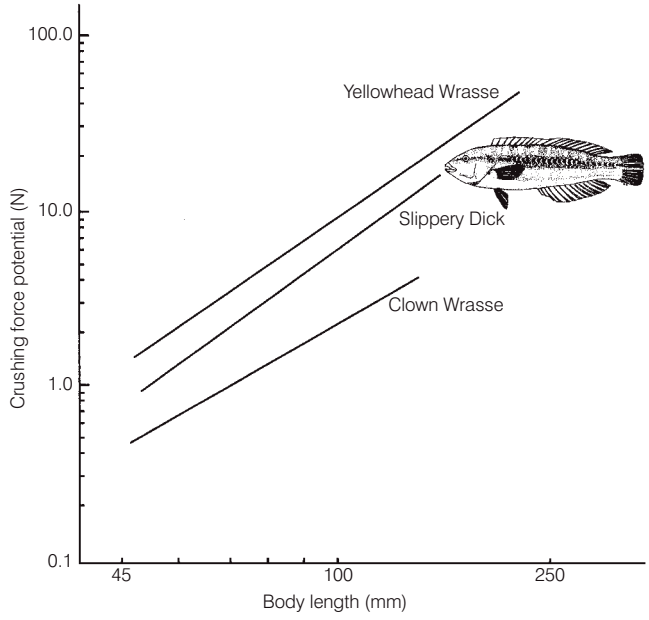


Figure 8.6

Crushing ability of the pharyngeal jaws in three related wrasses as a function of body size. Larger wrasses can crush larger snails because of their stronger pharyngeal jaws, and differences among species also influence preferred food types. Clown Wrasses have relatively weak jaws and feed on relatively soft-bodied prey, particularly when the fish are younger. Slippery Dicks and Yellowhead Wrasses have strong jaws and feed on shelled prey throughout their lives. After Wainwright 1988a; fish drawing from Gilligan (1989).

increasing body size (Fig. 8.6). At any size, Clown Wrasses have smaller pharyngeal musculature than the other two species. Small Slippery Dicks and Yellowhead Wrasses can crush and eat snails that are unavailable to larger clown wrasses. Small Clown Wrasses cannot crush even small snails. These abilities are reflected in the natural feeding preferences of the species. Small clown wrasses feed preferentially on relatively soft-bodied crabs and other invertebrates; they shift to snails only after attaining a body length of 11 cm, when they eat hard-bodied prey that are smaller than those taken by equal-sized fishes of the other two species. Slippery Dicks and Yellowhead Wrasses feed extensively on snails beginning at a relatively small fish body length of 7 cm. Pharyngeal crushing strength accounts for inter- and intraspecific differences in feeding habits in these fishes; competitive interactions and optimal prey characteristics other than shell strength have little if any influence.

As is so often the case in evolution, an adaptation opens up opportunities that become selection pressures favoring additional innovations. In moray eels, a remarkable modification of the pharyngeal jaws occurs. Morays develop weak suction pressures in the mouth cavity, which limits the rearward pushing of prey, as mentioned earlier. This is additionally complicated by the crevices and other tight

places where morays often feed, which constrains jaw movements that would normally aid in swallowing. Morays have "solved" this dilemma by developing raptorial pharyngeal jaws. The upper, pharyngobranchial arch and the lower, ceratobranchial arch are equipped with sharp, highly recurved teeth not unlike those in the oral jaws. In the resting position, the pharyngeal apparatus sits far back in the throat, behind the skull. But when prey are grasped by the oral jaws, a series of muscles project the pharyngeal jaws far forward into the oral cavity, these jaws then grasp the prey and retract back, pulling the prey toward the esophagus (Mehta & Wainwright 2007).

Dentition

The prey a fish eats and how those prey are captured are often predictable from the type of teeth the fish possesses. Even within families, species differ considerably in their dentition types as a function of food type and foraging mode (e.g., butterflyfishes (Motta 1988), cichlids (Fryer & Iles 1972), surgeonfishes (Jones 1968)). Here we focus on general groups of foragers and how their dentition corresponds to food type.

Piscivores and feeders on other soft-bodied, mobile prey such as squid show five basic patterns of marginal (= oral or jaw) teeth:

1. **Long, slender, sharp** teeth usually function to hold fish (mako, sandtiger, and angel sharks, moray eels, deepsea viperfishes, lancetfishes, anglerfishes, goosefishes). In some groups (e.g., goosefishes, anglerfishes; also esocid pikes), elongate dentition is repeated on the palatine or vomerine bones. These medial teeth point backwards and may have ligamentous connections at their base, which allows them to be depressed as the prey is moved toward the throat but prevents escape back through the anterior jaws.
2. Numerous small, needlelike, **villiform** teeth occur in elongate, surface-dwelling predators such as gars and needlefishes, as well as in more benthic predators such as lizardfishes and lionfishes.
3. Flat-bladed, pointed, **triangular** dentition is usually used for cutting off prey and is found in such fishes as requiem sharks, piranhas, barracudas, and large Spanish mackerels. Piranhas have teeth that are remarkably convergent in shape with those of many sharks (Fig. 8.7). In sharks, the lateral margins of bladelike teeth are often serrated, which enhances their cutting function when the head is shaken or the jaws are opened and closed repeatedly. Sharks and piranhas, as well as other characins, have also converged on **replacement dentition**. Tooth replacement, regardless of dentition type, has evolved repeatedly and independently among bony fishes, occurring in brachiopterygian bichirs, amiiforms, lepisosteid gars, and most teleostean superorders and orders, including osteoglossomorphs, elopomorphs, protacanthopterygians, ostariophysans, paracanthopterygians, and numerous acanthopterygians (Roberts 1967; Trapani 2001; Hilton & Bemis 2005).
4. Recurved, conical, **caniniform** teeth with sharp points characterize such piscivores as Bowfin, cod, snappers, and some seabasses. Sharp, conical dentition serves to grasp and hold. It reaches its extreme form in the almost triangular, fanglike, slightly flattened teeth of the African Tigerfish, *Hydrocynus*.
5. Surprisingly, many highly predaceous piscivores have limited marginal **cardiform** dentition that has a rough sandpaper texture and consists of numerous, short, fine, pointed teeth (e.g., large seabasses, snook, Largemouth Bass, billfishes). The former species rely on large, protrusible mouths for engulfing prey fishes, whereas billfishes immobilize their prey by slashing or stabbing with the bill (see Box 19.1).

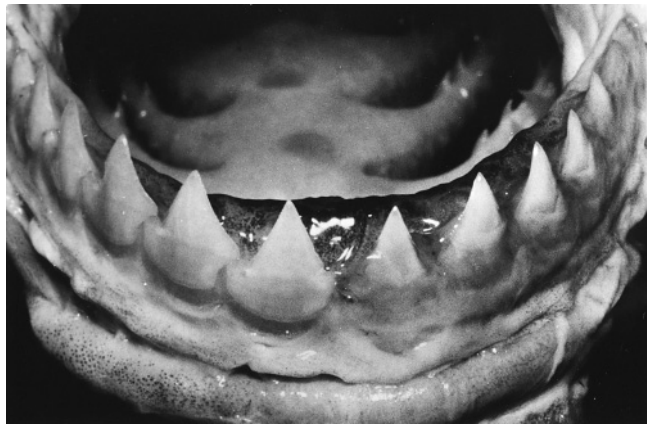


Figure 8.7
Convergence in dentition among predatory fishes. The triangular, razor-sharp teeth of a piranha, *Pygocentrus nattereri*, are remarkably similar in shape and action to those of many sharks. Note the small lateral cusps at the base of the teeth, a feature also shared with many sharks. Piranhas also replace their teeth as do sharks, but piranhas alternately replace all teeth in the left or right half of a jaw, rather than replacing individual teeth or rows of teeth. The teeth in the left side of the jaw (= right side of photo) have recently erupted. From Sazima and Machado (1990), used with permission.

Often, a predator will have a mixture of dentition types, such as anterior canines followed by or intermixed with smaller, needlelike teeth (e.g., the Pike Characin *Hepsetus*), or long canines intermixed with smaller conical teeth (e.g., some wrasses). Ultimately, and regardless of location in the mouth and whether teeth are of one or several types, primary dentition type reflects food characteristics. The primary biting teeth of ariid marine catfishes are palatine

Figure 8.8

Fishes that feed on hard-bodied prey crush their prey with molariform teeth located far back in their mouths, but often have different tooth types in different parts of the jaw. In the Wolf-eel, *Anarrhichthys ocellatus*, caninelike anterior jaw teeth grasp prey and molariform teeth farther back in the marginal jaws crush the prey. Photo by G. Helfman.

not marginal in location. Among 10 Australian species, piscivores have sharp, recurved palatine teeth, worm feeders have small, sharp, recurved palatine teeth, and molluskivores have globular, truncated palatine teeth (Blaber et al. 1994).

Fishes that feed on hard-bodied prey, such as mollusks, crabs, and sea urchins, often have teeth and jaw characteristics that represent a separation of the activities of capturing versus processing prey. Many such fishes have strong conical dentition in the anterior part of their jaws for plucking mollusks from surfaces. The prey are then passed posteriorly to flattened or rounded, **molariform** teeth located posteriorly in marginal or pharyngeal jaws. Convergence is apparent when comparing mollusk-eating fishes from different taxa, such as horn sharks and wolf-eels. Horn sharks (*Heterodontus*) have small conical teeth anteriorly, which grade posteriorly into broad, rounded pads for crushing and grinding (see Fig. 12.11). Wolf-eels have strong, conical canines anteriorly and rows of rounded molars posteriorly in each jaw (Fig. 8.8). Similar anterior–posterior differences occur in Freshwater Drum, Sheepshead, cichlids, and wrasses.

A suction versus chewing arrangement occurs in many fishes that feed on sand-dwelling mollusks. Suckers such as the river redhorse, *Moxostoma carinatum*, are ostariophysans in which the molarlike teeth occur on the pharyngeal arches. In ostariophysans, only the lower arch develops dentition, and these teeth usually occlude against horny pads in the roof of the mouth. In higher teleosts, the pharyngeal teeth are composed of both dorsal and ventral pharyngeal arch derivatives, such as in cichlids and the Redear or "shellcracker" Sunfish, *Lepomis microlophus*. Analogously, stingrays suction mollusks off the bottom and then crush them in pavementlike dentition. Fishes that remove attached invertebrate prey (such as sponges, ascidians, coelenterates, and chitons) from surfaces tend to have powerful oral jaws with incisorlike dentition (e.g., triggerfishes) or with teeth fused into a parrotlike beak (e.g., parrotfishes, pufferfishes). In parrotfishes, the beak bites off algae or pieces of coral that are then passed to the pharyngeal mill for grinding.

Another means of dealing with both soft- and hard-bodied prey has arisen in some sharks such as the hemiscylliid bamboo sharks. These sharks have the classic sharp, spiky teeth expected of a feeder on soft-bodied prey such as fish and squid. However, when feeding on harder items such as crabs, ligaments at the base of each tooth allow it to hinge backward, overlapping the replacement tooth that sits immediately behind it in the jaw. The multiple rows of depressed teeth then form a functionally flat surface more appropriate for crushing hard prey. The teeth spring back up after a bite is taken (Ramsay & Wilga 2007; see also Summers 2006).

In addition to marginal, medial, and pharyngeal teeth, fishes have one other mouth region where hard structures aid in the capture or retention of prey. These are the **gill rakers**, which are bony or cartilaginous projections that point inwards and forwards from the inner face of each gill arch. As with the various teeth, gill raker morphology corresponds quite closely to dietary habits. Piscivores and molluskivores, such as seabasses, black basses, and many sunfishes, tend to have short, widely spaced gill rakers that prevent the escape of large prey out the gill openings. Fishes that eat zooplankton of large and intermediate size, such as the Bluegill Sunfish and Black Crappie, have longer, thinner, and more numerous rakers. Feeders on small zooplankton, phytoplankton, and suspended matter have the longest, thinnest, and most numerous rakers; menhaden, *Brevoortia* spp., filter phytoplankton, detritus, and small zooplankters and have >150 rakers just on the lower limb of each gill arch. Among related species, gill rakers differ according to diet. In North American whitefishes (Coregoninae), the Inconnu (*Stenodus leucichthys*) feeds on small fishes and has 19–24 rakers, the Shortnose Cisco (*Coregonus reighardi*) feeds on mysid shrimp, amphipods, and small clams and has 30–40 rakers, whereas the Cisco (*C. artedii*) eats small zooplankters, midge larvae, and water mites and has 40–60 rakers (Scott & Crossman 1973). In most filter-feeding fishes, particles are captured by mechanical sieving, whereby large particles cannot pass through the narrow spaces between gill rakers. Electrostatic attraction, involving the capture of charged particles on mucous-covered surfaces, is also suspected (Lauder 1985).

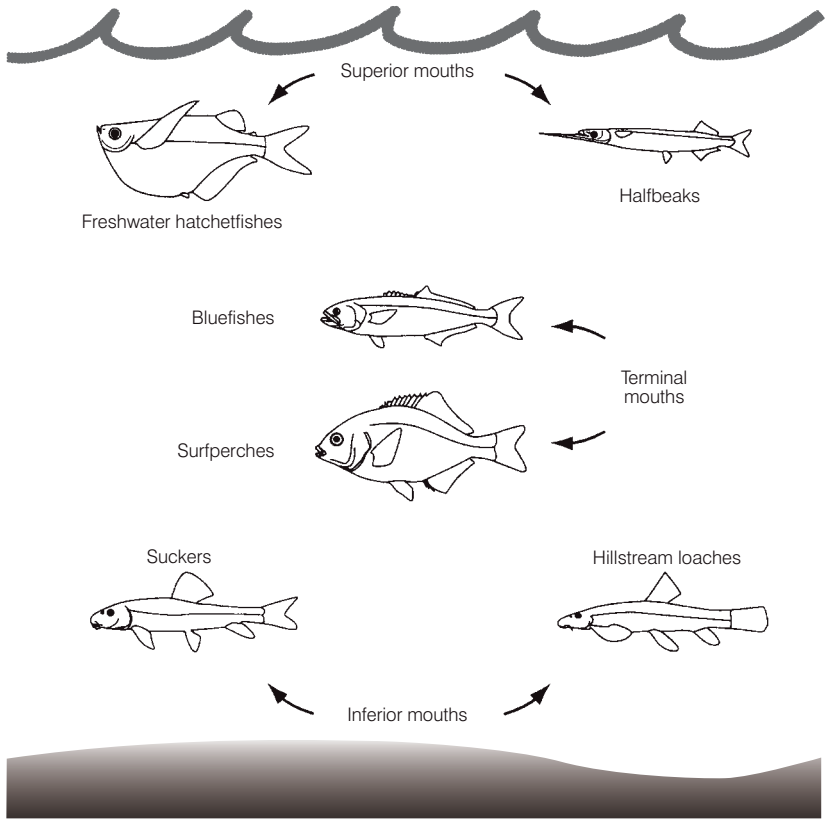


Figure 8.9
Correspondence among mouth position, feeding habits, and water column orientation in teleosts. Fishes with "superior" mouths frequently live near and feed at the surface, whereas fishes with "inferior" mouths often scrape algae or feed on substrate-associated or buried prey. Fishes with terminal mouths often feed in the water column on other fishes or zooplankton, but are also likely to feed at the water's surface, from structures, and on the bottom. Fish drawings from Nelson (2006), used with permission.

Mouth position and function

Mouth position, in terms of whether the mouth angles up, ahead, or down, also correlates with trophic ecology in many fishes (Fig. 8.9). The vast majority of fishes, regardless of trophic habits, have **terminal** mouths, which means that the body terminates in a mouth that opens forward. Deviations from terminal location usually indicate habitat and feeding habit. Fishes that swim near the water's surface and feed on items at the surface often have mouths that open upwards, termed **superior** or **supraterminal** (e.g., African butterflyfishes, freshwater hatchet or flyingfishes, halfbeaks, topminnows). Some predators that lie on the bottom and feed on prey that swim overhead also have superior mouths (e.g., stonefishes, weaverfishes, stargazers). Mouths that open downward, termed **subterminal** or **inferior**, characterize fishes that feed on algae or benthic organisms, including sturgeons, suckers, some North American minnows, suckermouth armored catfishes, Chinese algae eaters, some African minnows and cichlids, clingfishes, and loach gobies. Upside-down catfishes feed on the undersurfaces of leaves, but do so while swimming upside down and not surprisingly have inferior mouths. Fishes that do not have to visually fix on their prey (e.g., algal-scraping clingfishes, catfishes, loaches, cichlids), or that take somewhat random mouthfuls of sediments that are then sifted orally (e.g., suckers, mojarras), may gain an antipredator advantage by having an inferior mouth. A terminal mouth in such fishes would require that they angle head down each time they scraped or sampled the benthos, which would make them less able to escape rapidly if surprised by a predator.

Specialized **suctorial** mouths characterize unrelated fishes that scrape algae from rocks, particularly if they also live in high-energy environments. This ecological grouping includes hillstream loaches, suckermouth armored catfishes such as the familiar Plecostomus of the aquarium trade, Southeast Asian algae eaters, and the loach gobies of Australia. The gyrinocheilid algae eaters live in swift streams where they rasp algae from rocks with their lips while remaining attached with their suctorial mouth. Gyrinocheilids have evolved an additional in-current opening dorsal to the operculum that opens into the gill chamber. They breathe in through the dorsal opening and out through the operculum. Drawing water in through the mouth in the more normal manner would require the fish to detach from the substrate, at which moment it might risk being swept downstream. Mouths are not the only way for algae feeders to remain attached in wave-swept habitats. Gobiesocid clingfishes accomplish this via pelvic fins modified into a suction disk (Wheeler 1975; Nelson 2006).

Summary

SUMMARY

1. Functional morphology focuses on how structures work in the context of the daily tasks and interactions experienced by organisms. Locomotion and feeding offer many intriguing examples of the structure–function relationship. Locomotion in water presents very different physical challenges than are experienced by terrestrial animals. Density and drag are much greater in water, making locomotion energetically expensive and leading to the general hydrodynamic, streamlined shape of most fishes.
2. Swimming in fishes usually involves alternating contractions and relaxations of muscle blocks on either side of the body that result in the fish pushing back against the water and consequently moving forward. Many variations on this basic theme exist, and about 10 different modes of swimming have been identified that involve either undulatory waves or oscillatory back-and-forth movements of the body or fins. Body and fin shape correlate strongly with locomotory mode and habitat, the most extreme examples being the rapid swimming, highly pelagic mackerel sharks, tunas, and billfishes with streamlined bodies and lunate, high aspect ratio tails.
3. Locomotory adaptations create trade-offs. Maneuverability is often achieved at a cost in fast starts and sustained speed and vice versa. Versatility is achieved by using different modes for different purposes (fin sculling for positioning, body contractions for fast starts and cruising), which causes most fishes to evolve generalist rather than specialized swimming traits. Highly specialized locomotion includes fishes that can "walk" across the bottom or on land, climb terrestrial vegetation, leap, glide, and even fly.
4. Sharks, being cartilaginous, cannot rely on muscles attached to a rigid bony skeleton for propulsion. They instead undulate via contractions of their body muscles, which are firmly attached to a relatively elastic skin; the skin functions as an external tendon and provides propulsive force by rebounding. Some propulsive force comes from changing hydrostatic pressure inside the cylinder of the shark's body. The spacing of the two dorsal fins aids the tail in propulsion, and the tail works in concert with flattened ventral surfaces in the head region to counteract the weight of the body and to provide forward thrust.
5. Food-getting in fishes involves adaptations of the jaw bones and muscles, teeth, pharyngeal arches, gill rakers, and digestive system, as well as modifications in body shape, sensory structures, and coloration.
6. Food type can often be predicted from jaw and body shape and dentition type, regardless of taxonomic position. Zooplanktivorous fishes are usually streamlined, with compressed bodies, forked tails, and protrusible mouths that lack significant teeth. Lurking, fast-start piscivores are generally elongate, round in cross-section, with broad tails, posteriorly placed median fins, and long, tooth-studded jaws that grab prey. Alternatively, many piscivores that pursue prey for short distances are more robust, with fins distributed around the body outline, and with large mouths for engulfing prey. Many specialists that depart from these norms can be found.
7. An important food-getting innovation among modern fishes, particularly in teleosts, was the development of protrusible jaws and the pipette mouth. Modifications to jaw bones, ligaments, and muscles allow a fish to shoot its upper jaw forward and increase the volume of the mouth cavity, both creating suction forces and increasing the speed with which a fish overtakes its prey.
8. In addition to anterior, marginal jaws, and dentition on the roof of the mouth and tongue, teleosts have their gill arches modified into a second set of posterior, pharyngeal jaws. Pharyngeal jaws help move prey towards the throat and in many fishes serve to reposition prey for swallowing and for processing via crushing, piercing, and disarticulation. Pharyngeal teeth facilitate the eating of hard-bodied prey (mollusks, arthropods) and plant material.
9. Dentition type corresponds strongly with food type and is often repeated on the marginal jaws, vomer, palate, and pharyngeal pads. Piscivores and other predators on soft-bodied prey variously possess long, slender, sharp teeth, needlelike villiform teeth, flat-bladed triangular teeth, conical caniniform teeth, or rough cardiform teeth. Mollusk feeders have molariform teeth. Gill rakers also capture prey and may be numerous, long, and thin in plankton feeders, or widely spaced, stout, and covered with toothlike structures in predators on larger prey.
10. Mouth position also correlates with where a fish lives and feeds in the water column. Water column feeders typically have terminal mouths that open forwards, whereas surface feeders often have superior or supraterminal mouths that open upwards. Fishes that feed on benthic food types have subterminal or inferior mouths that open downward and that may generate suction forces that allow a fish to attach to hard substrates while feeding.

Supplementary reading

SUPPLEMENTARY READING

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Website

University of Massachusetts, Biology Department, www.bio.umass.edu/biology/bemis/FAOV_PPTS/FAOV3.htm.

Chapter 9

Early life history

Chapter contents

CHAPTER CONTENTS

Our chief emphasis in this and the next chapter is on the earliest stages of development, namely gametes, embryos, and larvae, transitional stages between larvae and juveniles, and various aspects of the growth process. Adult biology is explored primarily with respect to reproduction (determination, differentiation, maturation, longevity, and senescence). Related topics concerning the timing, effort, and behavioral interactions associated with reproduction are detailed in Chapters 21 and 24.

Complex life cycles and indeterminate growth

Two general traits shared by most fishes set them apart from the majority of vertebrate species and also underlie many of their more interesting adaptations. These two traits are indeterminate growth and a larval stage. Many fishes emerge from an egg as a larva, which bears little anatomical, physiological, behavioral, or ecological resemblance to the juvenile or adult into which the fish will eventually transform. In fact, continual growth moves each individual through a progression of life history stages that differ in most traits, creating a spectrum of continually changing structures and characters upon which natural selection has operated.

Indeterminate growth describes the continual increase in length and volume that occurs in most fishes throughout their lives. Although this growth may slow considerably as a fish ages, the potential for continuing increase profoundly affects many if not most aspects of a fish's life. With regard to most traits, larger body size appears to confer an advantage, at least within a species. Reproduction is intimately tied to body size in terms of egg number and size, larger females producing more and bigger eggs (see Chapter 24, Life histories and reproductive ecology). Mate choice by both males and females often favors larger individuals, and larger fish are better able to defend a spawning territory (see Chapter 21, Sexual selection, dimorphism, and mate choice). Swimming energetics and shoaling interact with body size: fish tend to shoal with individuals of like size (see Chapter 20, Responses of aggregated prey), and larger fish can swim faster and migrate over larger distances (see Chapter 23, Annual and supra-annual patterns: migrations). Predation rate is typically greater on smaller fish, and small fish may be constrained from feeding in profitable areas by predators or larger conspecifics. Indeterminate growth leads to size-structured populations in which different size individuals essentially function as different species, the so-called **ontogenetic niche** (Werner & Gilliam 1984; see Chapter 24, Population dynamics and regulation). Physiological limitations of small body size can be explained by **allometric** (proportional) **growth** of many structures, such as the increased visual acuity and sensitivity that occur as a fish grows. Foraging is also affected by body size, not only because many fish are gape-limited and hence only able to eat things they can swallow whole, but also because many prey types are not available to young fishes until muscle attachment sites and muscle masses reach a size

capable of overcoming prey defenses (see Chapter 8, Pharyngeal jaws).

Early life history: terminology

> [named] Stages are arbitrarily chosen moments in an essentially continuous process of development . . .
> Osse and van den Boogaart (1995, p. 23)

Given the diversity and complexity of stages, states, phases, or intervals in the early life history of fishes, it is not surprising that several classification systems have been developed to describe these stages, each differing slightly or greatly in terminology (Fig. 9.1). These schemes all attempt to subdivide about one dozen recognizable, general events during development into a coherent, descriptive progression. The simplest classification recognizes an **egg** (which after fertilization or activation contains a developing embryo), which hatches into a **larva**, which metamorphoses into a **juvenile**. Subdivisions of this basic sequence generally involve endpoint events, some of which occur quickly, others gradually (Fig. 9.1). Significant endpoint events include closure of the blastopore and lifting of the tailbud of the developing embryo; absorption of the yolk sac, independent feeding, and flexion of the notochord of the larva; development of fin rays, scales, and pigmentation; and changes in body proportions of the juvenile (Fig. 9.2). These general descriptions overlie a more complicated sequence of events involving changes in the anatomy, physiology, behavior, and ecology of a developing fish (Fig. 9.3). From a systematics standpoint, most fish species are readily distinguishable as such from the earliest stages. Early life history stages have consequently played an important role in fish systematics (Cohen 1984; Moser et al. 1984).

Part of the controversy over developmental terminology arises from the great diversity of embryonic and larval types, developmental rates, and transitional stages or events that exist among the 27,000+ species of fishes. Attempts at generalization are frustrated by exception and nuance, and by whether research focuses on marine or freshwater species, pelagic or demersal young, live- or egg-bearers, and embryology or taxonomy. Some workers maintain that development is a continuous and gradual process and that designating exact stages is an arbitrary process. Others maintain that development is **saltatory**, that it occurs with periods of gradual change punctuated by significant events or thresholds that allow for rapid change, such as the shift from dependence on yolk or maternal secretions to independent, exogenous feeding. This disagreement will not be resolved in the short space available here, but the interested reader should consult references by Balon (1975a, 1975b, 1980, 1984), Richards (1976), and Kendall et al. (1984) for a review.

Eggs and sperm

Gametogenesis

Most fishes have paired gonads, although one member of the pair may be consistently larger than the other in some species or only one gonad may be functional. Hagfishes and lampreys are unique in that only one ovary develops, from the fusion of two primordia in lampreys and from the loss of one ovary in hagfishes (see Chapter 13). Unlike sharks and other vertebrates, testes and ovaries in jawless fishes and bony fishes develop from only the cortex of the peritoneal epithelium, not from both the cortex and medulla. Testes in immature males are typically reddish and take on a smooth texture and creamy-white coloration as the fish matures and spawning time approaches. The testes generally account for <5% of body weight (see below). Follicles within the testes produce the developing spermatozoa (= **spermatogenesis**) through a series of meiotic and developmental transformations typical of vertebrates (**spermatogonia**, **primary spermatocytes**, **secondary spermatocytes**, **spermatids**, **metamorphosis**, **spermatozoa**) (Hoar 1969; Hempel 1979; Gorbman 1983; Adkins-Regan 1987; Jamieson 1991).

Fish sperm vary in size, shape, number of flagella (none to two), and presence or absence of acrosomes and other structures. Fish sperm are highly diagnostic of higher taxa and of some species (Jamieson 1991) (Fig. 9.4). Sperm heads range in length from about 2 mm (Bowfin, burbot, medaka) to 70 mm (Australian Lungfish). The caplike **acrosome** at the anterior end of most primitive fish sperm is lost in practically all neopterygian fishes (gars, Bowfin, teleosts). Two African families of osteoglossomorph fishes, the Mormyridae (elephantfishes or mormyrs) and Gymnarchidae, lack a flagellum. Their sperm may move by some form of ameboid motion. Typical ejaculates during spawning contain millions of sperm. Sperm is released in seminal fluid in species with external fertilization, or in packets called **spermatophores** in internal fertilizers. It is commonly stated (e.g., Box 21.1) that males produce an excess of sperm and consequently male reproductive success is limited more by access to females than by ability to produce gametes (the opposite is considered limiting in females). However, under circumstances where males mate daily over a prolonged breeding season, **sperm depletion** can occur and mating may in fact be delayed until sperm stores are replenished (e.g., Nakatsaru & Kramer 1982; Jamieson 1991; see also Shapiro et al. 1994).

Oogenesis, the development of eggs, occurs within the ovary and also progresses through various stages involving **oogonia**, **primary and secondary oocytes**, and finally **ova** or eggs (Wallace & Selman 1981) (Fig. 9.5). Oogones develop from primordial sex cells in the germinal epithelium of the ovary wall. Proteinaceous yolk granules are deposited

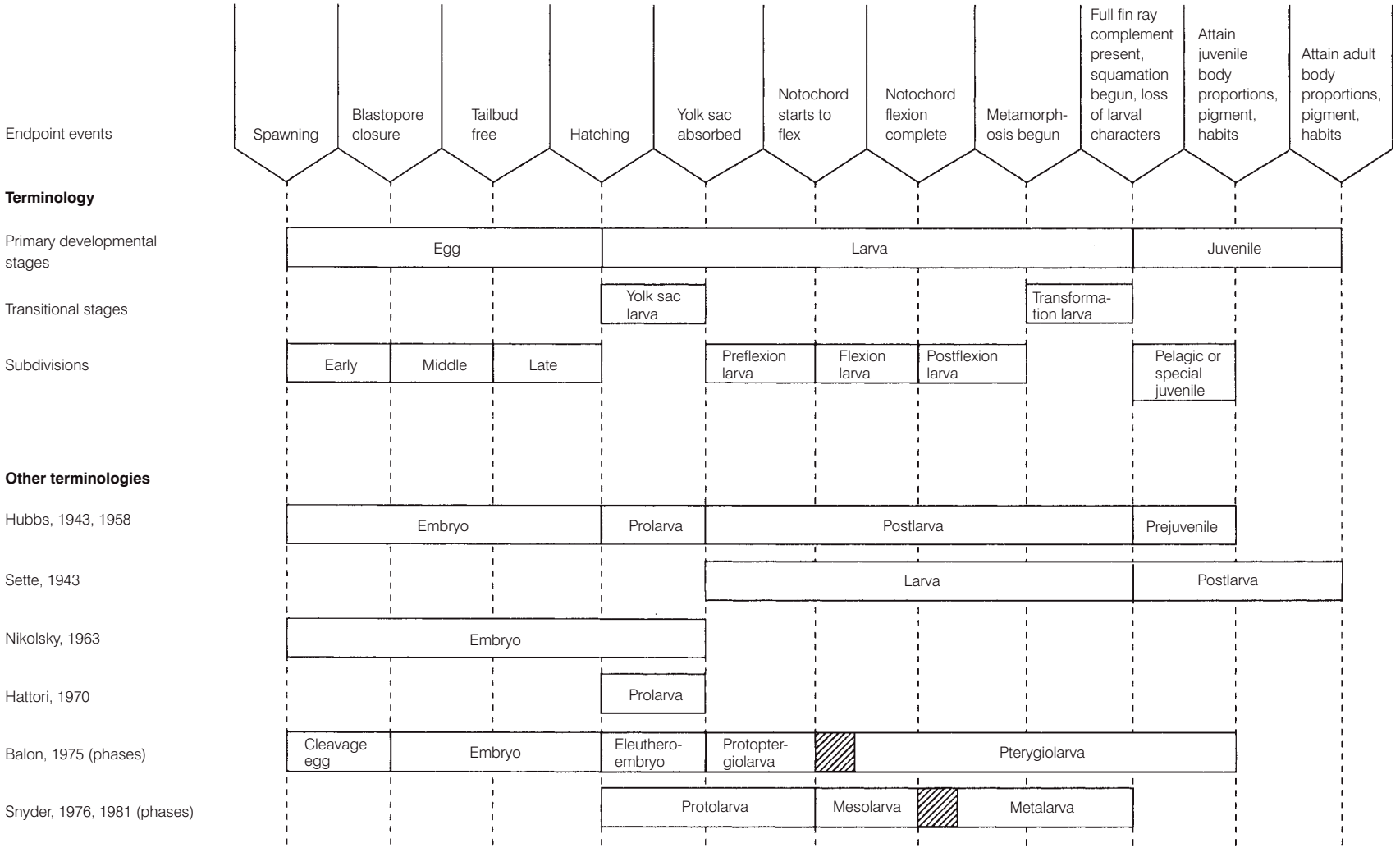


Figure 9.1

Events during, and terminology describing, the early life history of teleost fishes. The three basic stages – egg, larva, juvenile – can be further subdivided depending on definable events that occur during development and growth. The top half of the diagram summarizes one commonly used set of terminology, particularly for pelagic marine larvae. Alternative systems for describing these events are given in the lower half of the diagram (see Kendall et al. (1984) for reference details); the approach of Balon (1975b, second from bottom) may be more descriptive of many freshwater taxa. From Kendall et al. (1984), used with permission.

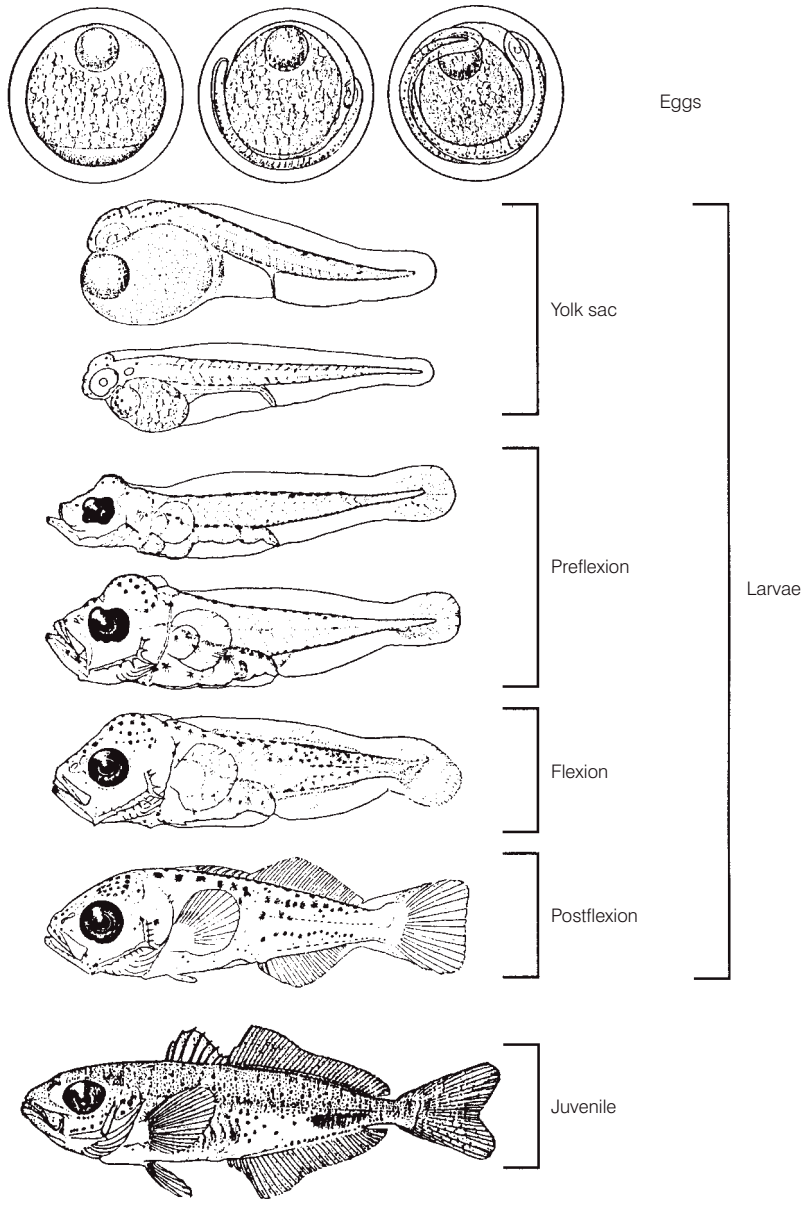


Figure 9.2
Stages during the early life history of the Horse Mackerel, *Trachurus symmetricus*. From Ahlstrom and Ball (1954).

around primary oocytes during **vitellogenesis**, the precursors of yolk material being manufactured in the liver. Oil droplets are incorporated in the yolk. Ripe eggs pass from the ovary through the oviduct, which is a continuation of the ovarian tissue, to the outside via the cloaca. In elasmobranchs, no direct connection between ovary and oviduct exists and hence eggs pass through the peritoneal cavity on their way to the oviduct. In several osteoglossomorph bonytongues, a loach (*Misgurnus*), anguillids, salmonids, and galaxiids, the oviduct is greatly reduced or absent and eggs enter the body cavity prior to being shed (Blaxter 1969; Hempel 1979; Wootton 1990). Females that have spawned are termed **spent**; their ovaries are bloody and contain residual eggs which are resorbed by the ovary. Egg resorption is a general process. Usually, most of the ripe eggs in an ovary are spawned while a small proportion is resorbed and the proteins, fats, and minerals contained in them are reused by the female for maintenance, growth, or production of more eggs. The number resorbed varies greatly among and within species, depending on fish size, number of previous spawnings that season, and energy state of the female.

Fecundity, the number of eggs released by a female during a spawning bout or breeding cycle, varies from one to two in some sharks to tens of millions in the Tarpon, *Megalops atlanticus*, and European Ling, *Molva molva*, to 300×10^6 in the Giant Ocean Sunfish, *Mola mola*; seasonal and lifetime fecundities can also be calculated. Most larger,

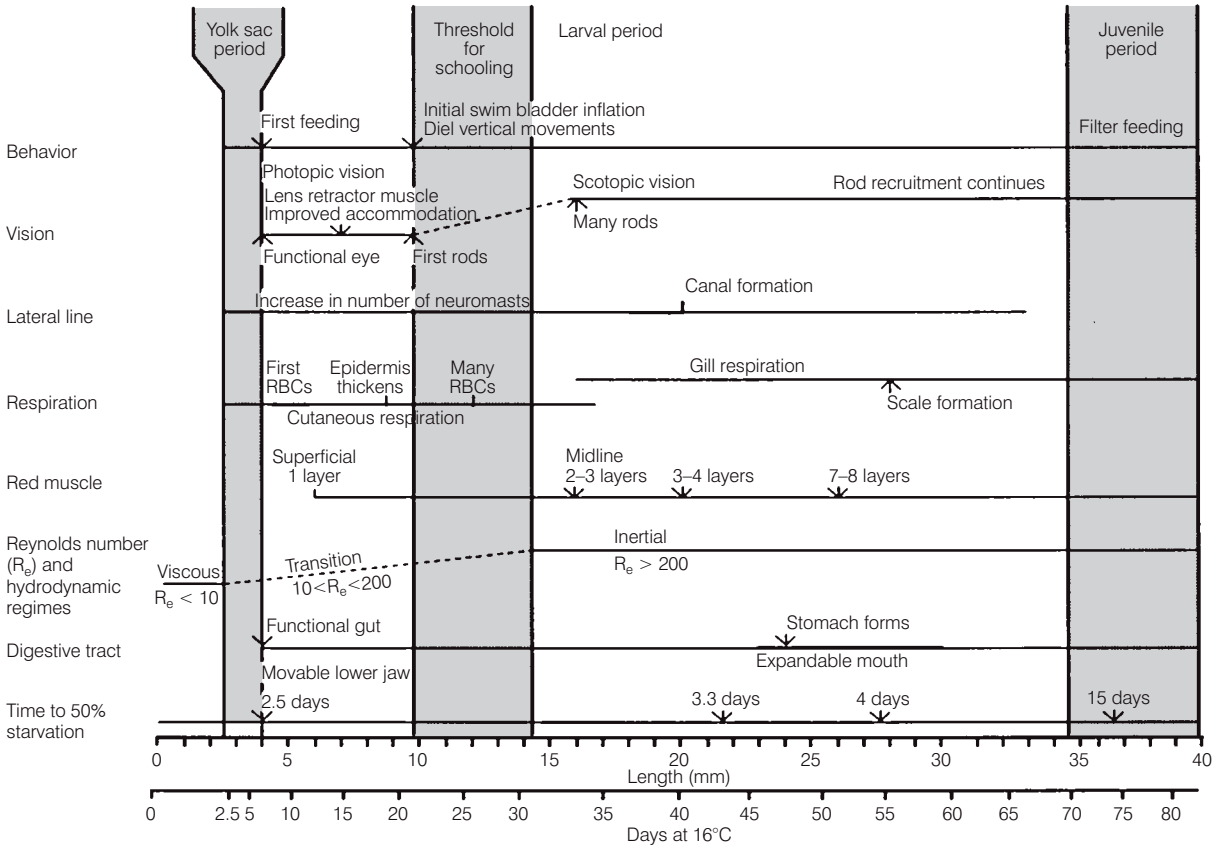


Figure 9.3

Behavioral, physiological, and anatomical events during the postembryonic early life history of a representative teleost, the Northern Anchovy, *Engraulis mordax*. The horizontal axis at the bottom represents days after hatching for larvae growing in 16°C water; events noted are those occurring after the larva begins exogenous feeding, when it is no longer solely dependent on yolk for energy. Photopic refers to daytime vision, scotopic refers to nighttime vision. Reynolds number is a measure of the difficulties that small larvae have with water viscosity (see below, Larval behavior and physiology). Time to 50% starvation refers to how long larvae can live without feeding, based on half of the larvae in an experiment dying after a given number of days without food. RBCs, red blood cells. From Hunter and Coyne (1982), used with permission.

temperate marine fishes produce tens of thousands to millions of eggs at a time. Fecundity generally decreases with increasing egg size and with increasing parental care, but increases with body size in an individual. Mouth-brooders such as sea catfishes and some cichlids produce only about 100 eggs at a time, and live-bearers such as the Four-eyed Fish, *Anableps*, contain about a dozen embryos. The relationship between egg number and body size is usually proportional to the mass of the female, reflecting the volume of a female's body that can carry the eggs. Hence egg number generally increases in relation to the cube, fourth, or fifth power of the length of the female (see Fig. 24.1). In addition to producing more eggs, larger females of many species produce bigger, better eggs that result in higher larval survival (e.g., in salmons, cod, haddock, Striped Bass, flounder) (Trippel 1995).

Exceptions show the premium placed on assuring survival of young rather than just on producing large numbers of eggs. In mouth-brooding cichlids, fecundity increases in relation to the square of the length of the female because mouth size increases only linearly with increasing body length (Breder & Rosen 1966; Hempel 1979; Lowe-McConnell 1987). Because of resorption, fecundity estimates based on counts of ripe eggs may not necessarily indicate true **fertility**, which is the number of viable offspring produced. Fecundity estimates for live-bearing fishes are further complicated by the consumption of eggs by developing embryos, a form of maternal provisioning (see below).

Certain generalizations apply to fish eggs, with a strong correlation between habitat and the characteristics of fertilized eggs. "Most marine fishes, regardless of systematic affinities, demersal or pelagic habits, coastal or oceanic distribution, tropical or boreal ranges, spawn pelagic eggs that are fertilized externally and float individually near the surface of the sea" (Kendall et al. 1984, p. 11). Among pelagic spawners, eggs are generally spherical in shape and have a single oil globule. Their diameters range from about

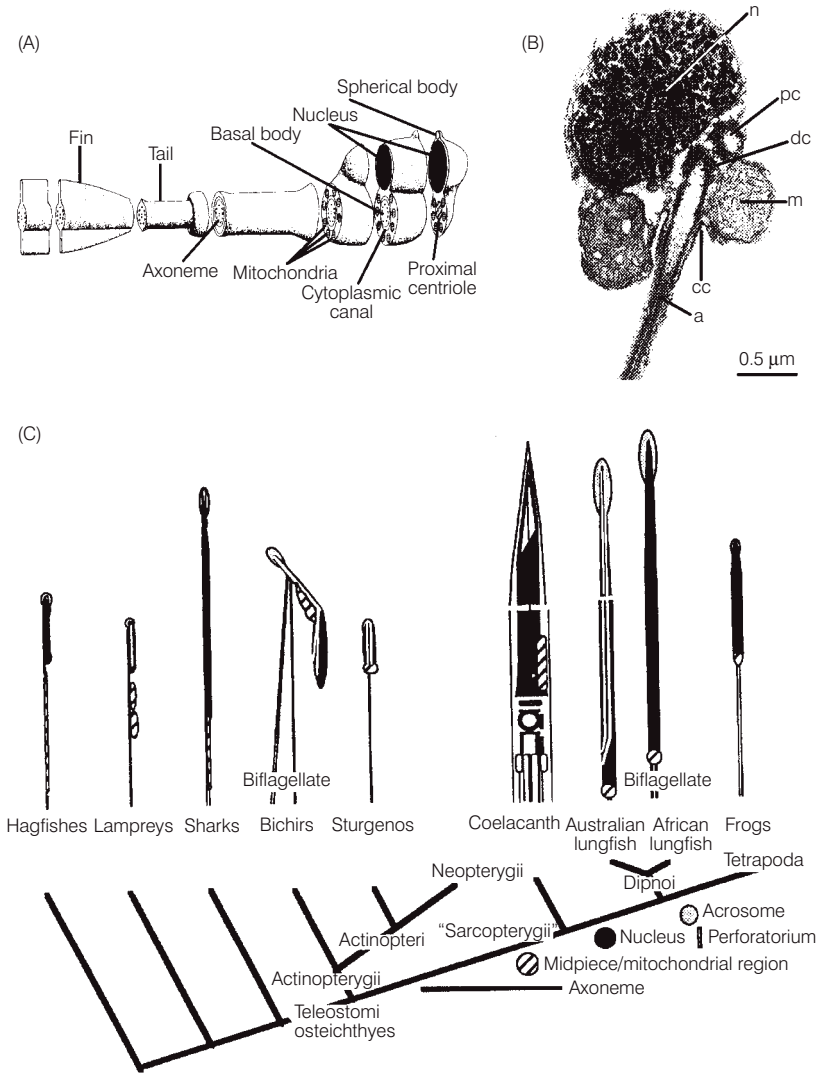


Figure 9.4

Fish sperm and their utility in constructing phylogenies. (A) Schematic diagram of the sperm of the percichthyid *Macquaria ambigua*; the entire structure is about 5 mm long. (B) Longitudinal section of the sperm of the Coral Trout, *Plectropomus leopardus* (Serranidae); a, axoneme; cc, cytoplasmic canal; dc, distal centriole; m, mitochondrion; n, nucleus; pc, proximal centriole. (C) Schematic diagrams of spermatozoa of non-neopterygian fishes and a cladogram based on sperm characteristics; the cladogram is basically similar to the one presented in Chapter 2, showing the parallel evolution of sperm and other taxonomically useful characteristics. From Jamieson (1991; C slightly modified), used with permission of Cambridge University Press.

0.5 mm (*Vinciguerria*, Photichthyidae) to 5.5 mm (moray eels), with a modal size of about 1 mm. This remarkable convergence among phylogenetically widespread taxa suggests a common, adaptive set of solutions to the selection pressures encountered by eggs that disperse passively in a near-surface environment and that contain an embryo dependent on yolk supplies for nutrition.

Most freshwater fishes and some coastal marine species diverge from this pattern and produce **demersal** eggs that are laid on the bottom. Many spawn in nests and engage in some form of parental care (see Chapter 21). Demersal eggs tend to be relatively large, up to 7 or 8 mm in salmon, anarhichadid wolffishes, and zoarcid eelpouts. The largest teleostean eggs are produced by mouth-brooding marine catfishes and range from 14 to 26 mm. Shark eggs are generally larger than osteichthyan eggs, whereas the largest bony fish eggs are produced by the Coelacanth, *Latimeria chalumnae*, with a diameter of 9 cm. Demersal eggs often have thick chorions and special coatings that may provide mechanical protection (ictalurid catfishes, North American minnows, killifishes, freshwater perch, blennies) (Boehlert 1984; Matarese & Sandknop 1984).

Departures from spherical shape are found in the elongate eggs of some cusk-eels, anchovies, minnows, cichlids, parrotfishes, and gobies. Congrogadid eel blennies have strangely cross-shaped eggs, and eggs of some darters are deeply indented and appear almost heart-shaped. Although usually smooth, the outer vitelline membrane of the egg, termed the **chorion**, may be sculptured (lizardfishes, deepsea hatchetfishes, mullets, some flounders), or have filaments, stalks, or spines (myctophiform lanternfishes and many atherinomorphs such as killifishes, flyingfishes, topsmelts, sauries, and halfbeaks). Filaments often help eggs attach to other eggs or to structures such as seaweeds, as in flyingfishes. Variation in other egg structures can help in species or family identification. The degree of segmentation and

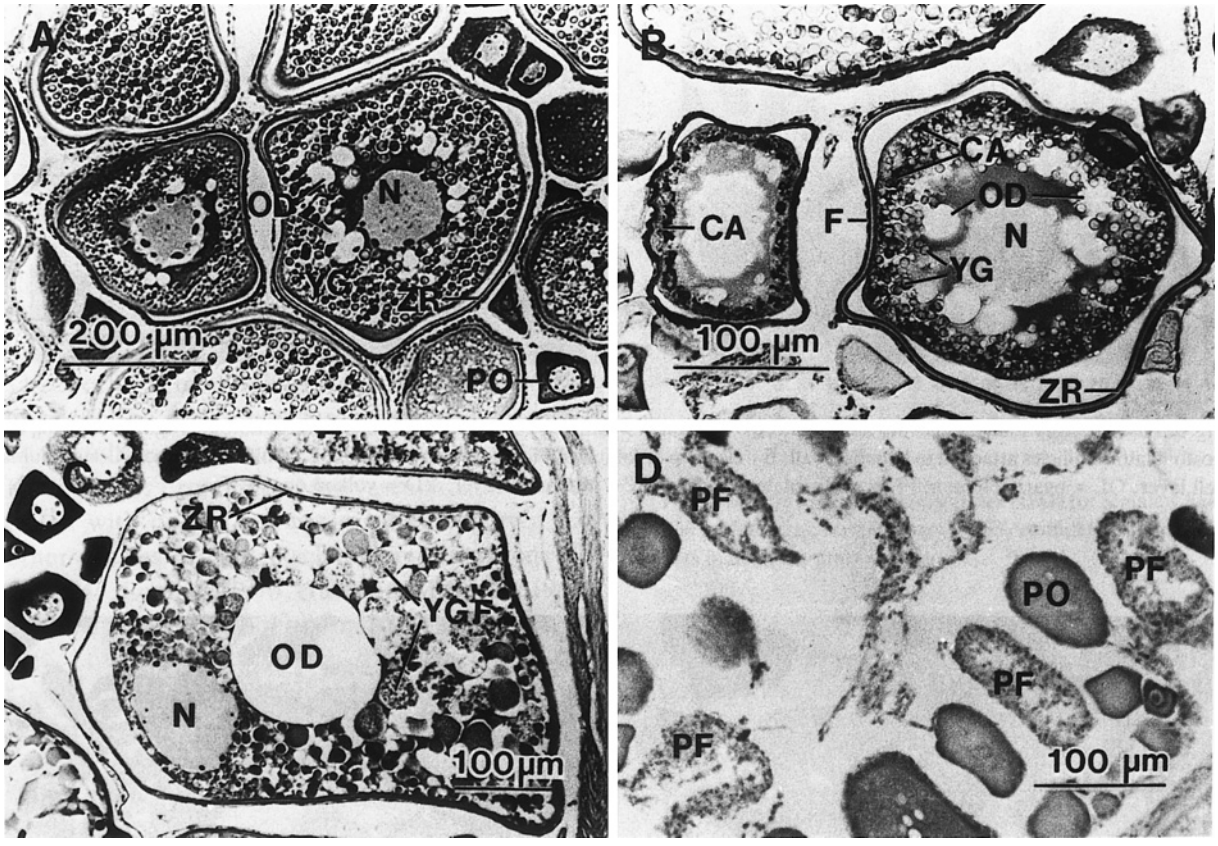


Figure 9.5

Stages in the development of teleostean eggs, as shown by the Multiband Butterflyfish, *Chaetodon multicinctus*. (A) Primary oocyte growth and yolk development (vitellogenesis). (B) Yolk vesicle or cortical alveoli stage (left cell), early vitellogenesis (right cell). (C) Maturing egg, where the nucleus has migrated to the cell periphery and the yolk granules have coalesced. (D) Postovulatory ovary, after the eggs are shed. CA, cortical alveoli; F, follicle that holds oocyte; N, nucleus; OD, oil droplets; PF, postovulatory follicle, from which egg has been released; PO, primary oocyte; YG, yolk granule; YGF, yolk granule fusion; ZR, zona radiata of the vitelline membrane. From Tricas and Hiramoto (1989), used with permission.

pigmentation of the yolk differs, with primitive teleosts such as many eels, herrings, and salmons having segmented yolks, whereas more advanced teleosts have homogeneous yolks. Pigmented yolks produce colorful eggs in gar, catfishes, and salmon. The occurrence, number, and location of oil globules in the yolk differ among species. Oil globules may serve as nutrition for embryos, as flotation mechanisms, and, when pigmented with melanin, may help protect sensitive developing structures from harmful radiation (F. D. Martin, pers. comm.). Oil globules in some species go through highly predictable patterns of movement (Malloy & Martin 1982). Eggs also vary among species in terms of the space between the chorion and the yolk, termed the **perivitelline space** or "around the yolk" space (Page 1983; Boehlert 1984; Matarese & Sandknop 1984).

An interesting aspect of reproduction is the effort and energy that different species and individuals expend, which often correlates with the life history pattern a species has evolved (see Chapter 24, Life histories and reproductive ecology). **Reproductive effort** includes food intake and its transfer to the gonads, as well as energy expenditure in somatic versus gonadal growth. In females, oocyte maturation involves mobilization of first lipids and then proteins from other parts of the body, such as fat deposits and body muscle, to the ovary. This maturation is also accompanied by as much as a 10-fold increase in oxygen consumption by the ovary until the final stage of oogenesis, when ovarian mass increases via water accumulation. True costs of reproduction must also account for energy expended during reproductive migrations, courtship, spawning, and internal brooding and other forms of parental care, among other factors. Energy expended in nongonadal growth can be substantial. For example, migratory female sturgeon and salmon use 80–90% of their body fat reserves during reproduction, much of which is expended during migration to the spawning grounds (Kamler 1991).

The difficulty of estimating reproductive effort accurately has led to the development of a variety of indices. Some indices depict characteristics of an individual at a given point in time (**instantaneous measures**), others over

the reproductive life of an individual (**cumulative measures**). One popular and simple instantaneous measure is the **GSI**, variously called the gonadosomatic, or gonadal-somatic, or gonosomatic index, a calculation of the percentage of the body mass of an animal devoted to gonadal material. The GSI can be calculated as gonad weight/total body weight, or as (gonad weight/body weight) – gonad weight (and sometimes minus gut weight). Values range greatly among species: cichlids < 5%, darters 11–23%, pupfishes 2–14%, American plaice 5–20%, sticklebacks 20%, salmonids 20–30%, and European eels 47%. The GSI of ripe females is a relatively accurate portrayal of effort for **total spawners** that spawn only once in a breeding season or lifetime, but it underestimates effort in **repeat, batch, or serial spawners** because only a fraction of the eggs or oocytes a female will produce are present at any moment (Heins & Rabito 1986).

GSIs in males are generally much smaller than for females, reflecting a lower effort directly expended in reproduction in males of many species. GSIs in male sticklebacks are 2% compared to 20% for females, and only 0.2% in male tilapia. Female Pike, *Esox lucius*, allocate 6–18 times more energy to ovaries than males do to testes. Intraspecific variation in male GSI can reflect differences in reproductive tactics. In Bluegill Sunfish, *Lepomis macrochirus*, some males guard nests and attract females with which they spawn; other males lurk at the periphery of the nests and sneak into the territory to join a spawning nest-guarder. GSIs for territorial males run at about 1%, but for sneakers are 4.5%. GSIs in male Bluehead Wrasses vary between 3% and 5%, the larger value characterizing males that previously engaged in group spawning, where sperm competition among males is likely (Gross 1982; Shapiro et al. 1994).

Measuring the GSI during different parts of the year can indicate ovarian or testicular cycles and spawning periodicities. Multimodal values would indicate protracted spawning seasons, whereas a single maximum would indicate a more defined spawning season. Not surprisingly, GSI values generally reach their maxima just before spawning (Page 1983; Wootton 1990; Kamler 1991). GSI calculations have been modified and improved to account for differences in body size among females and for females that do not shed all eggs at once (DeMartini & Fountain 1981; Erickson et al. 1985).

Fertilization

In most fishes, fertilization occurs outside the body of the female. Regardless, fertilization occurs when a sperm penetrates or is permitted to enter the egg membrane via a funnel-shaped hole in the membrane called the **micropyle**. The micropyle sits above the animal pole of the egg and is too narrow to allow the passage of more than one sperm. After sperm entry, the micropyle closes and the chorion tends to harden, which prevents **polyspermy** or entry of more than one sperm. Sturgeon eggs have several micropyles and polyspermy occurs. Micropyle presence and size is diagnostic of different species. A zygote is formed when pronuclei of the sperm and egg fuse (Hoar 1969; Hempel 1979; Matarese & Sandknop 1984; Jamieson 1991).

In species with external fertilization, gametes remain viable for less than a minute to as long as an hour, depending on temperature; longer viability generally occurs in colder water (Hubbs 1967; Petersen et al. 1992; Trippel & Morgan 1994). Studies of the proportion of eggs fertilized during natural spawning events indicates that at least 75% and often 90–95% of the eggs released are fertilized (Petersen et al. 1992, 2001; Marconato & Shapiro 1996). This number varies directly as a function of the volume of sperm released by the male. In water column spawners such as wrasses and parrotfishes, males can control sperm expenditure in response to female size and competition, releasing more sperm when spawning with larger females that release more eggs, or when other males are simultaneously attempting to spawn. Ejaculate volume also increases in the face of competition in internally fertilizing species such as live-bearing mosquitofish (Evans et al. 2003). In benthic, territorial spawners, however, sperm expenditure does not appear to increase when females release more eggs (e.g., sticklebacks; Zbinden et al. 2001), or in the face of competition from other males (gobies and cyprinid bitterlings; Candolin & Reynolds 2002; Scaggiante et al. 2005).

Females of some internally fertilized species are able to store sperm in the ovary. In the Dwarf Perch, *Micrometrus minimus* (Embiotocidae), newborn males are mature and inseminate but do not fertilize newborn females. The females store this sperm for 6–9 months until they mature and ovulate (Warner & Harlan 1982; Schultz 1993). Sperm storage is widespread in poeciliid livebearers, often involving more than one male partner (e.g., Evans & Magurran 2000; Luo et al. 2005). Some species store sperm and use it to fertilize multiple batches of eggs. Females of the Least Killifish, *Heterandria formosa*, store sperm from one copulation for as long as 10 months and use it to fertilize as many as nine different developing broods of embryos, several of which may be developing simultaneously – a phenomenon known as **superfetation**.

In a few species, activation of cell division is not synonymous with fertilization. Some poeciliid livebearers are **gynogenetic** in that females use sperm from males of other species to activate cell division, but no male genetic material is actually incorporated into the zygote (see Chapter 21, Gender roles in fishes). In some internally fertilized species, fertilization occurs but development may be arrested after a few cell divisions and then resumes when environmental conditions are more favorable for hatching. In some annual fishes, such as the South American and African rivulines, eggs are fertilized and then buried; they spend

the dry season in a resting state known as **diapause** (Lowe-McConnell 1987; see Chapter 18, Deserts and other seasonally arid habitats).

Internal fertilization is universal among sharks but is limited to about a dozen families of bony fishes, most notably the coelacanths; a silurid catfish; brotulids; livebearers; goodeids; three genera of halfbeaks; four-eyed fishes; the neostethids and phallostethids of Southeast Asia; scorpaenids in the genera *Sebastodes* and *Sebastes* (e.g., *Sebastes viviparus*); Baikal oilfishes; embiotocid surfperches; an eel pout, *Zoarces viviparus*; clinids; and labrisomids. An Asian cyprinid, *Puntius viviparus*, was originally described as a live-bearer, but subsequent examination of the type material indicated that predation on cichlid young, which were contained in the stomach, had been mistaken for developing young in the ovary (attesting to the value of depositing type material and voucher specimens in museums; see Chapter 2, Collections).

Internal fertilization requires that males possess an **intromittent organ** for injecting sperm. This structure has different names and is derived from different structures in different taxa. The pelvic fin of elasmobranchs is modified into **claspers**; the pelvic girdle, postcleithrum, and pectoral pterygial elements form the **priapium** of phallostethoids; the anal fin forms the **gonopodium** of cyprinodotoids such as goodeids, anablepid four-eyed fishes, jenynsiids, and poeciliid livebearers; brotulids and surfperches have an enlarged genital papilla. In some cardinalfishes, the female purportedly inserts an enlarged urogenital papilla into the male to receive sperm (Hoar 1969).

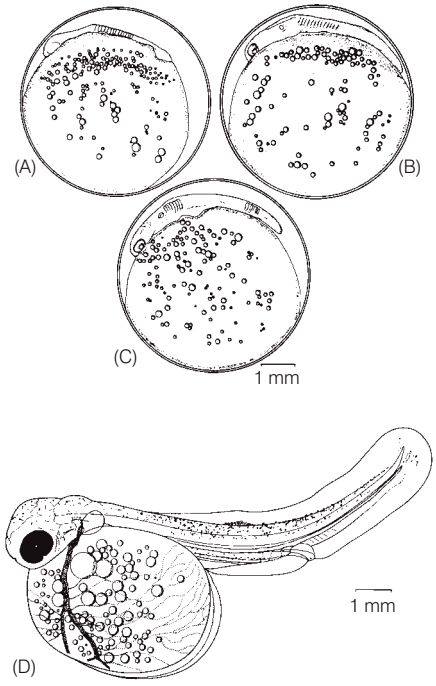


Figure 9.6

Embryonic development of the Lake Trout, *Salvelinus namaycush*. (A) At 17 days after fertilization (at 7.8°C), as the somites and brain ventricle just begin to form. (B) At 22 days, when the auditory vesicles and eye lens placodes have developed. (C) At 23 days the tail is lifting off and pericardial cavity is evident. (D) At 67 days, showing the fully formed embryo at about the time of hatching (at 4.4°C); note pigmentation, upturned notochord, gut tube, dorsal and ventral fin folds, pectoral fins, pigmented eye, and well-developed yolk circulation and large yolk sac. From Balon (1980), used with permission of Kluwer Academic Publishers.

Embryology

After fertilization, the chorion of the egg stiffens, a process known as **water hardening**, which serves to protect the developing embryo. Embryogenesis in fishes proceeds as in most vertebrates. The embryo develops on top of the yolk; yolk is concentrated at the vegetative pole and the fertilized egg is considered **telolecithal**. In hagfishes, elasmobranchs, and teleosts, cleavage is meroblastic in that cell division occurs in the small cap of cytoplasm that will develop into a fish, but not in the yolk. Lampreys have **holoblastic** cleavage, whereas bowfin, gar, and sturgeon exhibit an intermediate form, termed **semiholoblastic**. Cell division and differentiation continue in fairly predictable sequences, with many interspecific differences in the timing of appearance of different structures (Fig. 9.6) (see Lagler et al. 1977 and Lindsey 1988 for more thorough discussions of fish embryology).

Organs and structures that are at least partially developed in many embryos prior to hatching include: body somites, which are forerunners of muscle blocks; kidney ducts; neural tube; optic and auditory vesicles; eye lens placodes; head and body melanophores; a beating heart and functioning circulatory system, much of which is linked to circulatory vessels in the yolk; pectoral fins and median fin folds but not the median fins themselves; opercular covers, but not gill arches and filaments; otoliths; lateral line sense organs below which scales will later form; and the notochord. By the time of hatching, the head and the tail have lifted off the yolk, the mouth and jaws are barely formed, fin rays may be present in the caudal fin, but little if any skeletal ossification has occurred. The nonfunctional gut is a simple, straight tube and the gas bladder is evident as a small evagination of the gut tube. Advanced embryos curl around on themselves, their bodies making more than a full circle. In fish that hatch at a relatively undeveloped stage, the eye is seldom pigmented, maintaining the transparency of the helpless, newly hatched, free embryo with its very large and cumbersome yolk sac (Blaxter 1969; Hempel 1979; Matarese & Sandknop 1984; Lindsey 1988).

Just prior to emergence, **hatching gland cells** on the head of some fishes secrete proteolytic enzymes that aid in breaking down the chorionic membrane or "egg shell". Thrashing movements of the tail and body aid in the hatching

process. The time spent in the egg prior to hatching varies greatly among species, from around 12 h in some coral reef fishes; to a few days in Striped Bass, centrarchid sunfishes, some cichlids, and surgeonfishes; to a week or two in smelts, darters, mackerels, and flatfishes; to several weeks or months in salmons and sharks. In all fishes studied, hatching time decreases with increasing temperature (Blaxter 1969; Kendall et al. 1984). "**Hatching**" is a convenient landmark during early development, but it should be noted that the exact developmental stage at which the embryo frees itself from the egg varies greatly among species and even varies within species depending on temperature and oxygen content of the water, among other factors (e.g., Balon 1975a).

Species identifications of unfertilized or recently fertilized eggs can be a difficult task, often requiring electron microscopy. Embryos, especially those in advanced stages of development, are considerably easier to identify. Species-specific patterns of pigmentation often develop on the body and finfolds, particularly of marine species (e.g., codfishes, flatfishes). Other characters of use in identification include the general morphology of the head, gut, and tail, the number of body myomeres, and the existence of elongate or otherwise precocially developed fin rays (e.g., flyingfishes, ribbonfishes, sandfishes, weeverfishes) (Matarese & Sandknop 1984).

Species can be assigned to categories based on where embryonic development occurs and whether developing embryos are dependent on maternal versus yolk provisioning. If the mother releases eggs that then rely on yolk for nutrition, the species is **oviparous** or egg-laying, as is the case in chimaeras, some sharks and skates, and most bony fishes. If the young develop inside the mother and the mother provides nutrition via a placental connection, secretions, or additional eggs and embryos eaten by developing young, the species is **viviparous** or live-bearing. The young of viviparous fishes are generally born as juveniles, having bypassed a free larval stage. Viviparity characterizes about half of the 1200 species of Chondrichthyes and about 500 (2%) of the 25,000+ species of bony fishes (most of those with internal fertilization mentioned earlier). "Virtually every known form of vertebrate viviparity and possible maternal–fetal relationship may be found in fishes" (Wourms 1988, p. 4). Some researchers recognize **ovoviviparity**, whereby young develop inside the mother but depend primarily on the yolk that was laid down during oogenesis (e.g., some sharks, scorpaenids, zoarcid eelpouts, and arguably, guppies). However, many intermediate conditions exist involving both yolk and maternal secretions, blurring the distinctions and making ovoviviparity difficult to define (Breder & Rosen 1966; Hoar 1969; Kendall et al. 1984; Wourms 1988; Nelson 1994). Although live birth usually follows internal fertilization, the two are not synonymous. Many elasmobranchs have internal fertilization but lay eggs which develop for many months outside the female. The **priapium**, a bizarre and complex organ of male phallostethids and neostethids, is used for holding the female during copulation and for fertilizing eggs just before they are laid (Breder & Rosen 1966; Nelson 2006).

Meristic variation

Embryonic development generally progresses according to instructions laid down in the genetic blueprint, but the timing and even details of development are quite sensitive to environmental influences. Pollutants and chemical changes in the water often result in larval abnormalities and can be used to monitor environmental quality (see von Westernhagen 1988, Weis & Weis 1989, and Longwell et al. 1992 for reviews). But even natural variation in temperature, oxygen content, salinity, light intensity, photoperiod, or carbon dioxide can affect development. **Meristic** traits such as numbers of fin rays, vertebrae, lateral scale rows, myotomes, and gill rakers are known to vary in relation to environmental conditions.

The pattern of variation among meristic traits is not simple. The most commonly found relationship is for fin ray, vertebral, or scale numbers to increase with decreasing temperature (e.g., herrings, minnows, Rainbow Trout, grunions, killifishes, rivulines, and darters). This inverse relationship exemplifies a general phenomenon, termed **Jordan's Rule**, which applies to latitudinal effects on meristic numbers, although the actual determinant is water temperature (Lindsey 1988). However, an opposite pattern of increased meristic values with increased temperature has been observed for fin rays in Guppies and plaice. Another common pattern is the so-called **V relationship**, in which fewer meristic elements develop in fish raised at an intermediate temperature, but more elements are laid down at higher and lower temperatures (e.g., vertebrae or pectoral rays in Brown Trout, Chinook Salmon, rivulines, sticklebacks, paradise fish, snakeheads, and plaice). An **arched**, L or A, pattern of higher numbers at intermediate temperatures has been observed for the fin rays of Brown Trout and Chinook Salmon. The actual quantitative difference between experimental groups raised at different temperatures is in the range 0.1–3% difference in number of elements per Celsius degree of temperature. For example, a 1% per degree difference in vertebral count over a 5° temperature range for a fish with 100 vertebrae would translate into a five vertebrae difference between groups.

A **critical or sensitive period** often occurs during embryonic or larval development when effects on meristic characters are strongest. Vertebral counts in Brown Trout are most sensitive to temperatures at around the time of gastrulation and again as the last vertebrae are formed. Vertebral number is most sensitive to temperature before hatching in herrings and killifishes, but this sensitivity occurs later in paradise fish and plaice. Vertebrae form before fin rays, and have an earlier sensitive period (Blaxter

1969). Meristic characters may also be sensitive to events prior to fertilization, such as the temperatures at which parents are held and the age of the parents (Lindsey 1988). Causal mechanisms in these patterns are poorly understood. As an embryo develops, it differentiates via segment formation and grows via elongation. Environmental conditions may affect segment formation and elongation differently. Low temperatures may inhibit segment formation more than they inhibit elongation. Hence an embryo developing at low temperatures might be longer when differentiation occurred, causing more segments to be laid down and producing the pattern of more fin rays at lower temperatures (Barlow 1961; Blaxter 1969, 1984; Fahy 1982; Lindsey 1988; Houde 1989).

Larvae

Biologically, the larval stage or its equivalent is probably the most thoroughly studied period of the early life history of fishes. This results from the identifiability of larvae, their relative abundance, and their importance in determining the distribution and later abundance of many species, particularly those of commercial value.

Larval life generally begins as the fish hatches from the egg and switches from internal, yolk reserves to external, planktonic food sources. The free-swimming young may still have a large yolk sac and be termed a **free embryo**, **eleutheroembryo**, or **yolk-sac larva** until the yolk is absorbed. **Fry** is a nonspecific term often used for advanced larvae or early juveniles; **swim-up stage** often refers to free embryos or larvae that were initially in a nest but have grown capable of swimming above the nest.

The larval stage continues until development of the axial skeleton, fins, and organ systems is complete (Fig. 9.7). Median fin rays develop, first as short, fleshy interspinous rays; true fin rays and spines develop later between the interspinous rays. Scales develop, first along the lateral line near the caudal peduncle, then in rows dorsal and ventral to the lateral line, and then spread anteriorly (Fig. 9.8). Once the full complement of scales is attained, the number remains fixed. The end of the notochord, termed the urostyle, flexes upwards and a triangular hypural plate develops just below it. Caudal rays grow posteriorly from the hypural plate elements. Characteristic larval pigmentation patterns develop, the eyes become pigmented, and the mouth and anus open and become functional. Until gill filaments develop, the larva relies on cutaneous respiration, largely involving oxygen absorption across the thin walls of the primordial finfolds. The circulatory system is at first relatively open, and corpuscle-free blood is pumped through sinuses around the yolk and between the fin membranes (Russell 1976).

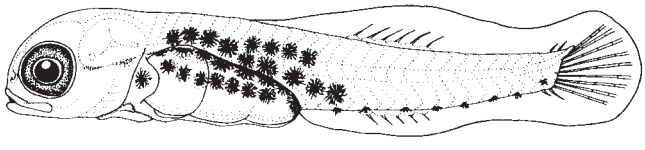


Figure 9.7
A recently hatched, marine teleost larva, as represented by a 6 mm clingfish, *Gobiesox rhessodon*. Note development of the mouth, eyes, median fin supports, and melanophores, and upward flexion of the notochord at the base of the tail. From Allen (1979).

Pelagic larvae, which are particularly common among marine fishes, also characterize lake and river species in fresh water (e.g., whitefishes, temperate basses, centrarchid sunfishes, percid pikeperches and perches). Larval periods in pelagic larvae vary widely in duration, from 1 to 2 weeks in sardines and scorpaenid rockfishes, to about 1 month in many coral reef species, to several months or even years in anguillid eels. A lengthy larval existence undoubtedly aids in the dispersal of these young to appropriate habitats (see below, Getting from here to there: larval transport mechanisms). Stream fishes, such as many minnows, darters, and sculpins, generally have demersal larvae with short larval periods. Young fish remain on the bottom among rocks or vegetation until they develop reasonable swimming abilities, reflecting the turbulent conditions of streams that can injure larvae or carry them downstream to suboptimal habitats such as lakes or the ocean. Once muscular and skeletal features are formed, many are captured in stationary drift nets, indicating a juvenile dispersal phase, as opposed to larval dispersal in pelagic, lake, and river species. Larvae of some rocky intertidal fishes (e.g., sculpins, pricklebacks, gunnels, clingfishes) may not disperse offshore but instead actively spend their entire larval existence within 5 m of the shoreline, which could guarantee their return to suitable habitat (Marliave 1986).

Larval periods are bypassed or very short in live-bearing fishes and in fishes that still possess considerable yolk reserves after hatching, such as salmonids. Arguably, no larval or juvenile phase exists in the viviparous Dwarf Perch, *Micrometrus minimus*, males of which are sexually mature when born (Schultz 1993). Development that involves a larval phase with distinct metamorphosis into the juvenile stage is termed **indirect. Direct development** occurs if a larval stage is very brief or not definable, i.e., the fish hatches into a miniature but immature adult, as in many coastal marine forms and in many catfishes, salmoniforms, and cottids (Youson 1988).

Larval feeding and survival

A defining event in a larva's life is when yolk supplies are exhausted and the fish becomes dependent on exogenous food sources, usually in the form of small planktonic organisms such as diatoms, larval copepods and mollusks, and

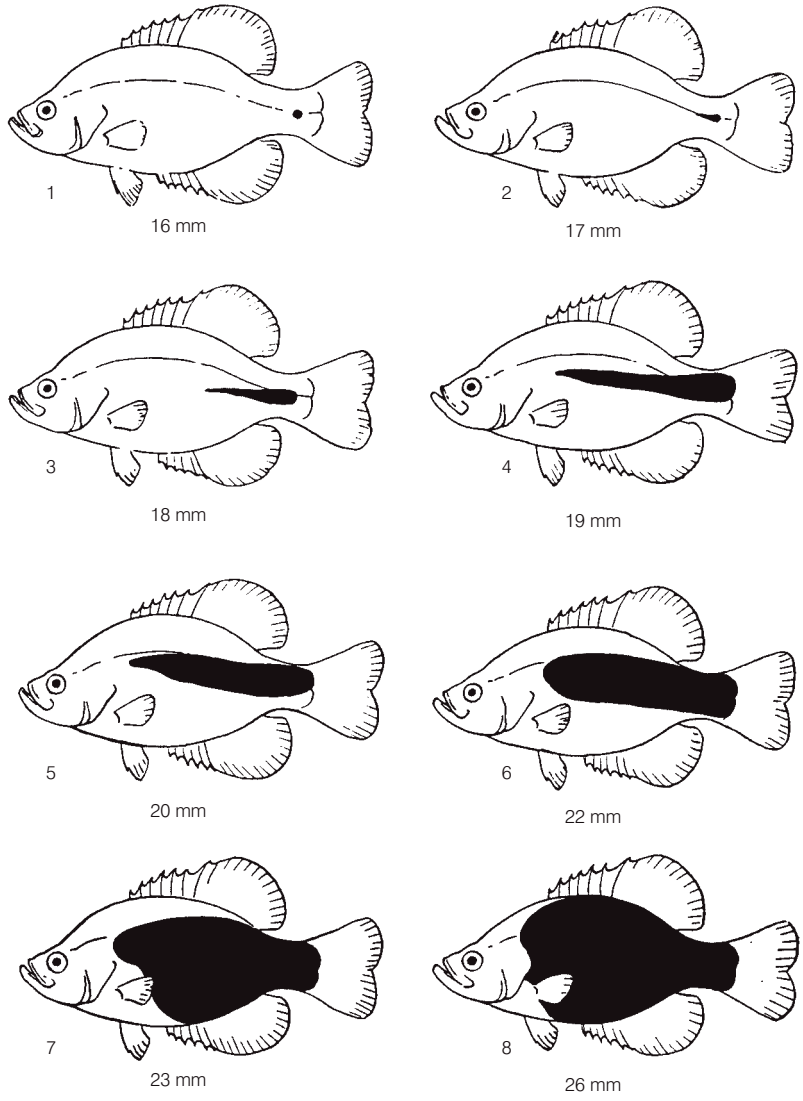


Figure 9.8
Development of scales in the Black Crappie, *Pomoxis nigromaculatus*, showing the general pattern of scales developing initially near the tail and spreading anteriorly. From Ward and Leonard (1954), used with permission.

adult euphausiids, amphipods, ciliates, tintinnids, appendicularians, and larvaceans. Even fishes that are herbivorous as juveniles and adults are usually carnivorous as larvae, as in rabbitfishes (Bryan & Madraisau 1977). This generalization may reflect the difficulty with which energy and nutrients are extracted from plants.

The potential importance of food availability at the onset of exogenous feeding has greatly influenced our thinking about sources of larval mortality and the subsequent strength of year classes of fishes. Several influential hypotheses address the relationship between early larval biology, food availability, and adult population size in marine fishes. Hjort (1914) proposed the **Critical Period Hypothesis**, which stated that starvation at a critical period, perhaps the onset of exogenous feeding, was a strong determinant of later year class strength. Blaxter and Hempel (1963) coined the phrase **point-of-no-return** to describe when larvae, as a result of starvation, are too weakened to take advantage of food even if it were available. Such irreversible starvation depends on larval condition and age: well-fed, young anchovy may last only 1–2 days before irreversible starvation sets in, whereas healthy, older flatfish larvae may be able to go 2–3 weeks without food. Cushing (1975) proposed the **Match–Mismatch Hypothesis**, which suggests that the timing of reproduction in many marine fishes has evolved to place larvae in locales where food will be available, i.e., that fish reproduction and oceanic production are synchronized. Since the cues of photoperiod and temperature that fish use to initiate spawning (see Chapter 23, Reproductive seasonality) are not necessarily the same ones that determine plankton production, mismatches can occur and result in high larval mortality (May 1974; Russell 1976; Hunter 1981; Blaxter 1984; Houde 1987).

Because of the relationship between larval survival and later population size, the actual causes and patterns of larval mortality are of considerable theoretical and obvious

practical interest. Literally billions of larvae are produced by most populations of marine fishes annually. In most species, >99% of these larvae die in their first year from the combined effects of starvation and predation; the average fish probably dies in less than a week (Miller 1988). Hence very minor shifts in mortality rates can have major implications for later year class strength and for recruitment into older, catchable size classes (Hobson et al. 2001).

The temperatures at which larvae develop affect individual growth and development rates, metabolic rates, and energy requirements, all of which can influence mortality (Houde 1989). Across a 25°C temperature range characteristic of the difference between tropical and temperate conditions (5–30°C), mortality rates of marine larvae can vary four-fold, being highest at the higher temperatures. Growth rates at these higher temperatures at any given size are six times faster. Larval duration at the lower end of the temperature range typically exceeds 100 days, whereas at 25–30°C, metamorphosis occurs in 1 month or less.

One might expect that spending the least amount of time as a small, vulnerable larva would lessen the chances of both predation and mortality. However, the metabolic requirements of small ectothermic animals such as fish larvae increase in direct relationship to temperature. **Gross growth efficiency** (weight increase/weight of food consumed) is constant despite temperature. A larva, because of its higher metabolic rate at higher temperatures, must consume more food to achieve the growth rate of a larva at lower temperatures. This is additionally compromised because gross growth efficiency declines with increased ingestion, and **assimilation efficiency**, which is how much of the food is actually useful to the larva, declines with increased temperature. To maintain the same average growth rate, a tropical larva has to eat three times more food than a temperate larva of the same species. Mismatching larvae with food availability becomes more critical at higher temperatures.

Spawning patterns among species appear to represent adaptations to these temperature relationships. Tropical fishes typically spawn over an extended period, producing multiple batches of young, rather than releasing all their eggs in one large spawning session. This kind of "bet hedging" strategy increases the probability that some larvae will encounter the kind of conditions necessary for successful growth, whereas a single spawning might lead to complete reproductive failure if food abundance were low, as it usually is in tropical pelagic areas. Temperate marine fishes that spawn in the summer, such as Atlantic mackerel and white hake, tend to spread their reproduction out over a longer period than do winter spawners such as herring and capelin at the same latitude (Houde 1989).

Pelagic larvae are particularly common among coral reef species. Whereas many nearshore temperate species have short larval periods or retain their larvae near the adult habitat, dispersal via a pelagic stage is almost universal among coral reef fishes. Of the 100 or so families that commonly inhabit coral reefs, 97 have pelagic larvae. The exceptions are instructive in that it is easy to postulate historical constraints or adaptive disadvantages to dispersal. Marine plotosid catfishes are a freshwater-derivative family with highly venomous spines. The brightly colored young form dense, ball-shaped shoals and probably gain predator protection from this behavior, a lack of dispersal helping keep siblings together and facilitating the formation of monospecific shoals. Many of the viviparous brotulas live in fresh or brackish water caves near coral reefs, a habitat that could be difficult to relocate by a settling larva. One species of damselfish, *Acanthochromis polyacanthus*, lacks a dispersed larval stage. It is also the only damselfish worldwide that continues to care for its young after they hatch; interestingly, *Acanthochromis* larvae develop more slowly than most other damselfishes (Kavanagh & Alford 2003). Other non-dispersers include batrachoidid toadfishes, the monotypic convict blenny (Pholidichthyidae), and apparently reef species of the croaker family.

The adaptiveness of a floating larva for the other 97 families probably results in part from selection for avoidance of abundant predatory fishes and invertebrates in benthic habitats, larvae generally not settling until they have developed avoidance capabilities. Dispersal may also reflect: (i) the possibility that successfully reproducing adults live in saturated habitats that offer few opportunities for settlement for their young; and (ii) the widespread and spotty distribution of coral reefs relative to immense oceanic expanses, necessitating the dispersal of offspring over as wide an area as possible. However, tagging, genetic, behavioral, and otolith chemistry methodologies are increasingly indicating that larvae are retained in nearshore gyres and currents and may actively return to parental regions. For example, marking and DNA genotyping studies of anemonefish on the Great Barrier Reef showed 15–60% of juveniles recruited back to their natal population, many settling <100 m from the anemone where they hatched (Jones et al. 1999b, 2005; see also below, Getting from here to there: larval transport mechanisms).

Pelagic existence is about the only thing these larvae have in common. Reproductive strategies include viviparity and oviparity, mouth-brooded eggs, nest builders, and demersal and floating eggs, some of the latter attached to seaweed. Larval periods range from 9 to >100 days, sizes at settlement from 8 to 200 mm. Some settle prior to metamorphosis to a juvenile stage, some after, and one family (Schindleriidae) is even mature at the time of settlement (Leis 1991).

Larval behavior and physiology

Depicting larvae as largely passive greatly oversimplifies their behavioral capabilities, which diversify as they grow older (Noakes & Godin 1988). Making meaningful

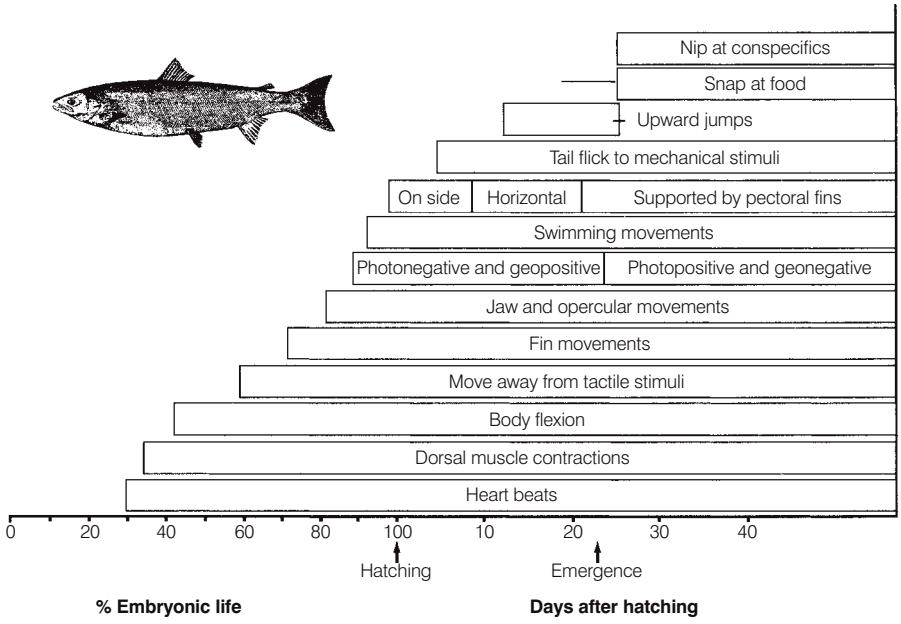


Figure 9.9
Anatomical and behavioral development of Atlantic salmon during embryonic life and the first 2 months after hatching. Note that even embryos are capable of avoiding aversive stimuli via fin and body movements. "Emergence" refers to yolk sac larvae moving up out of the gravel of the nest. From Huntingford (1993), after Abu-Gideiri (1966) and Dill (1977b), used with permission.

behavioral observations on very small, transparent larvae is understandably difficult, but successes point out the dynamics of larval development and the interdependence of morphology, physiology, and behavior. Larvae of reef fish swim actively, orienting to reefs and currents while moving vertically to remain in particular water masses (e.g., Paris & Cowen 2004). Atlantic salmon larvae hatch from eggs buried in gravel, and the larvae remain in the gravel for almost another month. Even during this early period, obvious behavioral responses occur (Fig. 9.9). The larvae can make coordinated swimming movements involving both body and fins. A general geopositive and photonegative response, moving them down and away from light, keeps them buried. They also orient toward water currents. Emergence occurs as these responses reverse to photopositive and geonegative, causing them to swim up and out of the gravel, but still into the current. They almost immediately react to food and interact with conspecifics, nipping at both, which helps obtain food and drive away potential competitors. They are also capable of swimming away if nipped.

The larvae of coral reef fishes are also being found to display surprisingly complex behavioral repertoires, especially as the time comes for them to drop out of the plankton and settle onto reefs. Surgeonfish larvae only 28 mm long that have just settled from the plankton can school, can use topographic reef features to avoid strong currents, can avoid predators, and can swim actively against currents as strong as 15 cm/s (Sancho et al. 1997). Kaufman et al. (1992) made behavioral observations of the larvae of 68 Caribbean reef species. These larvae, referred to as **transition juveniles**, were just settling onto reefs. Almost half of the species showed strong habitat specificity with respect to where they actually settled, and this specificity differed among species. Additionally, many species were able to prolong the settlement period for several days or even weeks while they apparently sought out appropriate habitats. Specificity of settlement habitat and species differences, even within families, has been shown in transition juveniles of other groups at other locales (e.g., Vigliola & Harmelin-Vivien 2001; Leis & Carson-Ewart 2002a). This stage in the life of reef larvae had generally been viewed as something of a parachute drop, with larvae exercising minimal if any habitat choice. In fact, the settling stage can be more accurately portrayed as a bungee jump.

Swimming capabilities in fish larvae in general are heavily dependent on the relationship of body size to water viscosity (its "syrupiness") and density (mass per unit volume). Small particles in a viscous medium such as water encounter tremendous friction forces with which larger particles do not have to contend. Such **Reynolds number** considerations (R_e = larval size × velocity × water density / water viscosity) mean that small larvae function at low Reynolds numbers (<1) and must swim sporadically and energetically, approaching 50 tail beats per second in anchovy and mackerel larvae, followed by long periods of rest. Larger larvae are able to swim and glide via inertial forces because viscosity is less of a factor (Purcell 1977; Hunter 1981; see Chapter 10, Body size, scaling, and allometry).

Accuracy of feeding strikes has been shown to increase rapidly with development in cichlids as well as herrings, carp, and seabass. Herring and anchovy larvae feed more efficiently as they grow, improving their success rate from 3–10% shortly after hatching to 60–90% in the later stages

of larval life (Blaxter 1969; Hunter 1981; Kamler 1991). In cichlids, many larvae and even juveniles are cared for by one or both parents. Many cichlid larvae form cohesive shoals almost immediately upon hatching, which obviously simplifies parental supervision. Some cichlid larvae feed on mucus produced by the parents and are attracted to the parents or to models with similar color patterns. By 25–40 days after hatching, shoals disband as individuals begin to charge, ram, and otherwise display at their siblings. Territory defense follows shortly thereafter (Huntingford 1993). Feeding in Mottled Sculpin larvae, *Cottus bairdi*, is strongly dependent on lateral line development. Sculpin as early as 6 days after hatching are able to detect vibrations produced by brine shrimp larvae in the dark, using free neuromasts that are located superficially on the skin of the head. With development, many of these neuromasts become enclosed in subdermal canals and sensitivity to minute disturbances, and ability to detect small prey, decreases (Jones & Janssen 1992).

More conventionally, ability to detect prey increases with age in most fishes, although some interesting specialized structures appear in larvae and then disappear during metamorphosis. In some weakly electric mormyrid elephantfishes of Africa, a special organ develops in larvae that produces electricity with a different discharge pattern than that shown in adults. This larval organ, which runs from the head to the caudal peduncle, degenerates after 2 months and is replaced by the adult caudal organ (Hopkins 1986).

More generally, many adult fishes have a duplex retina, one that contains both cones and rods (see Chapter 6, Vision). Cones function primarily by day, rods by night. The eye as it initially forms in embryos and larvae generally contains only cones, limiting feeding and other activities to daytime (e.g., herrings, many salmons and cichlids, soles). Herring do not develop rods until metamorphosis, which also coincides with the beginning of shoal formation, as does the development of the lateral line, which is also involved in shoaling behavior. Many aspects of visual capability – in terms of sensitivity to light, size of objects detected, resolving power, dark adaptation, and range of wavelengths detected – improve with growth in a number of species as a function of increased lens diameter, increased retina area, the addition of rods or sometimes of cones, the diversification and increased density of cones, and the addition of visual and screening pigments. Some fish larvae have unique visual structures not possessed by later stages. Stalked, elliptical eyes exist in larvae of 14 families of marine teleosts, including anguilliforms, notacanthiforms, salmoniforms, and myctophiforms (see Fig. 9.10A). Stalked eyes can increase 10-fold the volume of water viewable from any given spot, which could save energy spent searching for food as well as help in the detection of predators. Stalked eyes are lost during metamorphosis to the juvenile stage (Blaxter 1975; Weihs & Moser 1981; Hairston et al. 1982; Fernald 1984; Noakes & Godin 1988).

The larval phase is characterized by the onset of function of most of the organ systems an individual will use for the rest of its life, except for reproduction. The marked vulnerability of larvae to starvation and predation therefore decreases as these organ systems become functional. Not surprisingly, anterior and posterior parts of larvae grow faster than middle sections, reflecting the larva's need to feed, respire, and escape (Fuiman 1983; Osse & van den Boogaart 1995). An obvious interrelationship exists between feeding ability and development of the jaws, digestive system, vision, and swimming musculature, and these linked systems develop in synchrony.

A less obvious pattern holds for the development of predator avoidance. In White Seabass, *Atractoscion nobilis* (Sciaenidae), larvae between 3 and 7 mm long (4–23 days old) show little difference in predator escape behavior. Only about 25% of larvae react to approaching predators, usually by a startle response involving **Mauthner cells**, which are a pair of large, early-developing interneurons that connect the hindbrain with motor neurons in the spinal column and cause the body to flex suddenly. Responses change markedly in slightly older fish. Between 7 and 10 mm (23–30 days), the visual and acoustic systems of the larvae improve markedly. Visual acuity and accommodation improve, the optic tectum of the brain where visual information is processed develops, the gas bladder inflates, and the number of free neuromasts on the head and body increases. Both gas bladder and neuromasts are involved in detection of sound or of water displacement, perhaps allowing the larva to sense predatory motion as well as its own movements better. As a result, White Seabass larvae become much more adept at avoiding ambushing and hovering predators such as juvenile White Seabass and flatfishes. This behavior is augmented by a change to a demersal existence, which reduces the threat of predation by fast-swimming water column planktivores (anchovies, sardines, mackerel) to which they are still relatively vulnerable. Rapid development of neurosensory structures is therefore critical in the transition from a relatively passive target to a larva in which >75% actively avoid predators, over the course of less than 1 week (Margulies 1989). In herring (*Clupea harengus*) larvae, successful predator avoidance coincides with the appearance of lateral line neuromasts and the filling of the otic bulla with gas, both structures associated with hearing (Blaxter & Fuiman 1990).

Larval morphology and taxonomy

Whereas eggs tend to be generally similar across many taxa, the larvae that emerge are strikingly distinct and often rather bizarre when compared with our expectations of fish morphology. The challenges to ichthyologists include identifying and linking larvae with their adult counterparts. Equally challenging is understanding the adaptive significance of the various, seemingly incongruous, structures that

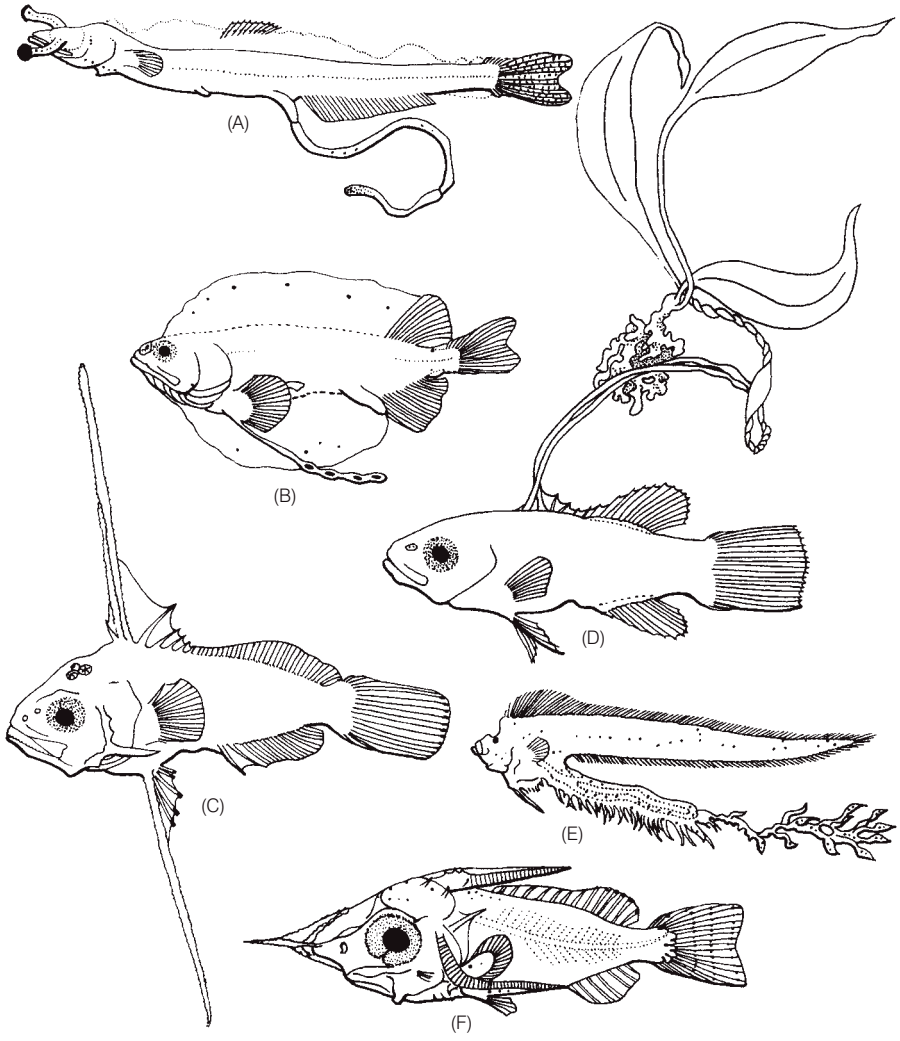


Figure 9.10

Larval diversity in marine fishes. Fish larvae often bear little external resemblance to the adults into which they grow. Spines probably make larvae harder to swallow, whereas trailing appendages could mimic siphonophore tentacles and therefore be avoided by predators, or may aid in flotation by slowing the sinking rate of the larva. (A) A 26 mm lantern fish larva, note eyes on stalks and trailing gut. (B) A 17 mm lanternfish larva (*Loweina*), note elongate pectoral ray and dorsal and anal finfolds. (C) An 8 mm seabass larva, note serrated dorsal and pelvic spines. (D) An 11 mm seabass larva, note elongate dorsal spine. (E) A 64 mm "exterilium" larva of an unknown ophidiiform, note trailing gut. (F) An 8 mm squirrelfish larva, note spines on head and snout. (A) from Moser and Ahlstrom (1974); (B) from Moser and Ahlstrom (1970); (C) from Kendall (1979); (D) from Kendall et al. (1984); (E) from Moser (1981), used with permission of Washington Sea Grant Program; (F) from McKenney (1959).

many larvae possess and then lose as they metamorphose into juveniles. One key is that larvae, although capable of locomotion, are at least initially relatively helpless and vulnerable. They are too slow to actively avoid most predators, other than those that also float with currents, such as various cnidarians with stinging cells. Many predators on pelagic larvae are small, gape-limited, and orient visually to their prey. To counteract these predators, larvae rely on structures that make them spiny and increase their body dimensions, or they mimic potentially noxious planktonic animals such as siphonophores (Fig. 9.10). Some structures such as extended fins, skin flaps, and gelatinous body coatings may also slow the sinking rate of larvae, keeping them in more nutrient-rich surface waters. Pigmentation patterns, which are often characteristic of larval stages and useful for identification, may screen harmful ultraviolet rays. This would apply particularly to the heavy melanistic pigmentation found on many species of **neustonic** or surface-dwelling marine larvae (Moser 1981).

Marine fish larvae have proven mysterious to ichthyologists, our knowledge having grown slowly and incrementally. Some of this history is reflected in the names given to larval stages, where many years of search were required to link larval and adult animals. Metamorphosis so radically alters many species that the two stages bear little obvious resemblance, attesting to different selective regimes and adaptations of different life history stages. The situation can be further complicated by stages intermediate between larvae and juveniles, sometimes called **prejuveniles**, which are also distinct. For example, the amphioxides larva of branchiostomatid lancelets and the kasidoron larva of the deepsea gibberfishes (Gibberichthyidae) once had familial status, the Amphioxididae and the Kasidoridae respectively. Generic status was initially given to a number of small fishes that are now identified as larvae or prejuveniles of well-known taxa, such as *Ammocoetes* (lampreys), *Leptocephalus* (anguilliform eels), *Tilurus* and *Tiluropsis* (notacanthoid halosaurs), *Querimana* (mullets), *Vexillifer* (pearlfishes), *Rhynchichthys* (squirrelfishes), *Dikellorhynchus* (tilefishes), *Acronurus* (surgeonfishes), and *Ptax* (snake mackerels). The scutatus larva of the Big-eyed Frogfish, *Antennarius radiosus*, was initially described as its own genus and species,

Kanazawaichthys scutatus. These and other distinctive larval stages are still given separate descriptive names, such as the exterilium ("external gut") stage of ophidioid cusk-eels (Fig. 9.10E), the "stalk-eyed" stylophthalmus larva of idiacanthid black dragonfishes, and the flagelloserranus larval stage of seabasses with elongate, ballooning second and third dorsal spines (Fig. 9.10D) (Richards 1976; Kendall et al. 1984; Pietsch & Grobecker 1987; Boschung & Shaw 1988; Eschmeyer 1990; Nelson 1994).

Getting from here to there: larval transport mechanisms

Many inshore marine fishes in temperate and tropical environments spawn offshore but their larvae or juveniles use shallow habitats such as bays, mangroves, and other estuarine regions as nurseries (Beck et al. 2003). This characterizes many coral reef species and anguillid eels, croakers, porgies, Bluefish, scorpionfishes, and flatfishes among temperate species. An important question therefore is how do such larvae, with their relatively limited swimming capabilities, move to shallow habitats? For coral reef species, many of which spawn at reef edges, luck may combine with behavior to determine dispersal. Active orientation, directed movement, utilization of favorable currents, and habitat choice are all implied by distribution and behavior of some species (Leis 1991; Kaufman et al. 1992; Cowen & Castro 1994; see above, Larval behavior and physiology).

For species along continents, however, adults may spawn 100 km or farther offshore, and larvae must traverse the continental shelf to arrive at nursery grounds in 2 or 3 months. Given that the average fish larva can swim only about 1 to 2 body lengths per second, or about 1 km/day, active processes such as directed swimming will be too expensive energetically as well as too slow to transport larvae such extensive distances or to fight the strong, outflowing currents that characterize embayments, sounds, passes, and many other estuarine locales. Additionally, once larvae find their way to a nursery ground, they frequently remain in specific regions, again requiring that they fight strong tidal, river, and wind currents that should flush them back out to sea. Behavioral adaptations of the larvae themselves are therefore implicated in finding and remaining in appropriate habitats.

The larval transport phenomenon has three main components: movement towards shore, location of and movement into nursery areas, and retention in nursery areas (Norcross & Shaw 1984; Boehlert & Mundy 1988; Miller 1988) (Fig. 9.11). Most interpretations of distribution patterns and behavior propose a combination of passive and active mechanisms. The degree of passivity decreases with age. Although young larvae may rely largely on passive transport of the water mass in which they hatched, older larvae can actively seek particular water masses with which they move. This larval habitat choice results from a surprising ability and tendency to swim actively against all but the strongest oceanic currents. Among 11 common Great Barrier Reef families studied, larvae in the latter half of their larval phase could swim at speeds greater than the mean current speeds found around reef areas and thus influence their dispersal "on a magnitude similar to the dispersing effect of oceanic currents" (Fisher 2005, p. 223).

The biggest mystery in larval transport has been the means by which larvae traverse hundreds of kilometers to get from offshore spawning grounds to inshore nursery areas (i.e., anguillid eels, bonefishes, menhaden, scorpionfishes, croakers, bothid and pleuronectid flatfishes). Of obvious significance is the spawning behavior of adults, especially their ability to place eggs in favorable locales. Spawning of many species on both the west and east coasts of North America occurs in winter when wind-driven, onshore currents are most common. Most marine eggs are buoyant and drift toward the surface. This places them in surface layers that are pushed shoreward by winds, either

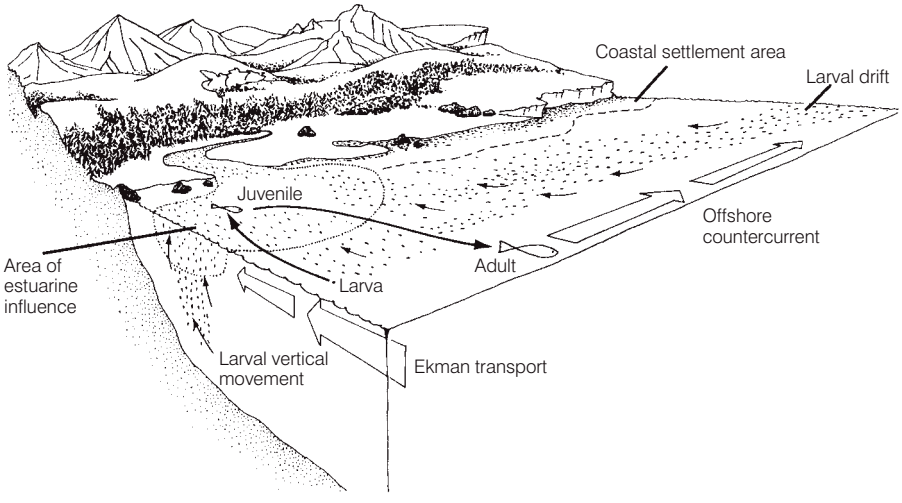


Figure 9.11
The general sequence of movement of marine larvae from offshore to inshore nursery grounds, as exemplified by events along the Oregon coast. Larvae are spawned offshore and carried onshore by shallow, wind-driven currents (e.g., Ekman transport). They then move alongshore by drifting with nearshore currents until encountering stimuli from estuaries, which they enter probably via selective tidal stream transport. From Boehlert and Mundy (1988), used with permission.

directly or as a result of Ekman transport, which involves wind-generated water movement that varies with depth. Some larvae may be carried by portions of major currents such as the Gulf Stream; the smaller water masses spin off from the main current and move shoreward as "warm core rings" (Hare et al. 2002).

Active behavioral mechanisms must also influence distribution because larvae of different species that spawn in similar locales may wind up in different places. For example, mullet, Bluefish, and dolphinfish spawn offshore, but larvae of the first two species use inshore nurseries, whereas dolphinfish larvae remain offshore. Vertical movements by larvae into upper surface waters could aid in retaining them in water masses that were moving shoreward (Norcross & Shaw 1984), although active swimming by older larvae of such species as Bluefish is also likely (Hare & Cowen 1996).

Shoreward movement is complicated by the larva's need to feed, so egg placement must also be in areas that are productive. Species that develop offshore often spawn in productive regions that are relatively stable, such as gyres, upwellings, fronts, or other circulating patterns that retain larvae where food availability remains high (e.g., pollock, Dover Sole). Some evidence suggests that coral reef fishes spawn at times and places that tend to retain larvae in local circulation patterns, which would promote their return to parental or nearby locales. Larval retention is at the heart of the controversy over whether coral reefs are **self-recruiting** or are dependent on upstream larval sources, a dichotomy with direct application to the design and placement of marine reserves (Mora & Sale 2002; Sponaugle et al. 2002; see Chapter 26, Biological preserves). Evidence is accumulating that at least for some locales and species, self-recruitment may be as common as widespread dispersal (e.g., Cowen et al. 2000; Hawkins et al. 2000; Taylor & Hellberg 2003). Given oceanographic features and currents and known larval behavior, between 37% and 80% of snapper larvae may self-recruit to Cuban waters (Paris et al. 2005). The pattern of currents and gyres around the Florida Keys would tend to aid retention of locally spawned larvae (Lee & Williams 1999). For isolated island regions such as Hawaii, larval retention might be insurance against dispersal into vast and uninhabitable oceanic regions (Norcross & Shaw 1984; Lobel 1989).

After the journey towards shore, larvae frequently accumulate along shorelines and at mouths of bays and estuaries, only to be found later inside these regions. Such pulsed, directional movement against the general net flow of water out of an estuary may involve **selective tidal stream transport**. During such transport, small fish ride favorable currents and avoid unfavorable ones, usually by moving up into the water column on flood tides and down to the bottom during ebb tides (see Chapter 23, Tidal patterns). This has been the suggested mechanism for movement into and retention within estuaries by young anguillid eels, herrings, shads, croakers, and plaice (Miller 1988).

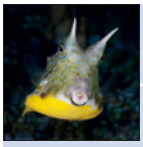
Once in a nursery area, a fish must fight currents that would distribute it offshore or to less desirable inshore habitats. This becomes less of a problem as a juvenile fish grows larger and stronger and can actively choose locales or currents, but remains a significant constraint for small larvae of species such as Atlantic Herring (*Clupea harengus*). Herring spawn in the estuary itself, and larvae first move to upstream areas but later reside in downstream areas. This distribution is achieved by vertical movement with respect to different currents. In most estuaries, surface waters are relatively fresh and move downstream, bottom waters are relatively saline and move upstream, and intermediate depths exhibit no net directional movement. In the St. Lawrence River estuary of Canada, young herring larvae remain near the bottom and are consequently carried upriver, whereas older larvae tend to move up and down twice daily and hence hold position in a relatively confined area of the estuary (Fortier & Leggett 1983). Species that spawn in estuaries (e.g., various herrings, cods, flatfishes, wolffishes, sculpins, gobies) tend to have large, demersal eggs and brief larval stages, all characteristics that would minimize export from the habitat (Hempel 1979; Norcross & Shaw 1984).

Larvae would have to respond to environmental cues that informed them when they were approaching appropriate or inappropriate habitats. Postulated cues that larvae might use to discriminate between water masses include odor, salinity, oxygen, turbidity, pH, geomagnetism, turbulence, light, food availability, temperature, and current speed and direction. An intriguing possibility is that larvae of coral reef species hear sounds associated with reefs and consequently orient toward those sounds. Larval traps that incorporated underwater speakers that broadcast natural reef noises (snapping shrimp, fish vocalizations) attracted significantly more larvae and a greater diversity of larvae than silent traps, especially at night (Leis et al. 2003; Simpson et al. 2004; Tolimieri et al. 2004). These and other studies lead to the conclusion that "sound emanating from reefs at night is a useable sensory cue for fish larvae trying to find settlement habitat" (Leis & Lockett 2005, p. 715). Similar evidence indicates that larvae are attracted to odors associated with reef areas (e.g., Atema et al. 2002). Clearly, multiple cues facilitate attraction to and settlement in appropriate habitat (Kingsford et al. 2002; see Chapter 24, Synthesis: what determines assemblage structure among coral reef fishes?).

Responses to any such cues are likely influenced by tidal, circadian, or lunar rhythms (see Chapter 23). Much discussion has focused on whether larvae can in fact detect minor differences in these factors among water masses and orient appropriately, and this remains an area of active research.

Many of our conclusions about larval transport remain conjectural because of a lack of confirming data. In addition, alternative explanations that view larvae as passive, drifting particles that regulate little more than their buoy-

ancy readily explain certain aspects of their distribution. For example, rivers commonly enter estuaries and create ebb tides that are less saline than flood tides. Increased buoyancy in saltier water would tend to move drifting particles inshore with the flood, with no behavioral selection of water mass necessary (Miller 1988). Such purely passive drift cannot be totally dismissed in explanations of larval transport, although most evidence points to some type of behavioral regulation at most stages of development, at least once the egg stage is past.



Summary

SUMMARY

1. Fishes experience indeterminate growth, growing throughout their lives, changing from larvae to juveniles to adults. They also change continually in terms of anatomical traits and ecological requirements and interactions. In most respects, large size confers physiological and ecological advantages on an individual.
2. Gametogenesis describes the development of sperm and eggs through a series of definable stages. Fish sperm vary in size, shape, and number of accessory structures (flagella, acrosomes). Fish eggs develop as oocytes that are invested with yolk. Females are able to resorb unshed eggs and reuse the materials that went into egg production. Fecundity, the number of eggs a female produces, generally increases with increasing body size within a species and varies among species from one or two in some sharks to many millions in large teleosts.
3. Most marine fishes produce pelagic eggs that are fertilized externally and from which pelagic larvae hatch. Most freshwater fishes deposit eggs on vegetation or on the bottom, often in nests.
4. Reproductive effort is a measure of the energy allocated to reproduction by an individual and can be characterized in part by gonad weight/body weight, adjusted for the frequency with which an individual spawns and the phase of the spawning cycle.
5. Fertilization occurs external to the body of the female in most bony fishes and internally in most elasmobranchs and in about a dozen families of bony fishes. Females of some internally fertilized species can store sperm for several months. Males of internally fertilizing species possess an intromittent organ, modified from fins or cloacal tissue, for injecting sperm into the female.
6. Embryonic development in fishes proceeds as in most vertebrates. Many species are identifiable at or just after the time of hatching, based on pigmentation and fin development. Although most fishes hatch from eggs (oviparity), some undergo internal gestation and are born live (viviparity), with various intermediate conditions (generally referred to as ovoviviparity).
7. Meristic (countable) traits may vary among developing fishes as a function of environmental conditions. Typically, fishes that develop in colder water lay down greater numbers of scales, fin rays, and vertebrae.
8. The larval period is most often the stage at which an individual disperses from the habitat of its parents. An important event in a larva's life comes when the yolk supply is exhausted and the young fish must forage on its own. Food availability during this "critical period" may determine the future size of a population and may determine many aspects of spawning locale and timing. Most larvae die from starvation or predation during their first week of life. Physiological tolerance and sensitivity, ecological and behavioral competence, and survivorship all increase with increasing age.
9. Fish larvae often bear little external resemblance to the adults into which they grow. Larvae often possess large spines and trailing fins and appendages that may give them protection from predators. Many fish larvae and juveniles were originally given different specific, generic, and even familial names before they were linked with the species into which they develop.
10. Many marine fishes spawn far offshore. The mechanisms by which their larvae move inshore to nursery habitats are a matter of debate. Onshore movement may involve passive transport via wind-driven surface currents. Movement into an estuary can involve selective tidal stream transport, where a small fish moves up into the water column on flood tides and then hugs the bottom during ebb tides.

Supplementary reading

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Chapter 10

Juveniles, adults, age, and growth

Chapter contents

CHAPTER CONTENTS

Juveniles

The numerical abundance of larval stages of many species and the processes that reduce this abundance have been a major focus of ichthyological research. But growth and change continue throughout the life of a fish. Since most commercially important fishes are exploited as adults, juvenile growth and maturation to adulthood have been extensively studied. Additionally, many fishes undergo a postreproductive period when organ systems degenerate, providing a comparative model for studying the aging process and old age, topics of importance in human biology.

Transitions and transitional stages

Hatching or birth and the onset of exogenous feeding represent two landmark events in the early life of a fish. Also of importance for many species is the change from larval to juvenile habitat, a transition that often involves settling from the water column and the assumption of a near-benthic existence. Traditionally, the larval phase is considered to end and the juvenile phase begin as larval characters are lost and the axial skeleton, organ systems, pigmentation, squamation, and fins become fully developed, at which time fish look essentially like a miniature adult. This transition can be brief and relatively simple, requiring minutes or hours in some damselfishes, or it can be very long and complicated, taking several weeks in salmons, squirrelfishes, gobies, and flatfishes (see below) (Kendall et al. 1984).

Some complex adaptations that essentially define major taxonomic groups do not appear until the juvenile phase. One example is the alarm reaction of the Ostariophysi (see Chapter 14, Subdivision Otocephala, Superorder Ostariophysi; Chapter 20, Discouraging capture and handling). Minnows and other ostariophysan fishes have a characteristic escape response to alarm substance, a chemical released from the skin of injured conspecifics. The alarm reaction appears relatively late in development, after shoaling behavior develops and after fish can already produce alarm substance in their epidermal club cells. However, the alarm reaction is genetically hardwired. After 51 days post-hatching, European Minnows, *Phoxinus phoxinus*, react to alarm substance in the water the first time they encounter it, regardless of experience with predators (Magurran 1986b).

Although eggs and larvae are by far the most vulnerable stages during the life history of an individual (see above and Chapter 24, Population dynamics and regulation), attainment of the juvenile stage still entails strong selection for successful food acquisition and predator avoidance abilities. The interplay between these factors is exemplified by juvenile Brook Trout, *Salvelinus fontinalis*. Brook Trout do not undergo the smolt transformation characteristic of many other salmonids, as discussed below. Instead they hatch in spring and take up residence in small, shallow

streams. Their chief task is acquiring sufficient energy stores during their first summer to get through the winter period of low food availability. Larger juveniles have a greater chance of surviving the first winter. To acquire energy and to grow, they must establish and defend a feeding territory. The best territories are in relatively shallow water, exposing the fish to both aquatic and aerial predators. Predators can be avoided by remaining motionless, but motionless fish can not chase prey or repel territorial invaders. Feeding and fighting distract an individual from avoiding predators.

Basically, smaller fish take more risks and tend to feed more extensively and openly, whereas larger fish are less willing to accept predation risks and are more willing to disrupt their feeding by taking evasive actions. The greater likelihood of winter starvation forces smaller juveniles to make the trade-off between predation risk and foraging differently from larger fish of the same age (Grant & Noakes 1987, 1988; see Chapter 20, Balancing foraging against predatory threat).

Transitional stages complicate the search for universally descriptive terminology about early life history. They also make it difficult to pinpoint when fish change from one developmental form to another. Transitional stages occur most commonly between larval and juvenile and between juvenile and adult periods. The transitional phase between larva and juvenile in reef fishes has been variously referred to as post-larval, late-larval, new recruit, juvenile recruit, pelagic juvenile, transition juvenile, and settler. The transitional phase may be variable in length, even within a species. This variability makes sense when it is realized that a young fish may not find a habitat appropriate to its next stage simultaneously with its ability to make the transition into that stage. Hence if it were forced to settle from the plankton at day 35 of development, or at the moment that skeletal elements became ossified and fin rays fully developed, a larva that was still far out at sea might have no choice but to sink to the bottom several kilometers down and starve or freeze to death.

Variability in larval period is evident in larvae of the Naked Goby, *Gobiosoma bosci*. These larvae settle from the plankton and take up a benthic, schooling existence for up to 20 days before transforming to solitary juveniles. Other gobies and a wrasse may have a 20–40-day "window of opportunity" during which they can search for appropriate habitat as larvae without transforming into the more sedentary juvenile form. Flatfishes can delay transformation to the juvenile form if they do not encounter an appropriate juvenile habitat; they do this by alternating between settling on the bottom and swimming above it. Substrate preferences, which imply active search for appropriate habitat, have been observed in numerous larvae (e.g., Sale 1969; Kaufman et al. 1992; Sancho et al. 1997). Direct observations of settling coral reef species indicate that such flexibility may be relatively widespread, and that settlement and transition from larva to juvenile should not be viewed as an all-or-nothing decision. Once settling competence is acquired, many larvae may have days or even weeks before they must settle and assume juvenile habits (Victor 1986; Breitburg 1989; Leis 1991; Kaufman et al. 1992; see Chapter 9, Larval behavior and physiology).

Complex transitions: smoltification in salmon, metamorphosis in flatfish

Metamorphoses by definition imply major changes in the anatomy, physiology, and behavior of an animal. The transition from larva to juvenile in many fishes involves complex suites of change that frequently include major changes in feeding habits and habitat. These alterations necessitate a breaking down and reworking of embryonic and larval structures and a rebuilding into adult structures that will function under very different environmental conditions. A brief example involves sea lampreys (see also Chapter 13, Petromyzontiforms). Larval lampreys, termed **ammocoetes**, are sedentary, blind, freshwater animals that reside in burrows in silty bottoms and filter suspended matter from the water. At metamorphosis to the juvenile stage, this animal is transformed into a predator/parasite with a suctorial mouth, rasping tongue, salivary glands that secrete anticoagulants, functional eyes, tidal ventilation, and an ability to live in sea water (Youson 1988). Many other taxa could be mentioned, but details of two well-studied groups, salmon and flatfishes, will serve to exemplify the complexity of the reworkings that go into changing an animal adapted to larval existence into one adapted to meet the challenges of later stages in its life history.

Smoltification

Widespread interest in salmonids has resulted in detailed knowledge and special terminology associated with different life history stages (see Fig. 23.11). Typically, salmon and trout spawn in gravel pit nests termed **redds**, the eggs hatch into **alevins** (yolk-sac larvae) that resorb the yolk and become **fry**. Fry develop species-typical patterns of vertical bars on their sides called **parr marks**, the fish now being called **parr**. After a few months or years depending on species and population, the parr of anadromous species that spend their juvenile lives at sea (Pacific and Atlantic salmons, Steelhead Trout) move downstream as silvery **smolts**. The processes associated with the downstream migration of smolts are among the most intriguing and best studied biological aspects of the early life history of fishes.

Smoltification is a complex phenomenon involving reworkings of just about every characteristic of a young salmon. An interesting feature of the changes is that they are preparatory: they occur as the animal changes from a parr to a smolt in fresh water, anticipating the environmental conditions that the young fish will later encounter after

it enters the ocean. Anatomically, smolts turn from countershaded and barred to silvery, which is a better form of camouflage in the open sea (see Chapter 20, Invisible fishes). They also take on a slimmer, more streamlined shape that involves a reduction in condition as body lipids are consumed. The silvering results from an increase in the density of purine crystals, mostly guanine but also hypoxanthine, which are deposited beneath the scales and deep within the dermis. Despite a loss of lipids, smolts are more buoyant than non-migratory conspecifics. Increased buoyancy results from increased gas volume in the gas bladder, which may reduce the energetic costs of migration. The complexity of hemoglobins in the blood increases, affecting oxygen affinity and the Bohr shift among other respiratory factors (see Chapter 5, Gas transport).

These alterations prepare a migrating smolt for oceanic conditions that often include reduced availability of oxygen compared with the cold, turbulent waters of a stream or river. Many changes occur in gill function, including increased chloride cell number and changes in ion permeability and enzymatic activity. These changes anticipate the move from the **hypoosmotic** freshwater environment where ion loss is the major problem to the **hyperosmotic** marine environment where water retention is the major problem (McCormick & Saunders 1987; Hoar & Randall 1988; Wedemeyer et al. 1990; see Chapter 7, Osmoregulation, ion balance and pH balance, and excretion).

Behaviorally, Atlantic Salmon parr are first highly territorial in shallow water, but then move into deeper water and form shoals, although a dominance hierarchy frequently exists in the shoals. Even this aggression decreases as fish start to move toward the sea. The movement is aided by a reversal in **rheotaxis**, the response to flowing currents that kept even embryos headed upstream (see above). Positive rheotaxis disappears as fish in large shoals drift downstream with the currents (Hoar & Randall 1988; Noakes & Godin 1988; Huntingford 1993). It is during smolting that young fish learn or **imprint** on the odor of their home stream, enabling them to identify it among hundreds of alternatives when they return from the sea during the spawning migration (see Chapter 23, Diadromy).

Many of the transformations that occur during smoltification can be linked to changes of circulating hormones (Fig. 10.1). Increases in corticosteroids, prolactin, and growth hormone respectively affect lipid metabolism, osmoregulation, and mineral balance. Cortisol and estradiol levels also increase. Thyroxin levels also increase naturally, and experimental injections of thyroid-stimulating hormone can induce many of the physiological and behavioral events of smoltification, such as purine deposition, gill enzyme activity, increased swimming activity, body growth, and lipid consumption. These changes suggest that thyroid hormone, interacting with photoperiod and endogenous rhythms, plays an important role in the process (Hoar & Randall 1988; Huntingford 1993).

Smoltification is by no means fixed in terms of age in a species or even a population. Atlantic Salmon may smolt at the ages of 1 to 7 years, depending on temperature and latitude. Onset of smoltification in siblings may vary by as much as a year. Feeding opportunities appear to be the key determinant of the onset of smoltification. Well-fed individuals smoltify younger, although genetic differences in feeding activity may cause some fish to cease feeding and consequently delay smoltification. Some evidence indicates a size threshold: Atlantic Salmon that do not attain a length of 10 cm by the fall of the first growing season are less likely to smolt the next year. Rate of growth and age interact with this hypothesized threshold length. Faster growing fish are more likely to smolt, and older fish may smolt at a smaller size.

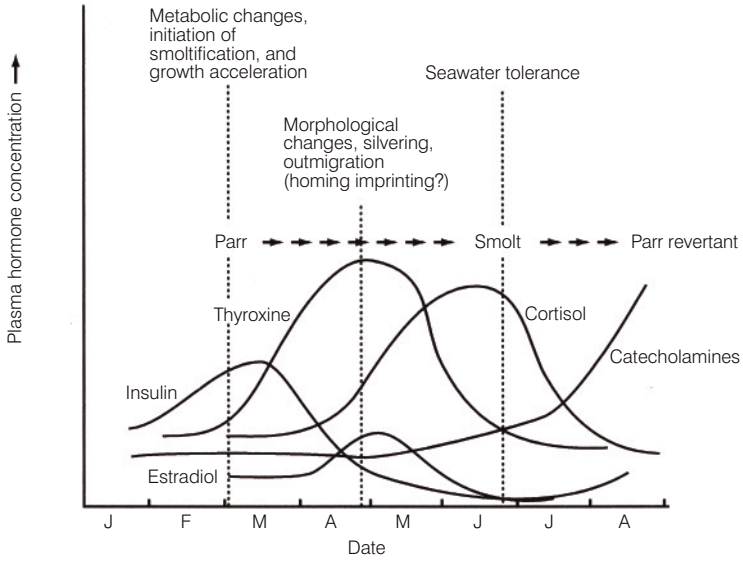


Figure 10.1

Sequence of events during smolting in the Coho Salmon, *Oncorhynchus kisutch*, and correspondence with changing levels of important hormones. Hormones implicated in the parr–smolt transformation tend to peak prior to, and may cause, the acquisition of the various anatomical, physiological, and behavioral traits that characterize the smolt stage. One group, the catecholamines, remains low throughout the smolting process but climbs if the fish does not migrate to sea and instead reverts to the parr stage. Drawing by W. W. Dickhoff, in Hoar and Randall (1988), used with permission.

Timing is also important. The smolt stage itself lasts a few weeks; if a fish does not enter the sea, the process will reverse and the fish will return to the parr condition. Although Pacific salmon (*Oncorhynchus* spp.) and Atlantic Salmon are considered anadromous and therefore undergo smoltification, these fishes can become **landlocked** and never migrate to sea. Also, some individuals within a population may bypass the smolt and migratory phases and remain behind in fresh water. When this happens in males, they may mature quickly at age 1 year and spawn with females that return the next season (see Chapter 21, Alternative mating systems and tactics). In Atlantic Salmon, the proportion of such **precocious** males differs among populations, ranging from 5% to >50% of the males. The factors determining precocious maturation in male salmons are widely debated, with evidence suggesting that food availability or genetic factors are determinant (Thorpe 1978; Hoar & Randall 1988).

Asymmetrical flatfish

Symmetry is an almost universal anatomical characteristic of animals. Most animals, regardless of phylum, exhibit **bilateral symmetry** in their morphology, having roughly mirror-imaged structures to the right and left of midline. Deviations from symmetry imply unexpected functions and adaptations. Biologists seek to understand the causation and function of asymmetry at the proximate level of genetic and environmental control of development and at the ultimate level of its possible adaptiveness.

Among the more startling examples of asymmetry is the "**handedness**" of flatfishes. The 14 families and about 680 species of pleuronectiforms (flounders, halibuts, soles, plaice, etc.) as a group are characterized by adults that lie on the bottom on one side of their body. Their flattened bodies are functionally analogous to many other benthic-living fishes such as angel sharks; skates; rays; banjo, suckermouth armored, and squarehead catfishes; ogcocephalid batfishes; platycephalid flatheads; and some scorpionfishes. The major difference is that all the other groups are flattened in a dorsal–ventral plane (= **depressed**), whereas flatfishes are laterally flattened (= **compressed**) (people often depress cockroaches and compress mosquitoes). Depressed fishes maintain their bilateral symmetry despite their extreme morphology. Most compressed fishes are deep-bodied, bilaterally symmetrical species that swim in the water column and use their flattened bodies to increase maneuverability or to increase their body depth against predators (e.g., serrasalmine characins, centrarchid sunfishes, many pompanos, monodactylid fingerfishes, butterflyfishes, ephippid batfishes and spadefishes, and surgeonfishes). Flatfishes are laterally compressed but lie on the bottom on either their right or left side and are therefore faced with the challenge of receiving sensory information from only half their sense organs, the other half being buried in the sand or mud. The most obvious accommodations to their unusual orientation can be seen in the structure and development of their visual apparatus.

Flatfishes begin life as normal, bilaterally symmetrical, pelagic larvae. In the Starry Flounder, *Platichthys stellatus*, larvae emerge from the egg when about 3 mm long and begin exogenous feeding. For the next month or two, they lead normal pelagic lives, until they reach a length of 7 mm. Then metamorphosis to a compressed shape begins (size at metamorphosis varies between 4 and 120 mm in different flatfishes). Most bones are incompletely ossified at this time, which apparently makes the transformation easier. The anterior neurocranium, brain, and eye sockets (orbits) rotate (Fig. 10.2). This allows one eye to actually migrate across the top of the head. In some species of bothids and paralichthyids, the eye moves through a slit that appears between the skull and the base of the dorsal fin. The dorsal fin remains in the midline or, in some species, grows forward until the first spine sits anterior to the eyes. The entire process happens quickly, over about a 5-day period in Starry Flounders, or in less than 1 day in some species.

Other asymmetries occur that reflect transformation to a benthic and compressed existence. The nasal organ on the blind side migrates to the dorsal midline; the blind side is usually unpigmented, may lack a lateral line, has smaller pectoral and pelvic fins, and squamation frequently differs on the two sides. During metamorphosis, the semicircular canals undergo a 90° displacement and the dorsal light reaction (see Chapter 6, Equilibrium and balance) also changes appropriately for a fish lying on its side. At the time of metamorphosis or shortly thereafter, the fish takes up a benthic existence and loses its gas bladder. In Windowpane, *Scophthalmus aquosus*, eye migration accompanies and is coordinated with a number of other developmental events, all culminating at about the time the young fish takes up a benthic existence (Fig. 10.3).

As a rule, families are characterized by having both eyes on a particular side of the head. Hence lefteye flounders (Bothidae) lie on their right side and have both eyes on the left side, the right eye having migrated; this is termed the **sinistral condition**. Occasional freaks occur because of presumed developmental abnormalities, and individual members of right-eyed species may be left-eyed. In such individuals, viscera may also be twisted and color patterns abnormal. Regular variation in such handedness also occurs. Starry Flounders, although members of the righteye (Pleuronectidae) family and usually right-eyed or **dextral**, often include left-eyed individuals. In California, 50% of the individuals may be left-eyed, and in Japan 100% of these pleuronectids are left-eyed! That these nonconformist individuals are in fact abnormal is evident in the development of their optic nerves. In all vertebrates, normal development results in a crossing of the optic nerves leading from the eye to the brain, such that the right side of the brain receives information from the left eye and vice versa. In left-eyed Starry Flounders, the optic nerve crosses twice,

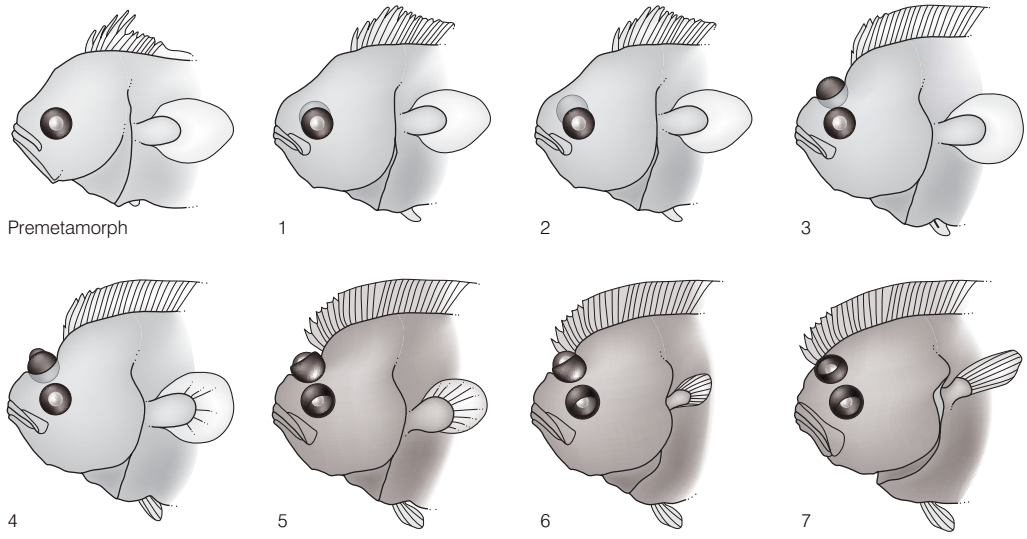


Figure 10.2

Progressive eye migration in a developing Summer Flounder, *Paralicthys dentatus*. When the flounder larva is about 10 mm long, the right eye begins to migrate over to the left side of the fish via a process that includes bone resorption and rotation of the fish's neurocranium. The entire process takes 3–4 weeks, during which time the larva grows 5–10 mm. The position of the right eye on the right side of the body is depicted in stages 1 through 3 (faint circle). Note other developmental changes, including development of eye structures, anterior migration of the dorsal fin, growth and elaboration of the pectoral and pelvic fins, and mouth growth. After Keefe and Able (1993), used with permission.

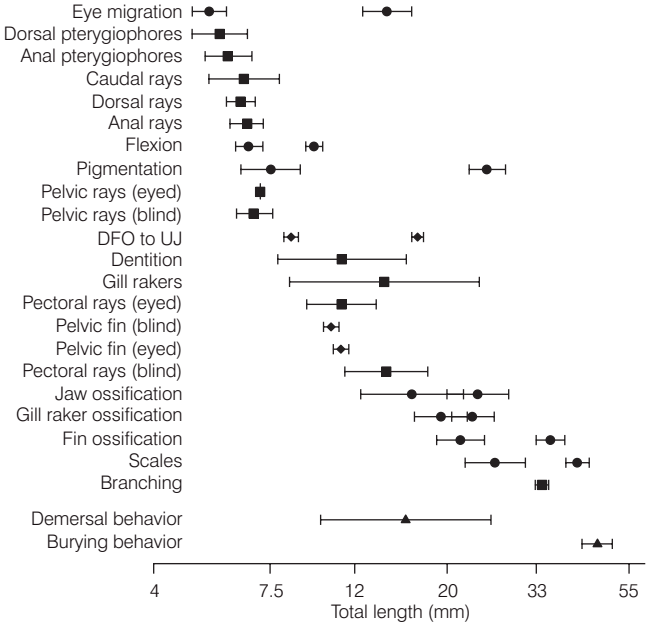


Figure 10.3

Metamorphosis from a pelagic to a benthic life in flatfishes involves numerous traits and behaviors. A sequence of changes occurs along with eye migration, some at different times and at different rates. eyed, traits on the eyed side of fish; blind, traits on the blind side; DFO to UJ, distance from dorsal fin origin to anterior edge of upper jaw; Branching, branching of dorsal fin rays. Slightly modified from Neuman and Able (2002), used with permission.

literally twisting around itself, a condition for which it is hard to assign any adaptive advantage. Experimental crosses of individuals from different populations have established that the determination of handedness in flatfishes is under complex genetic control, but no evidence exists to suggest that one side is adaptively better than the other (Policansky 1982a, 1982b; Ahlstrom et al. 1984).

Adults

Determination, differentiation, and maturation

The development of a reproductively functional individual involves three very different processes – determination, differentiation, and maturation – that occur at different times during life history (Fig. 10.4). **Sex determination** is the process by which the maleness or femaleness (**gender**) of an individual is decided, usually during early ontogeny. Determination can be either genetically or environmentally controlled. **Differentiation** involves the development of recognizable gonadal structures – ovaries or testes – in an individual, although maturing gametes are not necessarily present. **Maturation** implies the actual production of viable gametes, spermatozoa or ova. An individual's gender may be determined at fertilization, the fish may differentiate as a juvenile, but it is not technically an adult until it matures.

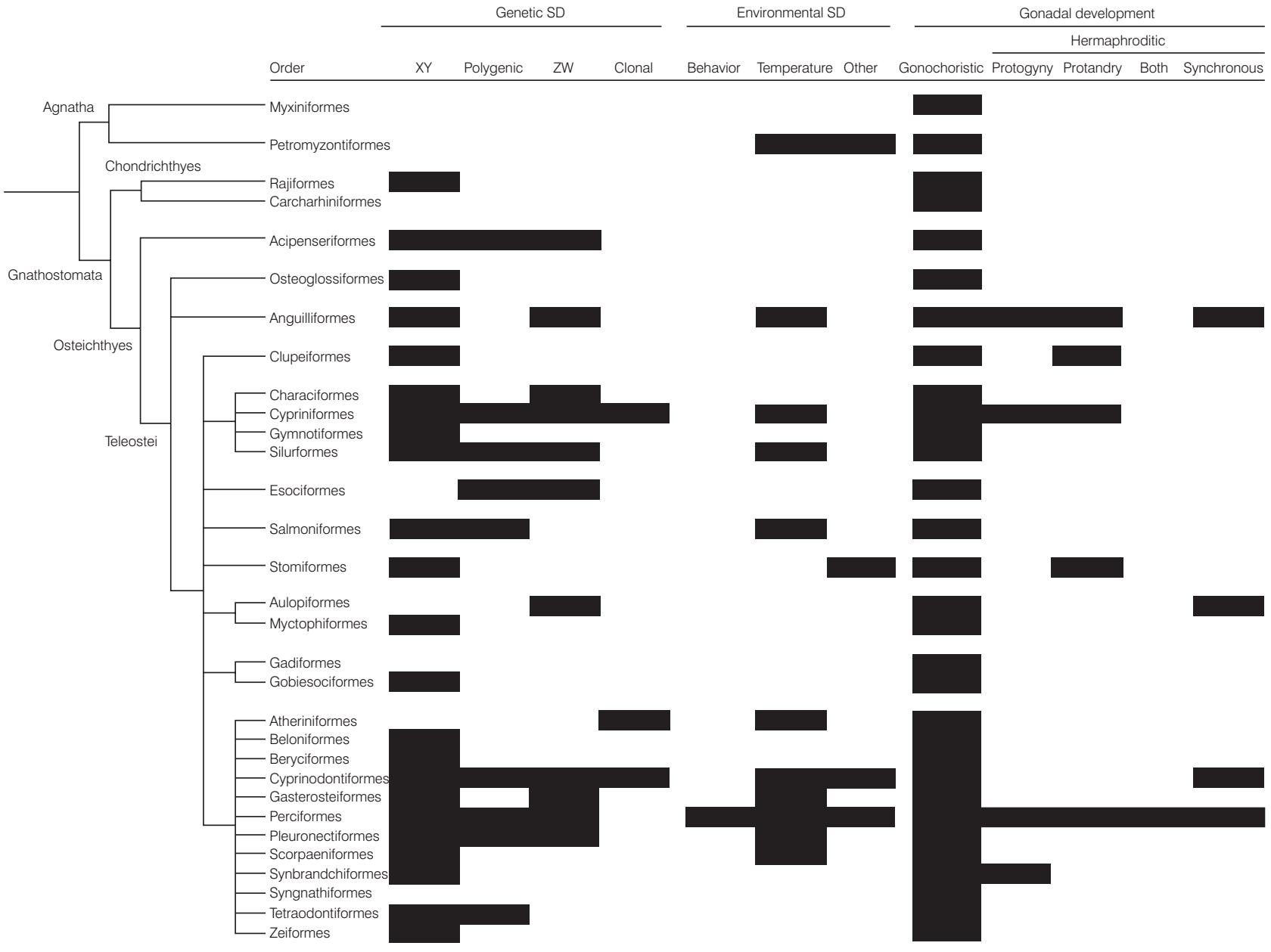


Figure 10.4

Patterns of sexual determination and maturation among fishes. Sex determination (SD) can be under genetic or environmental control, with sex-determining genes located on defined sex chromosomes (XY, ZW) or distributed among autosomal chromosomes. Among most sex-changing fishes, individuals mature as female first (protogyny) or male first (protandry). See text for details. From Devlin and Nagahama (2002), used with permission.

An interesting relationship exists between sex determination, sex change, and the existence of sex chromosomes in vertebrates. Birds and mammals have identifiable sex chromosomes. Male mammals are the **heterogametic** sex, possessing an X and a Y sex chromosome. The opposite holds for birds, in which the female is the heterogametic sex, known as ZW heterogamety. In birds and mammals, gender is determined and fixed at fertilization. The gender of individuals remains constant, and environmental conditions have no effect on sex determination. Some reptiles and amphibians have sex chromosomes, some do not. In turtles, males are generally produced at low temperatures; the opposite holds for crocodilians and lizards. In taxa in which such **environmental sex determination** or **ESD** occurs, sex chromosomes are relatively rare (Gorman 1973; Francis 1992).

Genetic determination of sex in fishes may involve monogenic or polygenic control, and sex-determining genes and factors can be located on autosomal chromosomes or on definitive sex chromosomes (Devlin & Nagahama 2002). Sex chromosomes are relatively rare among fishes, characterizing 176 species in 72 families, or about 10% of the approximately 1700 species for which chromosome number and morphology have been described, although this may underestimate the actual frequency of heterogamety. Examples of familes with sex chromosomes include several deepsea families, such as bathylagid smelts, sternoptychid hatchetfishes, neoscopelids, myctophid lanternfishes, and melamphaid ridgeheads. In shallow waters, heterogamety has been found in rajids; osteoglossids; anguillid and conger eels; characins; bagrid, silurid, and loricariid catfishes; trout; lizardfish; killifishes; livebearers; sticklebacks; sculpins and cichlids; gobies; white marlin; flatfishes; and triggerfishes (Gold 1979; Sola et al. 1981; Devlin & Nagahama 2002). The heterogametic gender can be either male (XY) or female (ZW), with male heterogamety being about twice as common as female heterogamety (Fig. 10.4).

As might be anticipated in a taxon where genetic determination of sex may be the exception, sex determination in fish is quite flexible and is influenced by a variety of external factors (Devlin & Nagahama 2002; Godwin et al. 2003). This lability has been exploited in aquaculture programs because it allows practitioners to produce monosex strains of economically valuable species where one sex grows faster or attains larger size than the other. A drawback of widespread ESD is that it makes fishes vulnerable to environmental degradation, including endocrine-disrupting chemicals and climate change (Strussman & Nakamura 2002).

The exact stage at which gender is determined in fishes is controversial. Although genetic determination probably applies to most species, in many fishes sex determination may not be fixed at fertilization or even during early ontogeny. Many fishes go through a **prematurational sex change**, differentiating but not maturing first as females, with some individuals later changing to males (Devlin & Nagahama 2002). This pattern is suspected or known from hagfishes, lampreys, minnows, salmonids, cichlids, butterflyfishes, wrasses, parrotfishes, gobies, and belontiid paradise fish. Such ambivalence is not altogether surprising when it is recalled that all gonads in agnathans and teleosts develop from a single structure, the epithelial cortex, that gives rise to ovaries in higher vertebrates. In sharks, ovaries develop from the cortex whereas testes develop from the medulla. Sharks consequently show no sexual lability.

Temperature may play a strong role as an environmental factor because sex determination in fishes is sensitive to thermal alteration (Devlin & Nagahama 2002). Experimental studies generally find **masculinization** of individuals or male-skewed sex ratios when the eggs or larvae of species of minnows, gobies, silversides, loaches, rockfishes, cichlids, and flounders are reared at higher temperatures, with the effect increasing as temperature rises. **Femininization** or female-biased sex ratios have resulted at higher temperatures in lampreys, salmon, livebearers, sticklebacks, and seabasses. The mechanisms underlying these effects appear to involve either altered enzyme activity or endocrine disruption (hormone synthesis or impaired steroid receptor function). Aromatase is an ovarian enzyme that converts testosterone to estradiol, a process vital to oocyte growth. In Nile Tilapia, *Oreochromis niloticus*, and Japanese Flounder, *Pleuronectes olivaceus*, elevated temperatures resulted in masculinization associated with reduced aromatase activity (Devlin & Nagahama 2002).

The possibility for ESD exists in all the fishes listed above, "environment" including climate, food availability, and social interactions. In the Paradise Fish, *Macropodus opercularis*, all individuals begin as females and some later differentiate as males, but these changes occur prior to maturation. Final determination is based on social status: dominant individuals become male and subordinate individuals become female as a direct result of social interactions. Anguillid eels, despite having ZW heterogamety, produce more males in dense populations as an apparent response to crowding (Krueger & Oliveira 1999). ESD has also been documented in Sockeye Salmon, Ricefish or Medaka (*Oryzias latipes*), poeciliid livebearers, rivulines, and Siamese Fighting Fish, all in response to temperature extremes (Francis 1992; Azuma et al. 2004).

ESD is best understood in the Atlantic Silverside, *Menidia menidia*. Northern populations have a limited spawning season and exhibit genetic determination, but southern populations have a longer season and are more sexually labile. Southern larvae spawned in the spring at low temperatures tend to become females, whereas those spawned in summer at higher temperatures become male. Spring-spawned individuals will have a longer growing period before the next spawning season than will late-spawned fish. Spring-spawned fish can therefore take advantage of the body size : egg number relationship and benefit more

from larger body size as females than as males (Conover & Kynard 1981; Conover & Heins 1987).

Many species change sex after initial maturation, referred to as **postmaturational sex change**; non-changers are called **gonochores** (see Fig. 10.4; see also Chapter 21, Gender roles in fishes). Maturing first as one sex and then changing to the other is referred to as **sequential hermaphroditism**. Changing from functional female to functional male is termed **protogyny**; a change from male to female is **protandry**. Protogyny is by far the more common form, accounting for 193 of the 235 species of sequential hermaphrodites surveyed by Devlin and Nagahama (2002). A few small serranids (*Serranus*, *Hypoplectrus*) and some gobies are **simultaneous** (or **synchronous**) **hermaphrodites**, producing viable sperm and eggs at the same time (Cole 1990; Oliver 1997; St. Mary 1998). Only the rivulid New World rivulines in the genus *Kryptolebias* (formerly *Rivulus*) fertilize their own eggs (Soto et al. 1992; Cole & Noakes 1997). Some species of live-bearers are **parthenogenetic**, having eliminated males from the reproductive picture, and female Bamboo and Bonnethead Sharks in captivity have laid fertile eggs or given birth to live young without having mated with males (e.g., Mayell 2002). The environmental and social conditions promoting sex change, hermaphroditism, and parthenogenesis are detailed in Chapter 21.

Maturation and longevity

Not surprisingly, age at first reproduction and longevity vary greatly among fishes (Finch 1990), making it difficult to identify patterns or draw conclusions (for an excellent overview of various classifications of maturation stages, see Pusey et al. 2004, table 5). The adaptive significance of differences in **age at first reproduction** relates to trade-offs between committing energy to somatic growth versus reproduction, combined with expected mortality rates and the probability of living long enough to reproduce. These trade-offs are discussed in Chapter 24, Life histories and reproductive ecology. Extremes in age at first reproduction include some embiotocid surfperches, the males of which are born producing functional sperm. Gobioid fishes in the genera *Schindleria* and *Paedogobius* have been shown to mature in less than 2 months, *Schindleria* maturing in as little as 3 weeks (Kon & Yoshino 2002a). Many small stream fishes mature in 1 year, being reproductively active the spawning season after they hatch (e.g., most darters), although maturation may take longer in populations at higher latitudes.

At the other extreme, sturgeons and some sharks may take 10–20 years to mature. Sturgeons may live 80–150 years. The slowest maturing shark is the Spiny Dogfish, *Squalus acanthias*, a species well known to students of comparative anatomy. Spiny Dogfish do not mature until 20 years old and have the longest recorded life span of a shark, upwards of 70 years. The record for naturally delayed reproduction among bony fishes is apparently held by American eels in Nova Scotia, which may not mature and undertake their spawning migration back to the Sargasso Sea until they are 40 years old (see Chapter 23, Catadromy).

Longevity patterns are only slightly more definable. With many exceptions, larger fishes generally live longer than smaller fishes. The oldest teleosts known are scorpaenid rockfishes of the northeastern Pacific. Radioisotopic and otolith analyses indicate that Rougheye Rockfish (*Sebastes aleutianus*) live for 140 years, Silver-gray Rockfish (*S. borealis*) for 120 years, and Deepwater Rockfish (*S. alutus*) for 90 years (Finch 1990; Leaman 1991). Among common sport species, European Perch can live 25 years and Largemouth Bass can live 15–24 years (Das 1994; Boschung & Mayden 2004).

Numerous species live for a year or less, including the so-called annual fishes of South America and Africa (see Chapter 18, Deserts and other seasonally arid habitats). Several gobies have remarkably short generation times and life spans. The Australian coral reef goby *Eviota sigillata* spends 3 weeks as a planktonic larva, settles and matures within 1–2 weeks, and lives for no more than another 4 weeks, for a total life span of less than 60 days (Depczynski & Bellwood 2005). The shortest known life span among freshwater fishes occurs in an African rivuline, the nothobranchiid *Nothobranchius furzeri*, with a life expectancy in the wild of a few months and a maximum life span in the laboratory of less than 12 weeks (Valdesalicil & Cellerino 2003). Other short-lived species include North American minnows in the genus *Pimephales* (Fathead, Bullhead, and Bluntnose Minnows), several galaxiid fishes from Tasmania and New Zealand, retropinnid southern smelts, Japanese Ayu, Sundaland noodlefishes (Sundasalangidae), a silverside, and a stickleback.

Death and senescence

Death in fishes usually results from predation, accident, opportunistic pathogens, or accumulated somatic mutations that lead to a slow decline in health and an increased susceptibility to environmental factors. However, some fishes age via the "programmed death" process of **senescence** that is more typical of mammals such as ourselves. Senescence refers to age-related changes that have an adverse effect on an organism and that increase the likelihood of its death (Finch 1990). Senescence includes the metabolic and anatomical breakdown that occurs in older adult animals following maturation and reproduction. Pacific salmon provide a dramatic example. Reproductively migrating fish in peak physical condition enter their natal river, mature, spawn, break down anatomically and physiologically, and die in a matter of weeks. Many of the anatomical and physiological changes that occur can be linked to the combined effects of overproduction of steroids and

starvation. **Interrenal** cells, which are steroid-producing cells associated with the kidney and are homologous with the adrenal cortex of mammals, secrete corticosteroids, producing blood levels of these substances five or more times higher than normal levels. This **hyperadrenocorticism** results in rapid degenerative changes in the heart, liver, kidney, spleen, thymus, and coronary arteries; the latter degeneration is strikingly similar to coronary artery disease in humans. The digestive tract including intestinal villi degenerates, fat reserves are depleted, and feeding ceases. Fungal infections and reduced resistance to bacteria occur, indicating loss of immune function. A conflict between reproduction and survival is evident in the breakdown of the immune system: elevated corticosteroids apparently serve to speed the mobilization of stored energy into reproductive activity, but have the "side effect" of suppressing immune function. In naturally spawning Pacific salmons, these side effects are irreversible. Castrated males and females do not produce the elevated corticosteroids, and do not spawn, but instead continue to grow to twice the length and live twice as long as intact fish. Precocious males, those that matured as parr and bypassed the smolt and marine phases, may survive spawning and breed again the next year (Finch 1990).

Equally spectacular senescence occurs in several other fish taxa. Reproduction in both parasitic and nonparasitic lampreys involves maturation accompanied by cessation of feeding and atrophy of most internal organs with the exception of the heart and gonads. Fats and muscle proteins are metabolized or transformed into gonadal products. Both males and females die shortly after spawning, probably from starvation. Anguillid eels live as juveniles for many years in rivers and lakes. They then undergo a reproductive metamorphosis that includes enlargement of eyes, changes in body coloration and fin proportions, gut degeneration, and cessation of feeding. After a reproductive migration to the sea that may take them thousands of kilometers, all adults presumably die (see Chapter 23, Catadromy). Laboratory manipulation of hormone functions indicate that, as with salmons, rapid senescence results from elevated corticosteroids and starvation. During maturation, conger and snipe eels also experience gut atrophy and in addition lose their teeth. The Ice Goby, *Leucosparion petersi*, which enters fresh water to spawn and then dies, develops enlarged adrenals and splenic degeneration. More gradual senescence has been observed in many multiply spawning species, such as herrings, haddocks, Guppies and other livebearers, annual killifishes, and Medaka. Anatomical and physiological indicators of gradual senescence include reduced or even negative length and weight change, reduced egg output, corneal clouding, disordered scales, malignant growths such as melanomas, spinal deformities, and impaired regenerative capability. Such senescent changes are more common in small, short-lived species that mature at relatively early ages (Lindsey 1988; Finch 1990; Kamler 1991).

Age and growth

Age

Many of the phenomena described above include fairly precise statements of the age of the fish involved. How are such ages determined? Although size is generally correlated with age, sufficient variation in size at any particular age exists in most species (see below), making it difficult to estimate one from the other with much precision, especially in long-lived or slow-growing fishes. Researchers interested in determining a fish's age therefore look for structures that increase in size incrementally, in relation to some periodic environmental phenomenon. Many body parts meet this criterion, differing among fish species and among age groups (Fig. 10.5). The most commonly used techniques involve counting naturally occurring growth lines on scales, otoliths (statoliths in lampreys), vertebrae, fin spines, eye lenses, teeth, or bones of the jaw, pectoral girdle, and opercular series. Researchers validate the periodicity of growth by labeling growing structures with dyes or radioisotopes, as part of catch-and-release programs. Representative growth patterns that can be used to age fishes include annual growth rings on scales and **daily growth increments** on otoliths (Brothers 1984).

Scales in most fishes begin to develop during the late larval stage or during metamorphosis to the juvenile stage. They arise as bony plates in the dermis. Bone-forming cells, termed **osteoblasts**, lay down layers of roughly concentric circles of bone, termed **circuli**, along the midbody, starting in the region of the developing lateral line. Scales grow by accretion as more bone is added along their periphery, increasing in thickness but particularly in diameter. Diameter increase reflects body growth; circuli are closer together during periods of slow growth, such as winter at higher latitudes, and wider apart during rapid growth, such as during spring and summer, analogous to the growth rings of trees. This growth pattern creates alternating dark and light bands in the scale that correspond to periods of slow and fast growth, respectively, particularly when viewed with transmitted light (e.g., backlit). In a habitat with distinct growing and non-growing seasons, such as most temperate lakes, one thick and one thin band constitute a year's growth. The band is referred to as an annular mark or **annulus**. The number of annuli on a scale therefore gives a record of fish age in years.

In reality, many factors can confuse or interrupt annulus formation. Growth typically slows down when fish enter spawning condition, reflecting the allocation of energy away from growth and into gamete production and reproductive behavior. Decreased growth may result from a decrease in feeding that occurs in many species that engage in parental care (see Chapter 21, Parental care). Such **spawning checks** will appear as dense bands and can be

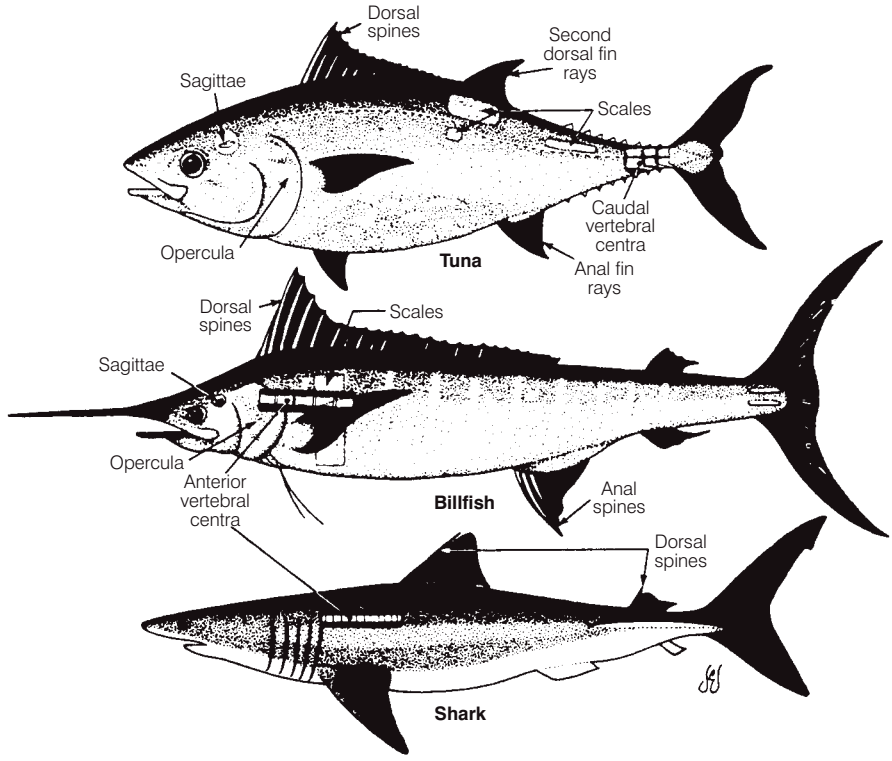


Figure 10.5
Methods for determining fish age. Growth lines are added periodically to hard body parts, but the best body part to count differs among taxa. Scales, otoliths, fin rays, and vertebrae are the most commonly investigated structures. Body parts used for determining growth of pelagic oceanic fishes are shown in the figure. From Casselman (1983).

mistaken for annuli, leading to overestimation of age. Bands resembling annuli, termed **false annuli**, can also result from multiple wet and dry seasons, as occur in many tropical locales, as well as from disease, recovery from injury, responses to pollutants, and forced periods of inactivity and nonfeeding. Feeding often slows down or ceases during summer periods of high water temperature and low oxygen.

Underestimation of age can also result if scales do not begin to develop until the fish is a few years old, as in anguillid eels, or if older fish reach a growth asymptote and hence grow little if at all. Based on scale ages, Pacific Sablefish, *Anoplopoma fimbria*, were generally thought to live 3–8 years and were managed as a fast-growing, short-lived, productive fishery. Subsequent studies, involving otolith sections and experimental injections of oxytetracycline into tagged fish, showed that the fish instead lived for 4–40 years, and some for as long as 70 years. However, older fish had essentially stopped growing, both in terms of increasing body and scale sizes, causing underestimation of age. These new analyses forced a major revision in the management strategies applied to the fishery. They point to a widespread realization, namely that different parts of a fish's body can grow at different rates (e.g., Casselman 1990). **Validation** of the annular nature of growth rings on scales and other structures is now generally recognized as essential (e.g., Hales & Belk 1992). Validation involves injection of vital dyes or radioisotopes that are quickly incorporated into one circulus of a scale, followed by periodic examination, or some other method whereby the actual time interval represented by an incremental mark can be verified (Beamish & McFarlane 1983, 1987; Stevenson & Campana 1992).

The semicircular canals of the inner ear contain **otoliths**, which are calcareous structures of characteristic shapes and sizes depending on the species. Otoliths form earlier than scales, often appearing in the otic capsules of embryos prior to hatching (Brothers 1984). Otoliths grow via the accretion of layers of fibroprotein and calcium carbonate crystals. In many fishes, this deposition occurs on a daily basis, relatively independent of most environmental conditions. Hence a one-to-one correspondence of rings (**lamellae**) to days exists on the otoliths, allowing highly accurate estimates of fish age, particularly in larvae and juveniles (Pannella 1971; Brothers et al. 1976). The width of the daily increments can be a useful indicator of growth conditions and can offer valuable information about when significant events occur during the early life history of an individual, such as length of larval period (Brothers & McFarland 1981). Of the three otoliths, the sagitta is usually largest and the most useful for aging studies.

As fish age, lamellae may grow too close together to allow resolution of daily increments. However, seasonal and annual records are still evident on these hard body parts. Changes in spacing of larger zones may indicate not only age but also when fish move among habitats that are

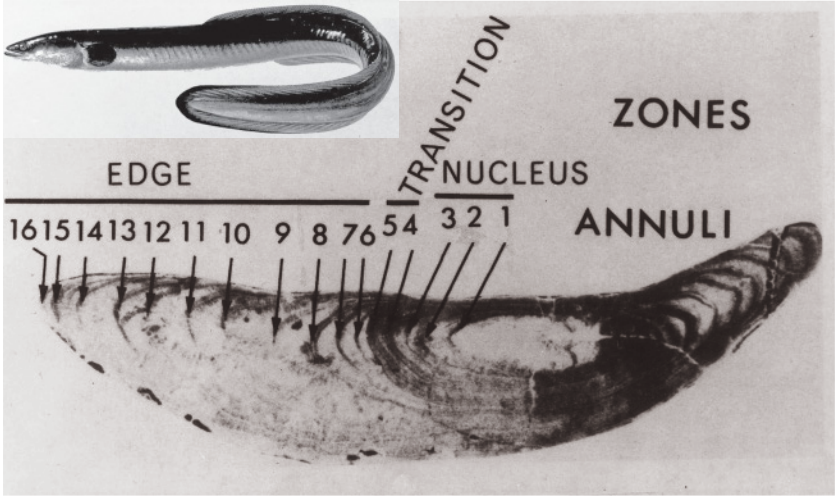


Figure 10.6

The correspondence between growth zones on an otolith and habitat use in an American eel, *Anguilla rostrata*. This sagittal otolith indicates that the eel was 16 years old when captured. It spent 3 years at sea or in the estuary of the St. Lawrence River (fast-growth nucleus zone), migrated upriver over a 2-year period (slow-growth transition zone), and finally took up residence in the upper St. Lawrence–Lake Ontario area (fast-growth edge zone). Habitat use was confirmed by measuring strontium : calcium ratios in the different zones of the otolith, using an electron microprobe associated with an electron microscope. Different ratios arise when an animal inhabits oceanic versus fresh water. From Casselman (1983); American eel drawing from Bigelow and Schroeder (1953).

more or less favorable for growth, as when eels migrate upriver or salmon smolts move from food-poor freshwater rivers to food-rich and saline estuaries (Fig. 10.6). Because the chemistry of the accreted layers reflects the chemistry of the water in which a young fish develops, the otolith has been likened to an event recorder, allowing determination of when and which habitats growing fish occupy. Such information can be useful in determining the geographic origins of recruits to an area or into an exploited or depleted population, as well as periods of occupancy of different water masses and pathways of dispersal (Thorrold et al. 2002; Palumbi et al. 2003; Patterson et al. 2005).

Growth

Among vertebrates, most growth in mammals and birds is **determinate**, ceasing after an individual matures. Lower vertebrates exhibit **indeterminate growth**: growth continues throughout the life span of an individual, although at a constantly decelerating rate. Hence older animals are generally larger, all other things being equal. The caveat here of equality among growth-controlling factors points out another crucial aspect of growth in fishes, namely its plasticity. "**Size at age**" varies enormously in fishes, whether we are comparing species, populations, individuals within populations, or individuals within cohorts and clutches.

Just about any factor that might possibly influence growth has been shown to have an effect, including temperature, food availability, nutrient availability, light regime, oxygen, salinity, pollutants, current speed, predator density, intraspecific social interactions, and genetics (reviewed by Wootton 1990, 1999). These factors, often working in combination, create large variations in the size of fishes of the same and different ages, leading to so-called size-structured populations, age differences in ecological roles and the ontogenetic niche, and cannibalism (Beverton & Holt 1959; Beverton 1987; see Chapter 24).

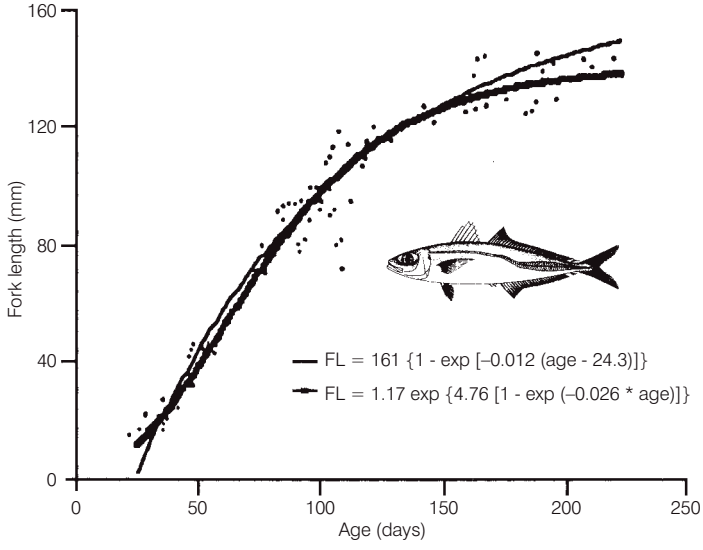


Figure 10.7

Growth curves and their statistical description. The plotted lines indicate growth over time for the Round Scad, *Decapterus punctatus*. The thin line and the upper equation are calculated from the von Bertalanffy equation; the thicker line and lower equation are based on a related calculation, the Gompertz equation. The von Bertalanffy equation predicts asymptotic growth; the Gompertz equation predicts a sigmoidal curve where growth increases and then decreases. The two lines are statistically similar, showing how growth slows with age and eventually approaches an asymptote. From Hales (1987), used with permission of the author; Round Scad drawing from Gilligan (1989).

When plotted against age, growth curves for fishes appear asymptotic, meaning they tend to flatten out at older ages, although the degree of flatness varies greatly among and within species (Fig. 10.7). This variation forms the basis of an equation commonly used to describe individual growth in most fishes, known as the **von Bertalanffy growth equation**, which in its simplest form can be written:

$$L_t = L_{\max}(1 - e^{-gt}),$$

where L is length, t is a point in time, $L_{\max}$ is the maximum or asymptotic length attained by the species, e is the base of natural logarithms, and g is the all-important constant that describes the rate at which growth slows. The von Bertalanffy equation is based on bioenergetic considerations, viewing growth as a result of anabolic and catabolic processes by which a fish takes in oxygen and energy to build tissues, and uses up energy and tissue over its life. Many refinements of the equation have been made and alternatives proposed that take into account age- and weight-specific differences in growth, food consumption rates, temperature, and overall energy budgets (see Brett 1979; Gulland 1983; Weatherly & Gill 1987; Busacker et al. 1990; Wootton 1999).

The von Bertalanffy growth coefficient (K) can be useful in assessing fishery management approaches because slower growing fishes with lower K values tend to be more vulnerable to overfishing. Some typical values of K for a variety of fishes are as follows (data courtesy of J. Musick from various sources):

Anchovies, Engraulidae:	0.80–1.40
Tunas, Scombridae:	0.42
Menhaden, Clupeidae:	0.39
Flounder, Paralichthyidae:	0.32–0.40
Spanish mackerels, Scombridae:	0.17–0.35
Epinepheline grouper, Serranidae:	0.18
Porgy, Pagridae:	0.09
Swordfish, Xiphiidae:	0.09–0.19
Ground sharks, Carcharhinidae:	0.04–0.078

The relationship between the increasing mass and length of a fish involves a power function. Mass increases as a function of the cube of the length of the fish, reflecting the universal relationship between the volume and the surface area of a solid, volume increasing faster. Hence the equation for the relationship between mass and length is typically,

$$M = aL^b,$$

where M is mass, L is length, and a and b are constants. The length exponent, b, usually takes values of around 3.0, indicating that the fish is growing isometrically, i.e., that its relative shape is remaining constant as it grows. Values greater or lesser than 3 indicate positive or negative allometric growth (see below), and can serve as an indication of the relative health or condition of the fish.

The equation

$$K = W/L^3$$

can be used to calculate the **condition factor**, K, of a fish, where W is weight or mass and L is length. Population or cohort measures of K can indicate whether populations or subgroups are growing or feeding at expected rates. Changes in an individual's condition factor could indicate periods of good versus poor feeding success, disease, or imminent spawning. K is obviously a rough and simplified indicator of general condition and lags far behind any actual events causing changes in relative condition. More precise and accurate indices can be calculated, such as relative condition factor, relative weight, or covariance analysis of mass and length change; much debate exists over which is the best measure (Ricker 1975, 1979; Anderson & Gutreuter 1984; Cone 1990; Wootton 1999).

Because the condition factor tells about an individual's history rather than its recent experience, measures that minimize the time lag between cause and effect have been developed, including biochemical analysis of protein uptake rate, energy content or intermediary metabolism (RNA : DNA and ADP : ATP ratios), lipid content, and various chemical and biomarker indicators of stress (Busacker et al. 1990; Wedemeyer et al. 1990; Morgan & Iwama 1997; Schreck 2000).

Body size, scaling, and allometry

As emphasized repeatedly in this book, body size has an overriding influence on most aspects of fish biology. During ontogeny, fish can grow from a larva a few millimeters long to an adult several meters long. An individual must perform all life functions at all sizes in order to reach the next stage; hence size-related phenomena are constant selection pressures on growing fish. Central to discussions of size are the concepts of **scale** and **allometry**, the latter topic forming the basis of a quantitative science of size (Gould 1966; Calder 1984; Schmidt-Nielsen 1983). **Scaling** refers to the structural and functional consequences of differences in size among organisms; allometry quantifies size differences among structures and organisms.

Changes in scale, whether over ontogenetic or evolutionary time, involve alterations in the dimensions, materials, and design of structures. A good example of scaling and its ramifications involves how an increase in body size affects the swimming speed and ability of large and small members of a species. The pelagic larvae of many marine fishes are small, elongate, and highly flexible, whereas adults take on a variety of shapes and swimming modes (see Chapter 8, Locomotion: movement and shape). The larvae of many herrings are almost eel-like and swim slowly, but adults have much deeper bodies and swim faster via the carangiform mode, in which the tail is the primary propulsive region. An increase in overall body mass, a **dimensional change**, requires the reworking of components. The internal skeleton changes from cartilage to bone, a **material change**. This corresponds to an increase in body musculature and a shift from anguilliform to carangiform swimming to take advantage of the stiffer nature of bone and

the more efficient transfer of energy from contracting muscles to the propulsive tail. This shift also corresponds to a **design change** from elongate with a rounded tail to a deeper, streamlined body with a forked tail, which is a more efficient morphology for a carangiform swimmer.

Allometry as a concept underscores a basic fact of growth and scaling, namely that the change in quantitative relationship between the sizes and functions of growing body parts is seldom linear. Linear relationships take the form:

$$y = ax,$$

indicating that structure y changes as a constant function of structure x, with a being the proportionality constant. A doubling of the size of a fish will not necessarily lead to a doubling of its swimming speed.

The relationship is more complex and depends on the measure of body size in question. For salmon, swimming speed increases approximately with the square root of the fish's length and with the 1/5th power of its mass (i.e., length$^{0.5}$, mass$^{0.2}$). Allometric relationships are described by equations of the nature

$$y = ax^b$$

or

$$\log y = \log a + b \log x.$$

The exponent b describes the slope of the line that results when the relationship between the structures is plotted on log-log paper. For simple, linear proportionalities, $b = 1$, which is biologically rare. More often, b will take on positive or negative values for regression slopes greater or less than 1, respectively, indicating that a structure is increasing in size faster or slower than the increase in the trait to which it is being compared. The equations for swimming as a function of body size in Sockeye Salmon have exponents of 0.5 for body length and 0.17 for body mass (Schmidt-Nielsen 1983).

Numerous examples of allometric relationships in fishes can be given, emphasizing the far-reaching implications of size in fishes as well as convergence in selection pressures and solutions among disparate taxa. Focusing on locomotion and activity, the relative cost of swimming decreases with body size in most fishes, both within and among species. Such a relation indicates that it is more expensive for a small fish to move 1 g of body mass a given distance than it is for a larger fish to do the same (measured as oxygen consumed/g body mass/km, $b = -0.3$). Heart size in fishes increases with body size in an almost linear fashion, taking on values of about 0.2% of body mass and having a slightly positive exponent (heart mass = 0.002 × body mass$^{1.03}$).

Not surprisingly, surface area of the gills relates to activity level. Very active fishes such as tunas have comparatively more gill surface than sluggish species such as toadfishes. But within species and even among species, the surface area of the gills (m^2) increases allometrically and positively with body size (kg), with an exponent of 0.8–0.9. Locomotion and respiration relate to feeding activity, which is eventually translated into growth. Gut length increases allometrically with body length in many species, with an exponent of >1. Growth rate also scales with size, being faster in larger species, with an exponent of 0.61 (measured as change in mass/day relative to adult body mass) (Schmidt-Nielsen 1983; Calder 1984; Wootton 1999).

Questions about size, scaling, and allometry are often linked to the idea of **trade-offs**, another recurrent theme in this book. What constraints are imposed on an animal by changing its size, both ontogenetically and evolutionarily? What are the advantages and disadvantages of being very small as opposed to being very large? Large size may confer many advantages, but an individual must be small before it is large. During growth, an individual must incur the costs of small size early in ontogeny as well as the energetic and efficiency costs of reworking its size and shape during growth. Juveniles of a large species are often inferior competitors to small adults of a small species. Rapid growth requires rapid feeding and high metabolic rate, which exposes a young fish to more predators and also often carries an increased risk of starvation. Size-related constraints also influence life history attributes such as whether a species will produce many small versus few large young, how extensive the parental care offered will be, and whether adults will mature quickly at small size or slowly at larger size.

One final topic with respect to size deserves mention. Fishes are supported by a dense medium and their support structures do not reflect the constraints of gravity as much as the necessity to overcome drag. The shapes of fishes then become explainable in terms of **drag reduction** and which area of the body is used in propulsion. Both are intimately related to the mode of locomotion used. An important size-related attribute is the **Reynolds number**, a dimensionless calculation that accounts for the size of an object, its speed, and the viscosity and density of the fluid through which it moves (see Chapter 9, Larval behavior and physiology). Calculations of Reynolds numbers help explain swimming speed, body shape, and locomotory type. In very small fishes, including larvae, the effects of drag are so great and the Reynolds numbers so small that inertia is impossible to overcome. Larvae seldom glide because their mass relative to water viscosity prevents them from developing inertia as they swim. They must continue to expend effort to gain any forward progress. However, their problems associated with overcoming inertia also mean that they are less likely to sink. Large fishes such as billfishes or pelagic sharks have high Reynolds numbers. They can use inertia to advantage and literally soar through the water, using their momentum to carry them forward.

The ontogeny and evolution of growth

Much of the emphasis in this and the preceding chapter has been on size relationships and the observation that indeterminate growth interacts intimately with many crucial aspects of fish biology. Growth processes – both general processes associated with length and mass increase but also in terms of changing body proportions – help explain many life history, behavioral, ecological, and physiological phenomena. We end this chapter by returning to the general question of how evolution has interacted with body growth processes to establish differences among life history stages and among species of fishes.

Ontogenetic differences within species

Throughout the above discussions, we have emphasized anatomical, behavioral, and ecological differences among size classes of a species. Ontogenetic differences are detailed in several other chapters, such as the tendency for larger fish to occur deeper in a habitat or region and for populations to show age structure (see Chapter 24), for different size fish to interact with different sets of predators and prey (see Chapters 19, 20), for shoals to be sorted by size (see Chapter 22), and for different size fish to have different foraging capabilities (see Chapter 8). Additional examples of ontogenetic differences are probably not necessary. The major point here is that larvae have to be adapted to larval life, juveniles to juvenile life, and adults to adult life. These different stages often differ in habitat and ecology and must function both during definable stages as well as during transitional periods.

Adaptations appropriate to one stage may therefore create **constraints** for other stages. Young fish may be constrained by structures and proportions that are primarily adaptive in later life. For example, small juvenile Largemouth Bass are morphologically miniature adults. Instead of feeding on fishes, for which their morphology would be best suited, they eat relatively small zooplankton. This puts them in direct competition with juvenile and adult Bluegill Sunfish, which are constructed to feed on zooplankton throughout their lives and hence have a competitive advantage over juvenile Largemouths (Werner & Gilliam 1984; see Chapter 24, Population dynamics and regulation). Conversely, later stages may retain characteristics of early ontogeny that may constrain them (see below). Regardless, the differing selection pressures on larval, juvenile, and adult fish within a species help clarify the general occurrence of differently appearing and behaving individuals.

An additional conflict exists during ontogeny, brought about by the need for each stage to be immediately functional at a variety of tasks, including feeding, locomotion, and predator avoidance. All tasks are important, but the balance shifts as a fish ages. Hence predator avoidance may take precedence over feeding efficiency among younger, smaller fishes that are more vulnerable to predators. Such a trade-off has been shown in a range of fish species (e.g., salmonids, sculpins, cichlids) with respect to muscular and skeletal development and action. Juveniles exhibit relatively high levels of performance of locomotory and other defensive traits (e.g., fast-start escape responses) relative to their feeding and foraging abilities. The opposite applies to adults of the same species, in which feeding performance is maximized (Herrel & Gibb 2006).

Although the life history of a fish appears as a continuum of events from birth through maturation to death, with each phase preparing the fish for the next, some evidence exists to suggest that adaptation to one phase actually inhibits progression into the next. For example, smolting and maturation in salmonids appear to be conflicting processes. Atlantic Salmon that smolt rapidly at 1 year of age may mature much later than fish that bypass the smolt stage and remain behind in fresh water. Administration of male hormones to young male Masu Salmon, *Oncorhynchus masou*, inhibits smoltification but causes maturation; castration of older fish causes them to undergo many of the transformations of smolting. The complexity, timing, and changes in habitat that occur during an animal's life cycle may function not only to prepare an individual for later phases but to also overcome inhibitory or conflicting influences of previous phases (Thorpe 1978).

Evolution via adjustments in development: heterochrony, paedomorphosis, and neoteny

Adjustments in developmental rates or timing may be a major way in which new species and even higher taxa evolve from old (Cohen 1984; Mabee 1993). Such a process may explain several phenomena, such as why some adult fish have apparent larval or juvenile traits, or why larval- or juvenile-appearing fishes are reproductively functional, or why closely related species may differ primarily in the duration of an early life history stage, in the time at which a particular structure changes, or in the rate at which different structures grow.

Such alterations in the time of appearance and the rate of development of characters during ontogeny are referred to as **heterochronic** events. Heterochrony results from modification of regulatory genes and processes. Juvenile traits in an adult animal are termed **paedomorphic** (="child form"); if juveniles become sexually mature, they are **neotenous**. Both paedomorphosis and neoteny are brought about as a result of heterochrony (Gould 1977; Youson 1988). Whether paedomorphosis or neoteny, or a related

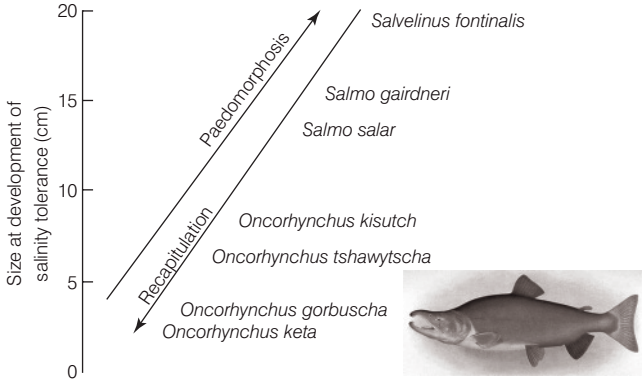


Figure 10.8

Salmonids differ in the minimum size at which they develop the necessary salinity tolerance to undergo the parr–smolt transformation. Observed differences among species could be explained by heterochronic shifts in the development of this trait. Such shifts might have changed the timing of the onset of the various physiological processes involved in salinity tolerance. It is not known what the ancestral condition was, and so either acceleration or deceleration of timing could be responsible. Hence either paedomorphosis (increasing size at smoltification) or recapitulation (decreasing size at smoltification), or both, could have affected the evolution of this trait. From McCormick and Saunders (1987), used with permission; salmon drawing from the US National Oceanic and Atmospheric Administration's Historic Fisheries Collection.

heterochronic phenomenon, produced a particular trait or condition is difficult to determine. Within fish families, differing forms of heterochrony occurring at different stages in life history may have produced different species, as is suspected among gobioid fishes (Kon & Yoshino 2002b). Regardless, distinguishing among possibilities is not critical to appreciating heterochrony as a major evolutionary process (Fig. 10.8).

Heterochronic changes in transitions between developmental stages, such as the timing of metamorphosis from embryo to larva or from larva to juvenile, is one means by which new species evolve (Youson 1988). Variation in duration of larval life affects age or length at metamorphosis. Elopomorphs as a group are characterized by unique leptocephalus larvae that remain as larvae for long periods, up to 3 years in European eels (e.g., Miller & Tsukamoto 2004). In cladistic terms, this synapomorphy defines the group. Long larval life may be related to the apparently unique ability of leptocephali to absorb dissolved organic matter from the water across a very thin epithelium (Pfeiler 1986). Within the elopomorphs, further variations in developmental rate characterize distinctive species and may suggest processes that led to their separate evolution. For example, Tarpon, *Megalops atlanticus*, metamorphose at earlier ages and smaller lengths (2–3 months, 30 mm) than most other elopomorphs.

Speciation may result from or be maintained by heterochronic shifts in larval characteristics. Intrageneric separation may have resulted from variation in larval period length in North Atlantic eels, *Anguilla rostrata* and *A. anguilla*. The different larval durations, less than 1 year in American eels and 2–3 years in European eels, have a critical effect on their respective distributions. Both species spawn at the same time and in the same Sargasso Sea locale (see Chapter 23, Catadromy). However, American leptocephali transform into juveniles and settle all along the Atlantic coast of North America. European larvae accompanying them in the Gulf Stream are unprepared to metamorphose and are therefore carried past North America and on to Europe. Hence a heterochronic shift in timing of larval metamorphosis helps keep the two species spatially separated.

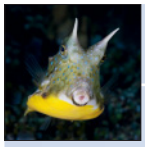
The evolution of many lamprey species may have also occurred via heterochronic shifts. Many nonparasitic lamprey species can be easily paired with ancestral, parasitic forms. The major differences between ancestor and descendant species involve the length of larval versus adult life, with derived, nonparasitic forms typically having much longer larval periods, rapid metamorphosis, and a relatively short, nonfeeding adult reproductive phase (see Fig 13.6). A delay in the time of metamorphosis would result in just such a difference, essentially creating small adults that retained many larval characters but were reproductively mature (Youson 1988; Finch 1990).

Miniaturization among fishes may often evolve via paedomorphic processes (Weitzman & Vari 1988). Two of the smallest fish species known, a goby, *Trimmatom nanus*, and a cyprinid, *Danionella translucida*, reach sexual maturity when only 10 mm long. They retain such larval features as incomplete squamation, limited pigmentation, and partial ossification of the skeleton (Winterbottom & Emery 1981; Roberts 1986; Noakes & Godin 1988). One family, the subtropical and tropical Pacific Schindleriidae, has many neotenic characters, including a functioning pronephros (the early embryonic, segmented kidney of fishes that is drained by the archenephric duct rather than by the ureter), a transparent body, and large opercular gills. *Schindleria brevipinguis* matures at less than 8 mm, and *S. praematura* attains sexual maturity when only 1 cm long, even before it transforms completely from a planktonic "larva" (Leis 1991; Johnson & Brothers 1993; Watson & Walker 2004; see Chapter 15, Suborder Gobioidei). Adults of what is arguably the world's smallest vertebrate species, the 7.8 mm Southeast Asian cyprinid *Paedocypris progenetica*, possess a number of larval traits, including a long caudal peduncle with a skin fold along its lower edge, many unossified bones, a translucent body, and a neurocranium lacking frontal and several other bones (Kottelat et al. 2006) (Fig. 10.9).

Characteristics of the deepwater, pelagic, ceratioid anglerfishes indicate that they evolved from shallow water, benthic species via neoteny that involved an extended pelagic larval or juvenile phase. Many ceratioids have

Figure 10.9
Paedocypris progenetica of Indonesia is the world's smallest vertebrate species, maturing at less than 8 mm length. It retains numerous larval traits, including minimal pigmentation, reduced squamation, and a largely cartilaginous skeleton with many bones absent. An 8.8 mm adult female is shown. From Kotellat et al. (2006), used with permission.

a gelatinous balloonlike skin as adults, which is also a pelagic larval trait. Mature males are distinctly larval in appearance, are even smaller than *Paedocypris*, and are parasitic on females 10 times their size (Pietsch 2005). Larval-like males also occur in the deepsea black dragonfishes and in the goby genus *Crystallogobius* (Moser 1981; see Chapter 18, The deep sea). Although large size confers an advantage in many species, the production of new species via heterochronic shifts that lead to the retention of small body size shows that small size is also advantageous under certain conditions.



Summary

SUMMARY

1. Although we recognize specific phases during the ontogeny of an individual, the transitions that occur between phases often require long time periods and can involve complex changes and reworkings of the anatomy and physiology of a fish. Examples of complex and protracted transitions include smoltification, when young salmon move from fresh water to the ocean, and metamorphosis, when flatfish change from symmetrical, planktonic larvae to asymmetrical, bottom-dwelling juveniles.
2. Reproductive development includes three very different processes: determination, differentiation, and maturation. Gender determination in most fishes is probably under genetic control and occurs at the time of fertilization. In some fishes, environmental conditions such as temperature can affect determination. Differentiation occurs when recognizable ovaries or testes appear in an individual. Maturation is synonymous with achieving adulthood and occurs when a fish produces viable sperm or eggs. Complicating this picture are many fish species that undergo postmaturational sex reversal, changing from functional females to functional males (protogyny) or from male to female (protandry). A few species are simultaneous hermaphrodites, functioning as males and females at the same time. Self-fertilization is exceedingly rare in fishes.
3. Age at first reproduction and longevity vary greatly among fishes. Some male surfperches are born mature, whereas some sharks, sturgeons, and eels may not mature until they are older than 20 years. Longevity also ranges from less than 1 year in annual fishes to more than 100 years in sturgeons and rockfishes. Death usually occurs as a result of accident or disease, but some fishes such as lampreys and salmons show programmed death (senescence) similar to that observed in mammals.
4. The age of a fish can be determined by counting growth rings on otoliths, vertebrae, fin spines, and other hard body parts. Such growth rings are usually added annually to a structure, but climatic and other environmental factors can lead to variation that can provide information about habitat shifts during ontogeny. Daily growth increments are often detectable on the otoliths of young fishes, allowing back-calculation to actual spawning dates.
5. Size at a particular age varies greatly in fishes. Growth curves that describe size/age relationships can be calculated using a number of equations, the von Bertalanffy growth equation being a commonly used indicator. The condition of a fish, calculated by dividing body mass by length, is one indicator of the kind of growth conditions an individual has experienced.
6. As a fish grows, the dimensions of its body change, as do the materials used in construction; together these modifications represent an alteration in the design of the individual. Changes in the relationship between body parts during growth or between body functions and body size can often be described by an

allometric equation. In most instances, the relationship is nonlinear.

7 Fishes undergo indeterminate growth and have complex life cycles. At each stage during its life, a fish must function physiologically, ecologically, and behaviorally. Such function is compromised by transitional periods, by alterations that are preparatory for the next stage, and by traits retained from previous stages. Evolution may occur through adjustments in the timing or rate of ontogenetic development. Such heterochronic changes include the rapid maturation of juveniles or retention of juvenile characteristics in adults (neoteny, paedomorphosis), and may explain the evolution of some of the smallest fish species as well as speciation in lampreys, elopomorphs, salmons, and deepsea anglerfishes.

Supplementary reading

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Figure III *(opposite)*

A Silvertip Shark, *Carcharhinus albimarginatus* (Carcharhiniformes: Carcharhinidae), with a Sharksucker (*Echeneis naucrates*, Perciformes: Echeneidae) attached. This symbiotic relationship between an elasmobranch (Chapter 12) and an advanced acanthopterygian teleost (Chapter 15) probably benefits both, the Sharksucker scavenging scraps from the shark's meals and in turn picking parasitic copepods off the shark. Remoras also attach to whales, turtles, billfishes, rays, and an occasional diver. Remoras generate sufficient suction to hang on even at high speeds via a highly modified first dorsal fin. Photo by D. Hall, www.seaphotos.com.

PART III

Taxonomy, phylogeny, and evolution

Chapter 11

"A history of fishes"

Chapter contents

CHAPTER CONTENTS

Fishes were the first vertebrates. Understanding the evolutionary history of fishes is therefore important not only for what it tells us about fish groups, but for what it tells us about evolution of the vertebrates and ultimately our own species. Innovations during fish evolution that were passed on to higher vertebrates include dermal and endochondral bone and their derivatives (vertebral centra, bony endoskeletons, brain cases, teeth), jaws, brains, appendages, and the internal organ systems that characterize all vertebrate groups today. During 500 million years of evolution, fishes colonized and dominated the seas and fresh waters and eventually emerged, at least for short periods, onto land. Major clades prospered and vanished, or were replaced by newer groups with presumably superior innovations.

Extant ("living") fishes therefore represent the most recent manifestations of adaptations and lineages that have their roots in the early Paleozoic. The more than 27,000 species of extant fishes constitute only a fraction of the diversity of fishes that has existed historically, as should be evident from the long lists of **extinct** forms given here (which in turn represent a select fraction of the diversity of former taxa). Many of the extinct forms are exotic in their appearance, whereas others are remarkably similar to living forms, at least in external morphology. A major challenge to ichthyology involves unraveling the evolutionary pathways of both modern and past fish taxa in the process of determining relationships among groups. Which of the many fossil groups represent ancestral types? Which were independent lineages that died out without representation in modern forms? What are the links between and among groups of the past and present? What do fossilized traits tell us about ancient environments? Where do similarities represent inheritance, convergence, or coincidence among extinct and living groups? And how have past adaptations influenced and perhaps constrained present morphologies and behaviors?

The focus of this chapter is on fishes that lived during the Paleozoic and Mesozoic eras, and on modifications that occurred during the evolution of different, major extinct groups, leading to the dominant bony and cartilaginous fishes of today. We deal first with jawless fishes, then with ancestors of modern bony fishes because these occur earlier in the fossil record, and finally with the cartilaginous sharks, skates, rays, and chimaeras. This presentation focuses on extinct rather than extant fishes, recognizing that the distinction is artificial, that many lineages arose hundreds of millions of years ago and still have modern, living representatives, and that direct ancestors of some extant forms arose before other groups that have since gone extinct (see below, Continuity in fish evolution). We follow the basic organization of Nelson (2006) because of its synthetic and broad approach, recognizing that Nelson's conclusions are one of many alternative interpretations of the literature.

Jawless fishes

Phylum Chordata[a]
- Subphylum Craniata
  - Infraphylum Vertebrata
    - †Superclass and Class Conodonta
    - †Superclass and Class Pteraspidomorphi (Diplorhina)
      - Subclass Astraspida
        - Order Astraspidiformes
      - Subclass Arandaspida
        - Order Arandaspidiformes
      - Subclass Heterostraci
        - Orders Cyathaspidiformes, Pteraspidiformes
    - †Superclass and Class Anaspida
    - †Superclass and Class Thelodonti
      - Orders Loganelliformes, Shieliiformes, Phlebolepidiformes, Thelodontiformes, Furcacaudiformes
    - †Superclass Osteostracomorphi
      - Class Cephalaspidomorphi (Monorhina)
        - Orders Cephalaspidiformes, Galeaspidiformes, Pituriaspidiformes

[a] Classification based on Nelson (2006).
† Extinct group. All subgroups within an extinct major taxon are also extinct.

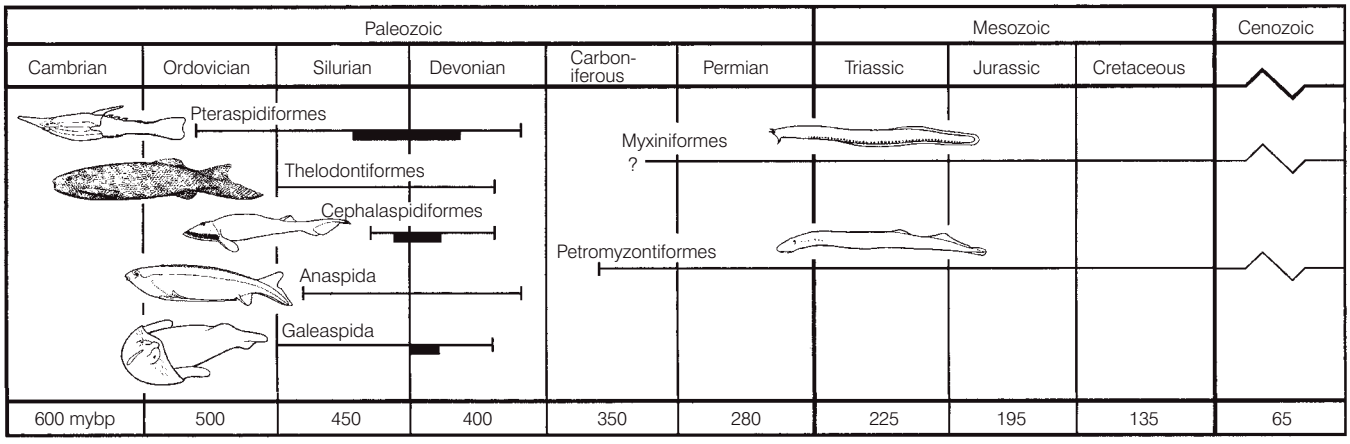


Figure 11.1
Periods of occurrence of major jawless fish taxa based on the fossil record. Thickened portions of lines indicate periods of increased generic diversity within a group. Time periods are not drawn to scale (e.g., the Cretaceous lasted almost 50 million years longer than the Silurian, but both are given equal space). Early Cambrian fossils that were arguably fishlike are not included (see text). Fossils are lacking for myxiniforms and petromyzontiforms during the Mesozoic. Data largely from Carroll (1988), Pough et al. (1989), Nelson (2006), and references therein.

The very first fishlike vertebrates undoubtedly evolved from invertebrates, perhaps a cephalochordate. However, the first "fishes" left no fossil record and their form and relationships remain a mystery. By the time fishlike fossils appear in Early Cambrian deposits, roughly 530 million years before present (mybp) (Fig. 11.1), complex tissue types had evolved, including filamentous gills, V-shaped myomeres, and a distinct dorsal fin. New discoveries are made almost annually, but the currently recognized oldest species, *Myllokunmingia fengjiaoa*, was found in the Chengjiang geological formation of Yunnan Province in southwestern China. *Myllokunmingia* was 3–4 cm long and is thought to be allied with (is a sister group to) ancestors of modern lampreys, although agreement is far from universal (Xian-guang et al. 2002; Shu et al. 2003).

If modern cephalochordates such as the lancelets (*Branchiostoma*) are considered fishlike – if not exactly fishes – then the ancestry of fishes can be traced farther back to the cephalochordate-like yunnanozoans (*Haikouella* and *Yunnanozoon*) from the Lower Cambrian, or to the much-heralded *Pikaia* with its dorsal nerve cord and notochord, from the Middle Cambrian Burgess Shale of British Columbia (see Chapter 13, Amphioxiforms).

Clearly recognizable fish specimens, such as the arandaspid pteraspidomorph *Sacabambaspis janvieri* from Bolivia, appear later, dating to 470 mybp (Gagnier et al. 1986; Gagnier 1989). This and related **jawless**, finless forms inhabited shallow seas or estuarine habitats in tropical and subtropical regions of the Gondwanan and Laurasian supercontinents (see Chapter 16). Their innovations include **true bone** (probably evolved independently in several ancestral groups) and a **muscular feeding pump**. The former adaptation, which existed only as an external covering, would have provided protection from predators to which softer ancestors were more vulnerable, as well as serving as a metabolic reserve for calcium and phosphate and an insulator of electrosensory organs (Northcutt & Gans 1983; Carroll 1988). A muscular feeding pump would have been more efficient for moving food-bearing water through a filtration mechanism than was the ciliary feeding mechanism of protochordates. Another major advance over the cephalochordates that preceded them was that, although lacking jaws, the early fossilized fishes were craniates. They had a head region containing a brain with specialized sensory capsules and cranial nerves, all contained in a protective skeletal braincase (Maisey 1996).

Subphylum Craniata, Infraphylum Vertebrata

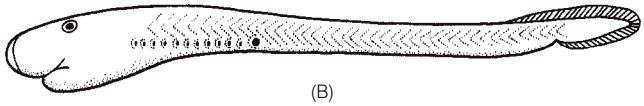
Vertebrate craniates possess, among other features, a **dermal skeleton** and **neural crest**, the latter describing regions of the developing nerve cord that are precursors to gill arches, pigment cells, connective tissue, and bone. Within the vertebrates are seven superclasses of fishes, five of which are extinct.

†Conodonta

Between Late Proterozoic and Late Triassic times (600 to 200 mybp), a group of animals known as **conodonts** ("cone-shaped teeth") arose, proliferated, and died in seas worldwide. The fossil remains, referred to as conodont "elements", consist of toothlike structures generally about 1 mm long and made from calcium phosphate (Fig. 11.2). Known since the mid-1800s, their abundance allowed them to serve as stratigraphic landmarks in determining the age of fossil beds. It was not until the 1980s that fossilized soft body parts were discovered, allowing speculation on true relationships (Briggs et al. 1983; Smith et al. 1987). Before these discoveries, the elements were identified variously as copulatory structures of nematodes, as radulae of snails, and as jaws of annelid worms, among other things. More conservative authors generally placed the animals in a separate, extinct phylum, the †Conodonta, with uncertain relationships (Clark 1987).

Axis of symmetry

(A)



(B)

Figure 11.2

Conodonts. (A) Conodont apparatus. The various elements (A–G) occur on the right (dextral) and left (sinistral) sides of the head region of the conodont animal and function as the feeding apparatus. (B) The 350-million-year-old, 40 mm long conodont animal. (A) from Clark (1987), used with permission; (B) as reconstructed by Aldridge and Briggs (1989).

The recent discoveries and subsequent reanalyses indicate that the earliest "protoconodonts" of the Paleozoic and Early Cambrian may likely have been invertebrates aligned to chaetognaths (Donoghue et al. 2000). Later euconodonts ("true conodonts") that arose in the Late Cambrian are true chordates, with V-shaped muscle blocks, a bilobate head and cartilaginous head skeleton, eyes contained in otic capsules, extrinsic eye muscles, a compressed body, axial lines suggestive of a notochord, and unequal tail fins supported by raylike elements (Donoghue et al. 1998) (Fig. 11.2B).

The total body length ranged between 4 and 40 cm. The conodont elements were contained in the head region and apparently functioned as teeth. Eyeballs and extrinsic eye muscles, chevron-shaped muscle blocks, and apparent bone cells in a dermal skeleton of some species strongly suggest that not only were conodonts chordates, but they may even be classified as vertebrates (Gabbott et al. 1995; Janvier 1995; Purnell 1995).

What are the affinities then of this ancient, highly successful, tooth-bearing, primitive chordate/vertebrate? Initially following the discovery of the actual animal, the popular interpretation was that the conodont elements were dentition homologous to the rasping, book-closing action of modern hagfishes, placing conodonts near the base of the hagfish lineage (Helfman et al. 1997; see Chapter 13). However, more complete, cladistic analysis incorporating multiple structures and taxa indicates that conodonts constitute a separate, extinct superclass and class that arose after the earliest myxine hagfishes and petromyzontomorph lampreys, i.e., they are more derived than hagfishes and lampreys and may even be basal to the jawed fishes that arose later (Donoghue et al. 1998, 2000).

†Ostracoderms

The first fishes, conodonts aside, were historically termed **ostracoderms** ("shell-skinned"), in reference to a bony shield that covered the head and thorax. But ostracoderm is now considered an artificial designation that includes perhaps four distinct superclasses of jawless craniate fishes, the **Pteraspidomorphi**, **Anaspida**, **Thelodonti**, and **Osteostracomorphi**. Relationships between ostracoderm groups and modern jawless fishes such as hagfishes and lampreys remain speculative, with revised interpretations appearing as new fossil discoveries are made.

†Pteraspidomorphi

Pteraspidomorphi (or Diplorhina = "two nares") derive their alternate name from impressions on the inside of the head plates indicating two separate olfactory bulbs in the brain. Pteraspidomorphs were jawless filter feeders in both marine and freshwater environments; they occurred from the Lower Silurian until the end of the Devonian. Three subclasses of pteraspidomorphs are recognized, the Astraspida, Arandaspida, and Heterostraci. Primitive forms, such as the Ordovician *Astraspis*, *Arandaspis*, and arandaspid *Sacabambaspis*, had symmetrical tails, full body armor, and multiple branchial openings (Fig. 11.3).

Heterostracans ("those with a different shell") had dermal armor that extended from the head almost to the tail, necessitating swimming by lashing the tail back and forth, much like a tadpole. The tail in most forms was **hypocercal**, in that the notochord extended into the enlarged lower lobe of the tail. Their body form, armor, and tail morphology suggest that heterostracans plowed the bottom, pumping sediments into the ventral mouth, and filtering digestible material through the pharyngeal pouches. The armor is generally **sutured** and shows **growth rings**, indicating incremental growth. Early pteraspidiforms were small (*c*. 15 cm), but some heterostracans reached 1.5 m. Two orders, seven families, and more than 50 genera are recognized (see Denison 1970; Carroll 1988).

Later heterostracans, such as the pteraspidiform *Pteraspis* from the Lower Devonian, had hypocercal tails, fused dorsal and ventral head plates, and single branchial openings (Fig. 11.3B). The Devonian also produced highly derived forms, such as the sawfishlike *Doryaspis* and the tube-snouted, blind *Eglonaspis*. Trends in the development of pteraspidiform lineages include the reduction of armor through fusion of plates, narrowing of the head shield, and development of lateral, presumably stabilizing, projections (**cornua**). These changes all suggest strong selection for increased mobility and maneuverability. While these anatomical changes were taking place, pteraspidiforms invaded freshwater habitats (Carroll 1988).

†Anaspida

The more fusiform, compressed anaspidiforms, such as *Pharyngolepis* (Fig. 11.4A), occurred from the Upper Silurian through the Late Devonian. They were seldom larger than 15 cm, and had pronounced hypocercal tails and terminal mouths. Anaspids originated in nearshore marine habitats and gradually entered fresh water. The anaspid body was covered largely with overlapping, tuberculate scales. One advance was the development of flexible, lateral, finlike projections that had muscles and an internal skeleton, thus giving these small fishes considerable

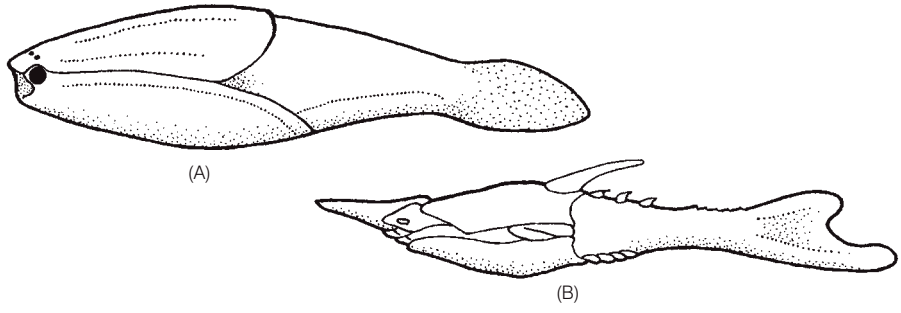


Figure 11.3
The earliest known fishes were jawless pteraspidomorphs with armored head shields. Pteraspidomorphs included such small, primitive forms as (A) *Arandaspis* (subclass Arandaspida) from Australia, as well as more advanced forms such as (B) *Pteraspis* (subclass Heterostraci) from Devonian Europe. (A) after Rich and van Tets (1985); (B) after Moy-Thomas and Miles (1971).

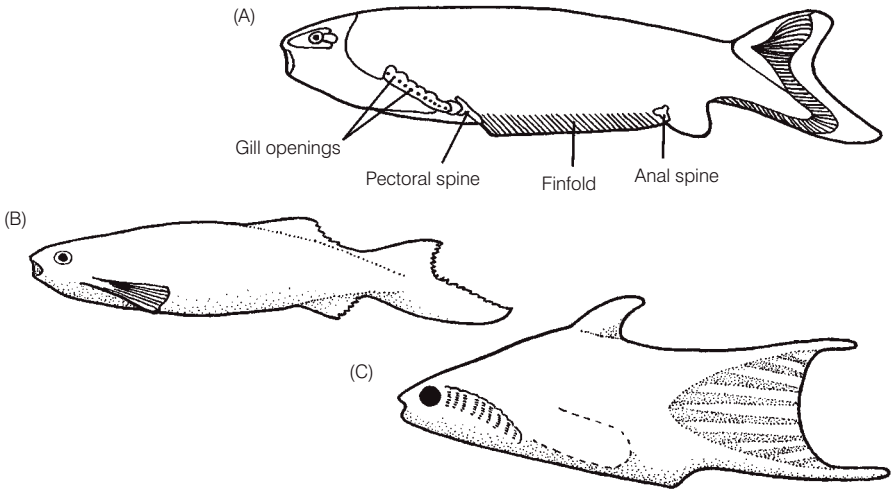


Figure 11.4
Other jawless fishes are placed in the superclasses Anaspida and Thelodonti. (A) Anaspids, such as *Pharyngolepis*, were convergent in body form with the thelodonts, but probably led a benthic existence. (B) Thelodonts were more streamlined, such as *Phlebolepis* with its hypocercal tail. (C) The furcacaudiform forktail thelodonts may be among the first fishes to occupy the water column. (A, B) after Moy-Thomas and Miles (1971); (C) after Wilson and Caldwell (1993).

maneuverability for their apparently suprabenthic existence.

†Thelodonti

Thelodonts ("nipple teeth", also known as coelolepids or "hollow scales") were diminutive (10–20 cm), fusiform, jawless fishes that were covered with denticles rather than bony plates (Fig. 11.4B). They were abundant and widespread, their denticles/scales serving as stratigraphic indicators in paleontological studies. Most were depressed, with a horizontal mouth, asymmetrical hypocercal tails, and a detectable lateral line that ran the length of the body. Many thelodonts had dorsal and anal "fins". Their mode of life was probably similar to pteraspidiforms, namely skimming and filtering small organisms from bottom sediments while swimming, although genera with a fusiform body shape and terminal mouths suggest they may have been water column swimmers. A suprabenthic existence is almost certain for the recently discovered furcacaudiform (literally "forktail") thelodonts of northwestern Canada (Fig. 11.4C). These were shaped like minnows or pupfishes and had compressed bodies, symmetrically forked tails, tubular mouths, and a stomach (Wilson & Caldwell 1993).

Five orders and perhaps 14 families are recognized, with representatives from the Upper Ordovician to the Upper Devonian. Early thelodonts appear in marine deposits but later groups invaded fresh water. Nelson (2006) summarizes the diversity of viewpoints that exist about thelodont position and relationships.

†Osteostracomorphi

The superclass Osteostracomorphi contains one class and three orders of jawless fishes. The highly diverse class Cephalaspidomorphi (or Monorhina = "single nostril") first appears in the Upper Silurian, approximately 100 million years after the appearance of the pteraspidiforms. They too flourished until the end of the Devonian. They had two semicircular canals and evidence of true bone cells. The alternative name Monorhina refers to the single, median, slitlike opening, the nasohypophyseal foramen, in the anterior region of the head shield, associated with the pineal body.

The best known cephalaspidomorphs are a predominantly freshwater group, the **Cephalaspidiformes** (Fig. 11.5). These were abundant and diverse fishes; nearly 100 species just in the genus *Cephalaspis* have been described (see Jarvik 1980). Rather than acellular bone, cephalaspidiform armor was cellular. Another cephalaspidiform innovation, also evolved in jawed vertebrates, is ossification of the endoskeleton. Paired lateral appendages in cephalaspidiforms are thought by some to be homologous to gnathostome pectoral fins (Nelson 2006). Unlike the armor of pteraspidiforms, cephalaspidiform head shields are sutureless and lack any apparent growth rings. In fact, all fossils of many species are the same size, suggesting a naked (nonfossilizing), growing larva that metamorphosed into an armored adult of fixed size. The head shield included one medial and two lateral regions (sensory fields) of small plates sitting in depressions and connected to the inner ear by large canals, for which either an acousticolateralis, electrogenerative, or electroreceptive function has been suggested (Moy-Thomas & Miles 1971; Carroll 1988; Pough et al. 1989). The tail was heterocercal, which may have made skimming along the bottom easier by counteracting the upward lift that the lateral appendages and flattened underside of the head would have generated.

The internal anatomy of the cephalaspidiform head shield is remarkably well known. Swedish paleontologist Erik Stensiö and colleagues painstakingly sectioned rocks containing cephalaspidiforms and worked out the anatomical details of the braincase and cranial nerves (Fig. 11.5B).

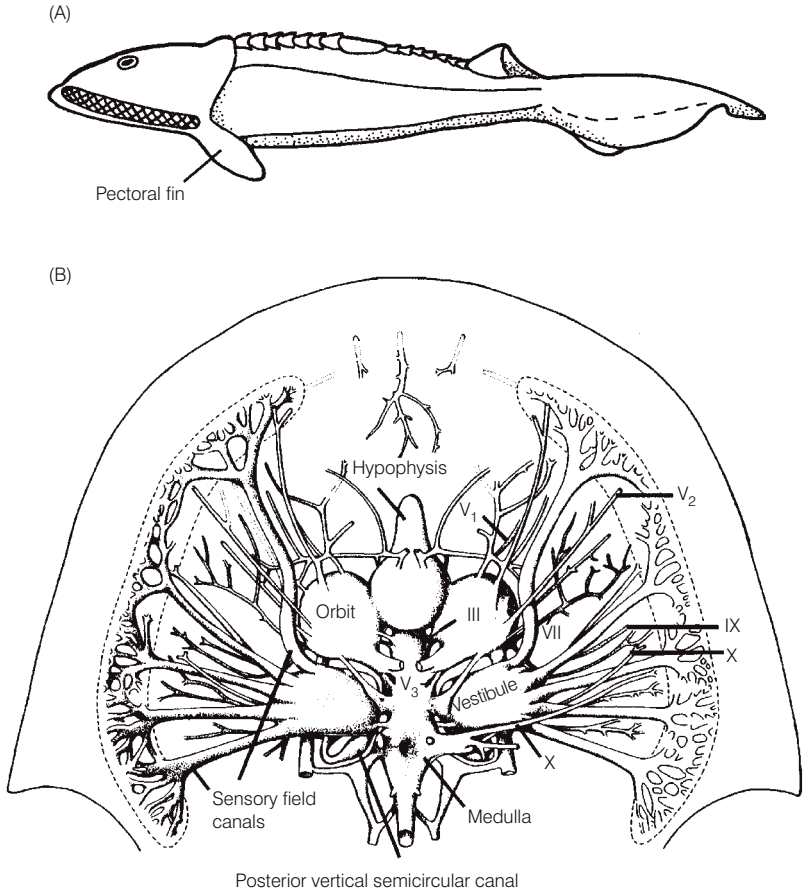


Figure 11.5
Cephalaspidomorphs were diverse jawless forms that appeared during the Silurian and lasted into the Devonian. The largest order was the cephalaspidiforms, including (A) *Hemicyclaspis*. (B) Thin sections of headshields clearly show brain differentiation and cranial nerves (roman numerals), organized similarly to modern lampreys. (A) after Moy-Thomas and Miles (1971); (B) from Stensio (1963), used with permission.

These efforts allowed identification of such structures as the olfactory lobes, diencephalons, and myelencephalon, the relationship of the hypophyseal sac to the olfactory opening, the relative sizes of the right and left ganglia, the alternation of cranial nerves, the separation of dorsal and ventral nerve roots, the location of blood vessels, the existence of two vertical semicircular canals, and other details (Moy-Thomas & Miles 1971).

The other two cephalaspidomorph orders are the recently discovered **galeaspidiforms**, with 10 families restricted to China, and the pituriaspidiforms, with two species found only in Australia. In galeaspidiforms, the median nasohypophyseal opening is large and anterior to the eyes. Paired gill compartments are numerous, up to 45 in number, which is the extreme among vertebrates. Bone was acellular rather than cellular (Halstead et al. 1979; Janvier 1984; Pan Jiang 1984).

Based on the detailed anatomical studies of Stensio, subsequent workers interpreted many cephalaspidiform head structures to be homologous with modern lampreys, concluding that an ancestral–descendant relationship existed. However, more recent analyses indicate that the osteostracomorphs are the closest jawless relatives to jawed vertebrates or gnathostomes, constituting a sister group (i.e., osteostracomorphs and gnathostomes are more closely related to each other than they are to any other clade, including lampreys).

Later evolution of primitive agnathous fishes

Although much has been written about possible descendants of the early agnathans, additional discussion of the interrelationships of these primitive groups is beyond the scope of this book, mainly because authorities disagree as to where the relationships lie. Different authors consider different characters as ancestral, derived, or convergent, and consequently arrive at different conclusions about relationships between and among jawless and jawed forms. One interpretation gaining acceptance, and the one presented here, is summarized in Fig. 11.6. For an historical overview of this controversy, the reader is referred to Jarvik (1980), Carroll (1988), Forey and Janvier (1993), Long (1995), Janvier (1996, 2001), Maisey (1996), Forey (1998), Donoghue et al. (2000), Clack (2002), Pough et al. (2005), and Nelson (2006).

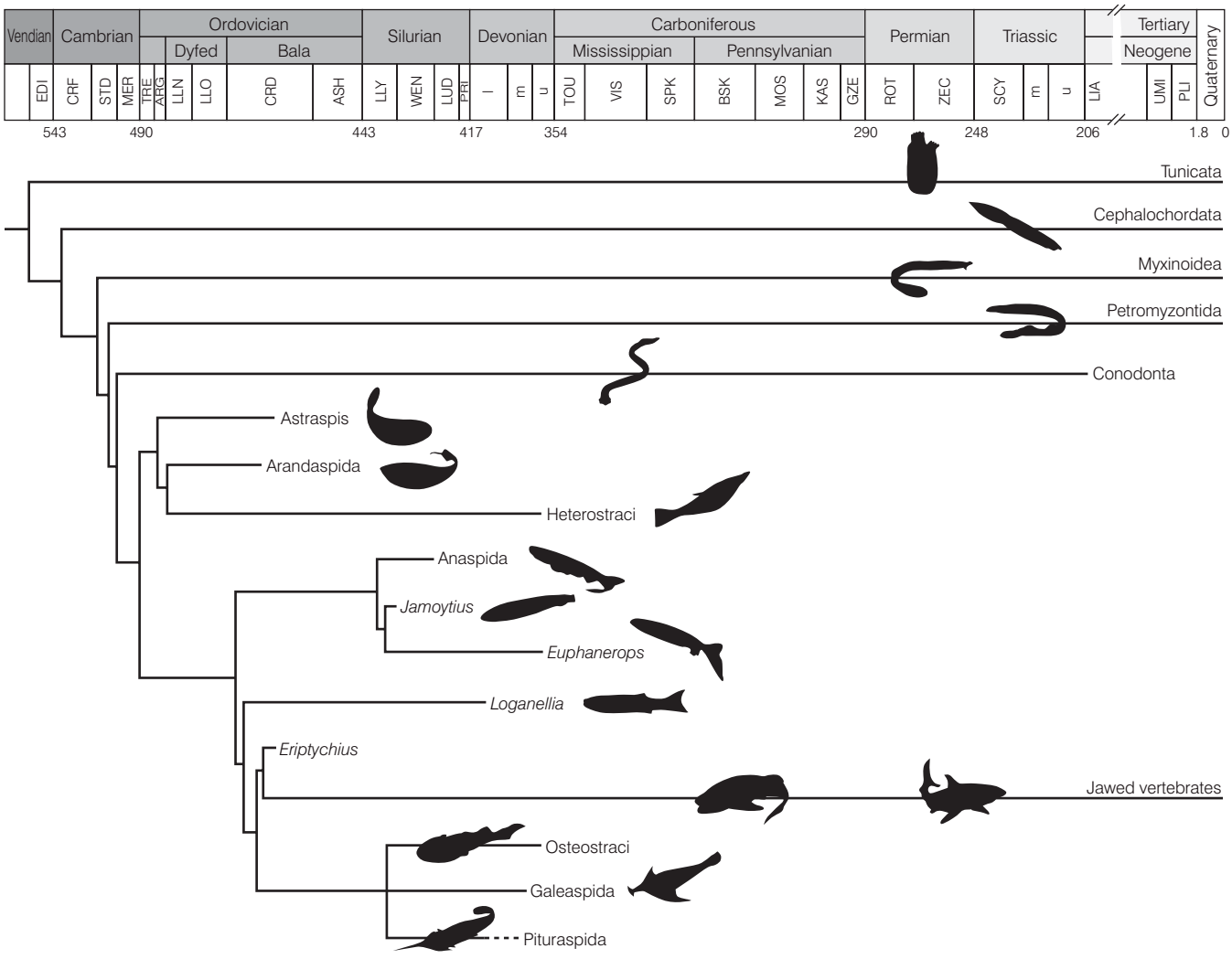


Figure 11.6

One view of relationships among early agnathous fishes, modern jawless forms, and jawed vertebrates. Notable here is the stem or sister position of cephalochordates relative to all craniates, of conodonts relative to all jawless vertebrates except lampreys, and of osteostracomorphs (Osteostraci, Galeaspida, Pituriaspida) relative to jawed fishes. Major geological time periods are given at the top of the figure, with abbreviated subdivisions immediately below. The time scale is millions of years before present. Most groups depicted are discussed in the text. From Donoghue et al. (2000), used with permission.

Gnathostomes: early jawed fishes

Phylum Chordata
  Subphylum Craniata
    Superclass Gnathostomata
      †Class Placodermi
        Orders Acanthothoraciformes, Rhenaniformes, Antiarchiformes, Petalichthyiformes, Ptyctodontiformes, Arthrodiriformes

† Extinct group.

The superclass **Gnathostomata** is characterized by a number of innovations lacking in jawless forms. **Jaws** are present, derived from gill arches. **Paired limbs** with skeletal support are usually present, as is **endochondral bone, three semicircular canals,** and **dentine-based** rather than horny teeth. However, no clearly intermediate fossils between jawed and jawless forms have been found. The origins of jaws and the other structures that characterized the early gnathostomes are buried in the fossil record, belonging to some group yet to be discovered. Homologies between the gill arches of osteostracomorphs and the jaws of later groups are unclear, and the early fossils of jawed fishes already possessed jaws, teeth, scales, and spines. To further complicate our understanding of chronology and phylogeny is the age of different fossils versus the widely held view that placoderms

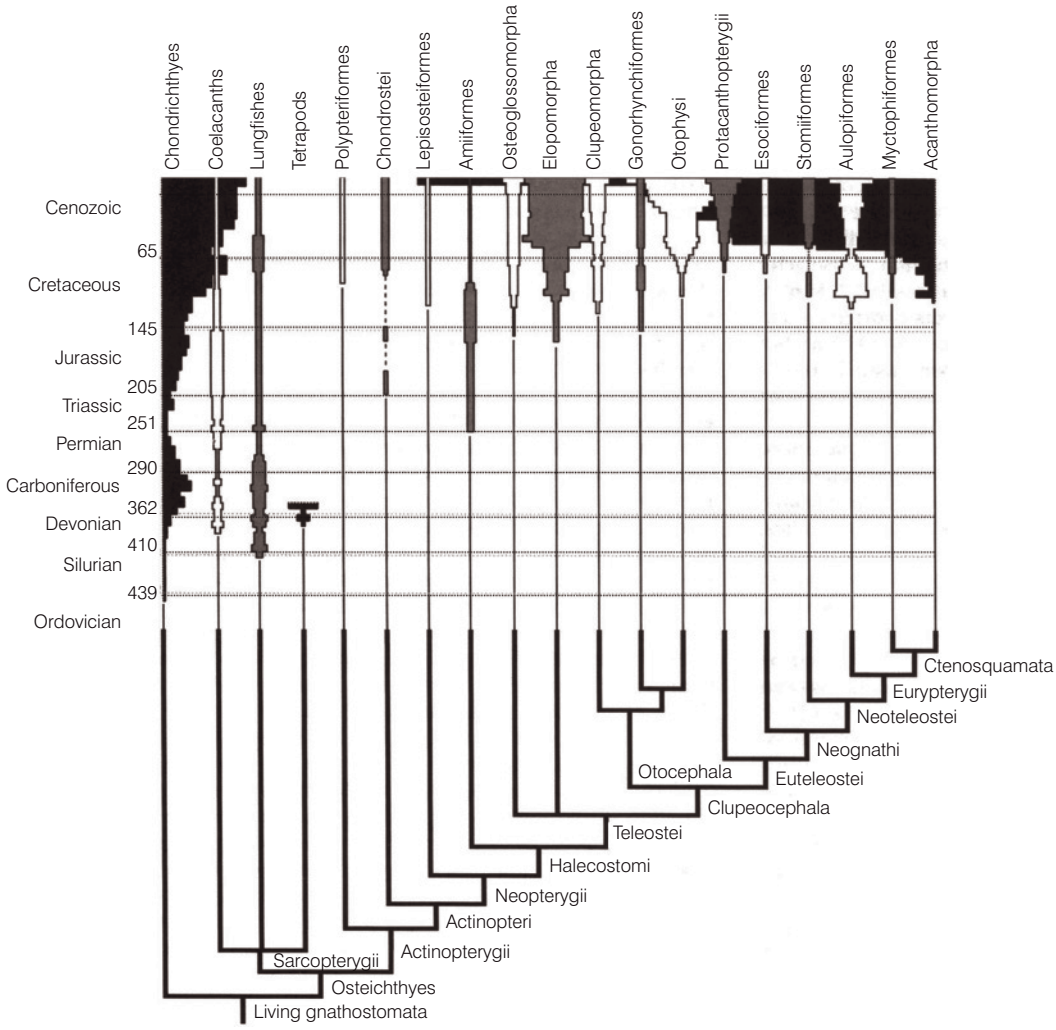


Figure 11.7

Periods of occurrence of major jawed (gnathostome) fish taxa based on the fossil record. Column width represents familial diversity within a group (only half of chondrichthyan and acanthomorph diversity is shown). The time scale is millions of years before present. A glance at the figure reveals why the Devonian is commonly referred to as the Age of Fishes: during the Middle Devonian, most major groups discussed in this chapter, including jawless forms shown in Fig. 11.1, were represented. Slightly modified from Stiassny et al. (2004).

preceded acanthodians and may have been ancestral to chondrichthyans. However, chondrichthyan scales and denticles have been found in Late Ordovician deposits, acanthodians show up later in the Lower Silurian, and the earliest placoderms do not appear "until" the Middle Silurian (Nelson 2006).

What we do have is an abundance of fossil material that gives us a clear picture of the diversity of forms that the innovation of jaws must have permitted, with groups proliferating and with many early groups giving rise to extant taxa (Fig. 11.7). The evolutionary importance of true jaws cannot be overemphasized: "perhaps the greatest of all advances in vertebrate history was the development of jaws and the consequent revolution in the mode of life of early fishes" (Romer 1962, p. 216).

This revolution included a diversification of the food types that early fishes could eat. Large animal prey could be captured and dismembered, and hard-bodied prey could be crushed. Agnathous fishes were probably limited to planktivory, detritivory, parasitism, and microcarnivory. Stomachs for storage of food evolved, probably as a consequence of jaws that could bite off pieces of food. With the advent of jaws, both carnivory and herbivory on a grand scale became possible, as reflected in the size of the fishes that soon evolved. Jaws also allowed for active defense against predators, leading to de-emphasis on armor, which in turn meant greater mobility and flexibility. This increase in agility was greatly enhanced by the development of paired, internally supported pectoral and pelvic appendages, "the most outstanding shared derived charac-

ter of the gnathostomes besides the jaw" (Pough et al. 1989, p. 235).

Class Placodermi

Placoderms ("plate-skinned") had tremendous success and diversity. Their name refers to the peculiar bony, often ornamented, plates that covered the anterior 30–50% of the body. Most placoderms had depressed, even flattened bodies, suggesting benthic existence. They may have preyed upon, and eventually replaced, pteraspidiform and cephalaspidiform fishes. As in ostracoderms, placoderms occurred first in marine habitats but later moved into fresh water. As in both ostracoderms and acanthodians (see next section), many placoderm groups show an evolutionary trend toward reduction in external armor, leading to a mobile existence in the water column. Placoderms had ossified haemal and neural arches along the unconstricted notochord and three semicircular canals. Placoderms arose in the Late Silurian, flourished worldwide in the Devonian, and disappeared by the Early Carboniferous. Their disappearance often correlates with the proliferation of chondrichthyans at the end of the Devonian, and ecological replacement is suspected.

Six orders, 25–30 families, and perhaps 200 genera of placoderms are recognized (Fig. 11.8). **Acanthothoraciformes** from the Lower Devonian are the basal group and are therefore the oldest known jawed vertebrates. **Arthrodiriforms** (arthrodires, "jointed neck") are the largest order, containing about 170 genera. They possessed a unique hinge at the back top of the head between the braincase and the cervical vertebrae, termed the **craniovertebral joint**. This joint allowed opening of the mouth by both dropping the lower jaw and raising the skull roof, thus increasing gape size. As the group evolved, this joint became larger and more elaborate, and dentition diversified into slashing, stabbing, and crushing structures. Arthrodires were among the largest of the placoderms. *Dunkleosteus* (Fig. 11.8E) was perhaps 6 m long, with a head more than 1 m high; some fossils suggest *Dunkleosteus* may have reached twice that size (Young 2003). Their large size and impressive dentition implicate the arthrodires as major predators of Devonian seas. Devonian arthrodires (e.g., *Groenlandaspis*) have also been found with fossilized silver and red pigment cells distributed in a pattern indicative of countershaded coloration. Red pigment cells suggest that color vision had already evolved in fishes more than 350 mybp (Parker 2005).

None of the other placoderm orders attained the success of the arthrodires. **Rhenaniforms** were extremely dorsoventrally depressed and bore a striking resemblance to modern skates, rays, and angel sharks (e.g., *Gemuendina*, Fig. 11.8D), although their lateral fins were too heavily armored to be undulated or flapped in the manner characteristic of modern skates and rays. The antiarchiforms (**antiarchs**, e.g., *Bothriolepis*, Fig. 11.8C) were predominantly freshwater, heavily armored, benthic fishes with a spiral valve intestine and jointed, arthropod-like pectoral appendages that had internal muscularization. **Ptyctodontiforms** greatly

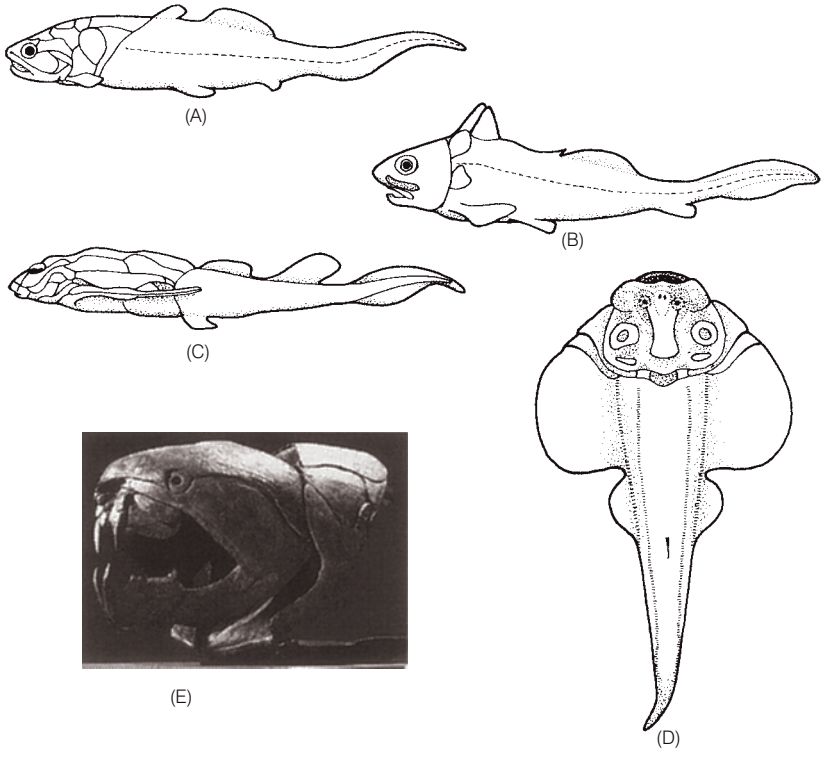


Figure 11.8
Placoderms. (A) The coccosteomorph *Coccosteus*, (B) the ptyctodontid *Rhamphodopsis*, (C) the antiarch *Bothriolepis*, (D) the rhenanid *Gemuendina*, and (E) *Dunkleosteus*, a giant arthrodire placoderm from the Devonian. In *Dunkleosteus*, the meter high head was followed by a proportionately large body, but actual lengths are unknown because fossilized remains of the posterior skeleton are lacking. (A–D) after Jarvik (1980) and Stensio 1963; (E) photo by Chip Clark, used with permission.

resembled modern holocephalans in body form (see Fig. 11.8B) and are the first fishes known to possess apparent male intromittent organs in the form of claspers associated with the pelvic fins, an indication of internal fertilization.

Although the craniovertebral joint of many placoderms afforded increased jaw mobility compared to forms with a fixed upper jaw, placoderms lacked **replacement** dentition. Placoderm "teeth" consisted of dermal bony plates made up of a unique dentinelike material attached to jaw cartilage. This bone was often differentiated into sharp edges and points, producing "fearsome blade-like jawbones, which wore away during growth like self-sharpening scissors, to leave a hardened core forming massive stabbing blades" (Young 2003, p. 988). However, these blades were subject to breakage and wear, with no apparent repair or replacement mechanism. Placoderm jaw morphology and hinging also prohibited them from developing suction forces when feeding. The innovations of serially replaced teeth and of jaws that could create suction characterize the fish taxa that evidently replaced the placoderms and acanthodians.

Advanced jawed fishes I: teleostomes (Osteichthyes)

The first bony fishes are represented by fragments and microfossils from the Late Ordovician. From these ancestors, three distinct classes arose: the **acanthodians**, **sarcopterygians**, and **actinopterygians**. The three together make up the grade **Teleostomi**, whereas sarcopterygians and actinopterygians together constitute the subgrade **Euteleostomi** (euteleostomes have historically been referred to as **Osteichthyes**, literally "bony fishes", but that taxon lacks official rank although it remains a sentimental favorite and is easier to remember than "euteleostomes").

Teleostomes are grouped together because they share cranial, scale, and fin similarities, but especially because both acanthodians and actinopterygians possess **three otoliths** (sarcopterygian lungfishes have two otoliths and coelacanths have only one). Acanthodians diversified in the Silurian and Devonian and lasted through the Permian. The euteleostome **Actinopterygii** ("ray-fins") are known first from scales in Late Silurian deposits, whereas **Sarcopterygii** ("fleshy or lobe fins") appear in the Early Devonian.

Euteleostomes share numerous characteristics, including the bone series in the opercular and pectoral girdles, the pattern of their lateral line canals, fins supported by dermal bony rays, a heterocercal tail with an epichordal (upper) lobe, replaceable dentition, and a swim bladder that developed as an outpocket of the esophagus. Sarcopterygians

Phylum Chordata
- Subphylum Craniata
  - Superclass Gnathostomata
    - Grade Teleostomi
      - †Class Acanthodii
        - Orders Climatiiformes, Acanthodiformes, Ischnacanthiformes
      - Subgrade Euteleostomi
        - Class Sarcopterygii
          - Subclass Coelacanthimorpha
            - Order Coelacanthiformes (coelacanths, Actinistia)
          - Subclass Dipnoi (Dipnotetrapodomorpha)
            - †Order Onychodontiformes
            - †Superorder Porolepimorpha
              - Order Porolepiformes
            - †Superorder Dipteramorpha
            - Superorder Ceratodontimorpha
              - Order Ceratodontiformes (living lungfishes)
        - Tetrapodomorpha[a]
          - †Order Rhizodontiformes
          - †Order Osteolepidiformes
        - (†)Infraclass Elpistostegalia
          - Subclass Tetrapoda[b]

[a] The unranked taxon, Tetrapodamorpha, lies below class but above infraclass and subclass.
[b] Nelson (2006), among others, uses cladistic principles to relegate the 26,734 species of tetrapods to a subclass of the fleshy finned sarcopterygians, declaring them a "divergent sideline within the fishes that ascends onto land and into the air and secondarily returns to water" (p. 87). It will be interesting to see how students of these higher vertebrate groups respond to this depiction. Pough et al. (2005) at least concur.
† Extinct group.

diversified into extinct and modern coelacanths, lungfishes, and tetrapodomorphs – the latter group including rhizodontimorphs, osteolepidimorphs, and the elpistostegalians that gave rise to tetrapods. Actinopterygians underwent tremendous multiple radiations, producing the cladistian bichirs, the chondrosteans (many fossil groups plus modern sturgeons and paddlefishes), and neopterygians, including gars and related fossil groups, Bowfin and related fossil groups, and ancient and modern teleosts.

Although we tend to view the more advanced fishes as improvements over the primitive taxa, in part because the former are represented today, placoderms and acanthodians existed literally side by side with the "more advanced" forms for more than 100 million years. At some point, for climatic or biological reasons that are unclear, the innovations of the more derived gnathostomes, or the evolutionary constraints placed upon the more primitive groups, led to a replacement of one group by the other. The result was an incredible series of explosions of species belonging to four or five very different lineages, derived forms of which are still alive today.

†Class Acanthodii

The oldest fossils of relatively advanced, jawed fishes belong to **Acanthodians**, or "spiny sharks", from Late Ordovician deposits. Their Latin name refers to the stout median and paired spines evident in most fossils; their similarity to sharks is largely superficial and few current authors feel they are related to modern chondrichthyans (but see Jarvik 1980). Acanthodians were generally small (20 cm to 2.5 m); occurred in both salt and fresh water, mostly in Laurasia (see Box 16.1); had cartilaginous skeletons; a body covered with small, non-overlapping scales; large heads; and large eyes. Their streamlined, round bodies, reduced armor when compared to ostracoderms, subterminal mouths often studded with teeth (including teeth inside the mouth and on the gill rakers), and fin placement indicate they were water column, not benthic, feeders. Given the success of ostracoderms in benthic habitats, it is not surprising that the next fish group to evolve would occupy the relatively unexploited water column.

Three orders, nine families, and at least 60 genera of acanthodians have been described, many from isolated spines and teeth (Carroll 1988). All three orders show interesting parallels in evolution. Early acanthodians had multiple gill covers, broad unembedded spines anterior to all fins except the caudal, as well as additional spine pairs between the pectoral and pelvic fins (Fig. 11.9A). More advanced species had single gill covers and lost the ancillary paired spines, the remaining spines being thinner and embedded in the body musculature (e.g., *Acanthodes*, Fig. 11.9B). Some specialized lineages were toothless and had long gill rakers, indicating a planktivorous habit. Because acanthodians possessed a third (horizontal) semicircular canal and neural haemal arches associated with the unconstricted vertebral column, and other shared, derived traits (otoliths, lateral line canals, ossified operculum, branchiostegals, cranial and jaw series, including the new interhyal bone), they are included within the Teleostomi (Lauder & Liem 1983; Maisey 1986). Acanthodians survived until the Early Permian, outlasting the major ostracoderm groups by 100 million years.

Class Sarcopterygii

Ancestral sarcopterygians remain one of the most actively studied fossil groups of fishes, in no small part because of their place in tetrapod evolution. In recent years, abundant discoveries have been made, often prompting reanalysis of relationships among fossil and extant groups. Agreement is far from universal: Forey (1998) summarized major hypotheses, presenting 13 different phylogenies proposed by different authorities in the last 20 years of the 20th century. Forey's concluding analysis is presented in Fig. 11.10 and is largely followed here. The debate revolves largely around

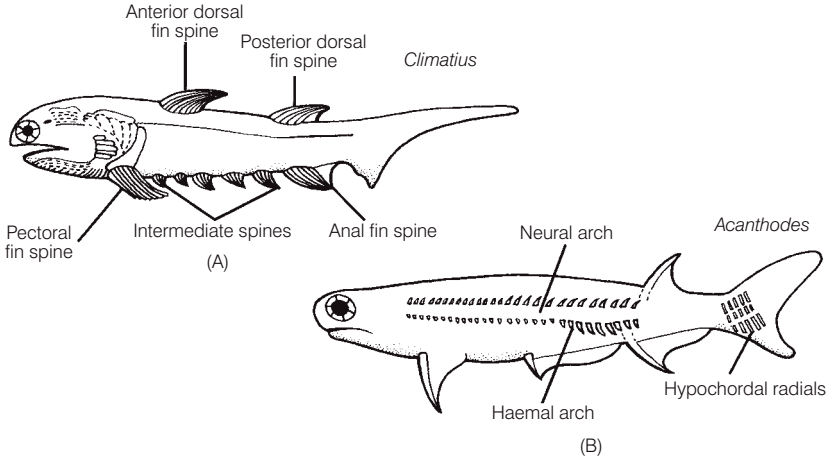


Figure 11.9
Acanthodians. (A) *Climatius*, a primitive acanthodian with multiple gill covers and multiple, unembedded spines. (B) The more advanced *Acanthodes*, with fewer, thinner, more deeply embedded spines, a single gill cover, and a more symmetrical caudal fin. After Moy-Thomas and Miles (1971).

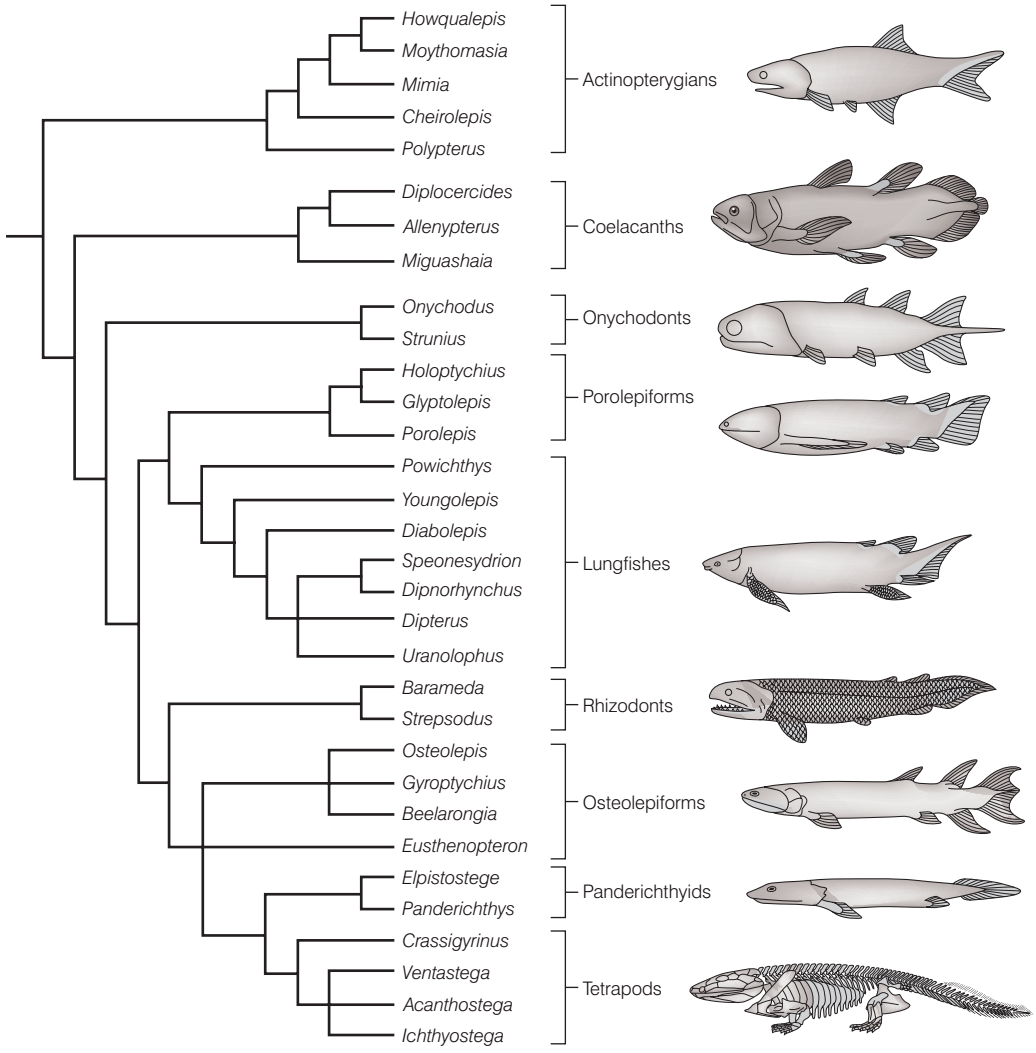


Figure 11.10

One view of relationships among euteleostome bony fishes ("Osteichthyes"), showing actinopterygians as the sister group to the various extant and extinct sarcopterygian taxa. After Forey (1998).

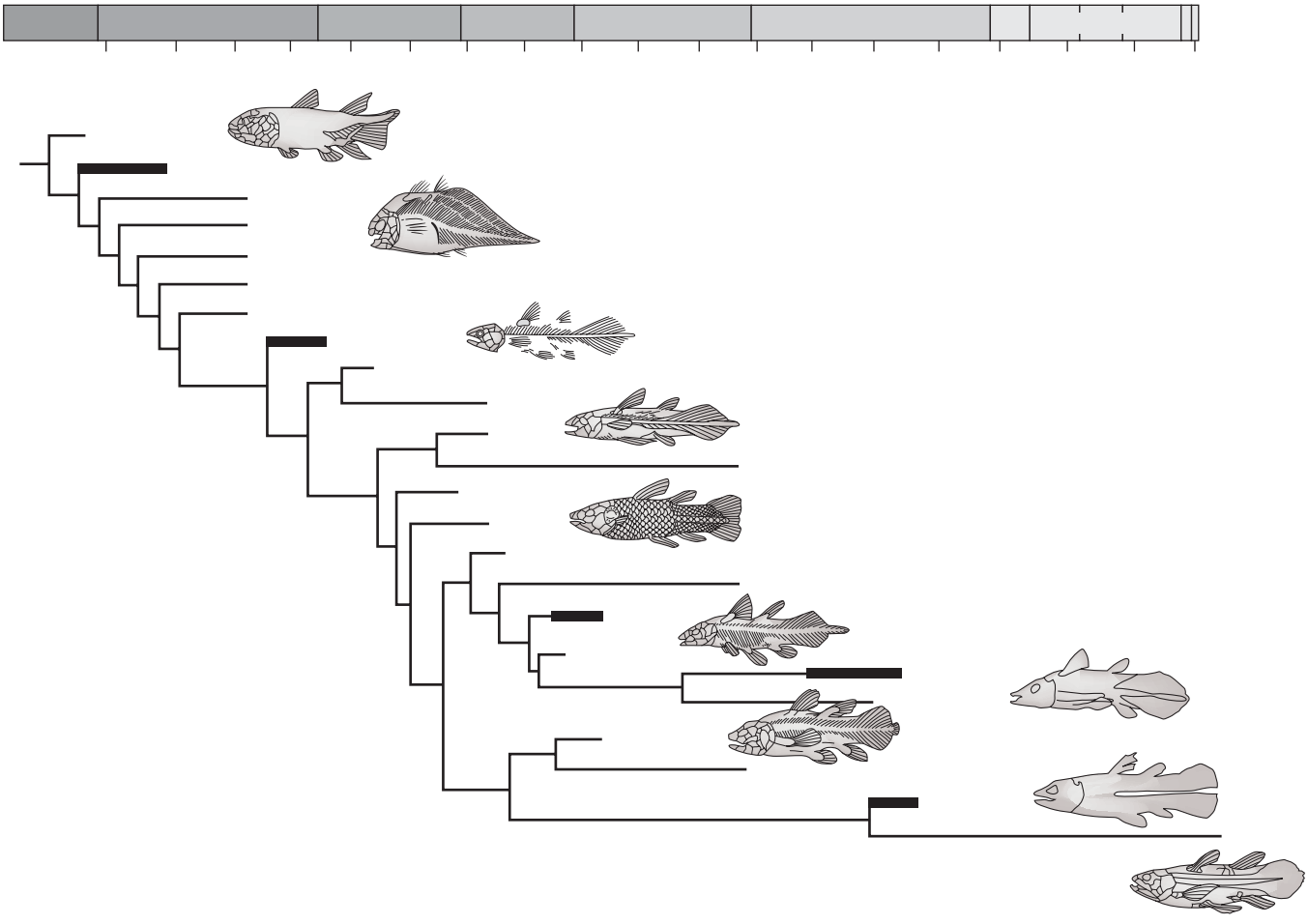
the relative positions of lungfishes, coelacanths, and the osteolepiform–porolepiform–panderichthyid lineages relative to tetrapods. Fortunately, discovery of a Devonian fish intermediate between the elpistostegalian/panderichthyid group and early tetrapods was published in early 2006 and *may* influence much of the debate (see Box 11.1 below).

Until the dust settles, many higher taxonomic groupings omitted from this treatment are listed as "unranked" and are given numerical designations 1a–4b in Nelson (2006). The exception is Tetrapodomorpha, which we include as "unranked" between class and infraclass. Most of the omitted taxa fall between the official rankings of subclass and superorder, but a formal designation does not yet exist. We fully expect that in the next few years, researchers in this exciting area will erect names and ranks for these groups, alleviating the confusion that currently plagues a student first encountering the admittedly bewildering array of unfamiliar names and serial numbers.

Subclass Coelacanthimorpha, order Coelacanthiformes

Fossil **coelacanthimorphs** (or Actinistia) appeared in the Middle Devonian and are not known after the Late Cretaceous. They occurred worldwide in both marine and fresh water. The fossil record of the group is extensive: at least 83 valid species in 24 genera and perhaps nine families are recognized. Diversity was maximal during the Early Triassic, when 16 described species existed (Forey 1998) (Fig. 11.11). All but one family and two species are extinct.

Coelacanths are in many respects more specialized than other sarcopterygians, possessing a unique spiny rather



than a lobate first dorsal fin; a three-lobed caudal fin with a middle fleshy, fringed lobe (the term "coelacanth" describes the hollow nature of the fin rays that support the tail); a rostral organ involving a rostral cavity with several openings on the snout associated with electroreception; and lacking internal choanae, cosmine in the scales, branchiostegals, and a maxilla. Most evolution in the group occurred during the Devonian (some early genera had a heterocercal rather than a diphycercal tail), and later species are surprisingly unchanged in body shape and jaw morphology from the early representatives, although trends of change (reduction in some bones, increases in others) have occurred (Cloutier 1991). Rapid evolution and morphological variation occurred in early coelacanths, including an eel-like species from the Middle Devonian (Friedman & Coates 2006). Prior to the discovery of the living Coelacanth in 1938 (see Chapter 13: The living coelacanths, at least for now), coelacanthimorphs were of interest primarily to paleontologists as a specialized, extinct group notable for its conservativism and its relationship to the reputed ancestors of tetrapods.

Subclass Dipnoi (Dipnotetrapodomorpha)

Besides coelacanths, sarcopterygians consist of two other subclasses: (i) the dipnoans (also called dipnotetrapodomorphs), consisting of a variety of extinct fishes with stout bodies and paddlelike paired fins (including the specialized, modern lungfishes); and (ii) the **Tetrapoda** that emerged onto land to become amphibians, reptiles, birds, and mammals. Major groups within the Dipnoi are the dipnomorphs (two fossil superorders aligned to lungfishes and the lungfish superorder itself) and the tetrapodomorphs (including the rhizodontomorphs, osteolepidomorphs, and the infraclass Elpistostegalia).

Dipnomorphs

Dipnomorphs are an unranked taxon made up of extinct fishes in the superorder **Porolepimorpha** (one order, two

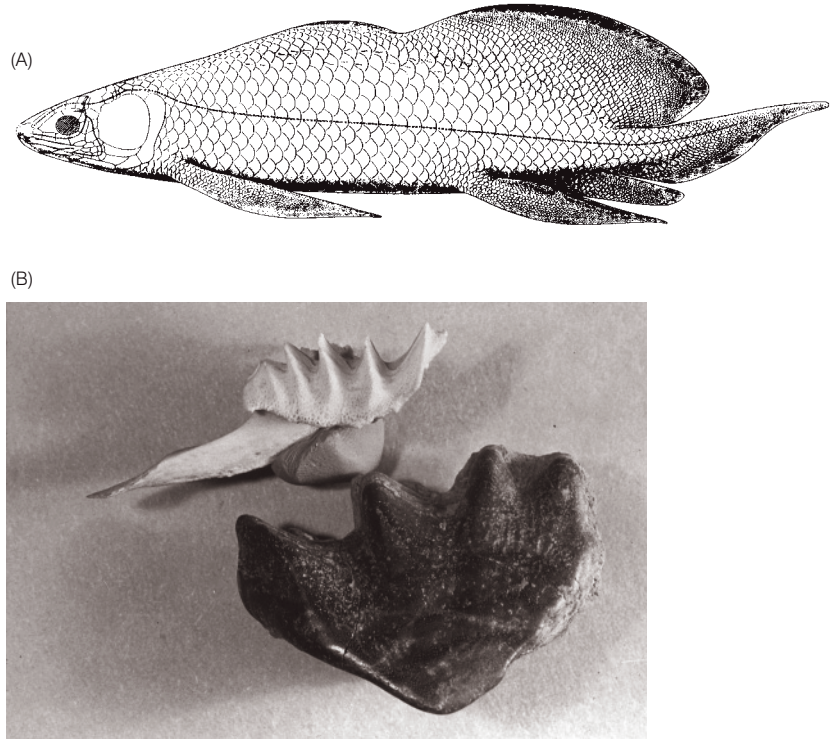


Figure 11.12
Extinct and extant lungfishes. (A) *Scaumenacia*, an Upper Devonian lungfish from eastern Canada; (B) Toothplates from a fossil lungfish, *Ceratodus*, from the Upper Triassic (*c*. 5 cm wide) and from the extant Australian lungfish, *Neoceratodus* (upper structure). The Australian lungfish is considered to be more similar to ancestral forms than are the living African and South American species. The *Neoceratodus* toothplate is mounted on a piece of modeling clay. (A) from Jarvik (1980), used with permission; (B) photo by G. Helfman.

families from the Devonian), plus two superorders of lungfishes, the extinct **Dipterimorpha** (10 families) and extant **Ceratodontimorpha** (one order, three extant families, with some extinct genera). Lungfishes as a group have been generally referred to as **Dipnoi** or dipnoans ("double-breathing"). Dipteramorphs arose in the Devonian in marine environments, expanded into freshwater habitats, and died out by the end of the Triassic. Primitive lungfishes were characterized by: two dorsal fins; fleshy, scale-covered, paired, leaflike **archipterygial** fins with a bony central axis and with fin rays coming off the central axis; a lack of teeth on the marginal jaw bones, but with tooth plates inside the mouth, and with the premaxilla, maxilla, and dentary missing; a solid braincase; and a pore-filled, cosmine coating on the dermal bones that covered the skull and scales and that may have been associated with electroreception (Fig. 11.12). Later species occupied fresh water, and trends in lungfish evolution include loss of the first dorsal fin, fusion of the median fins (second dorsal, caudal, anal) to form a symmetrical tail (earlier forms had heterocercal tails), elaboration of the tooth plates and development of replaceable dentition, replacement of ossified centra with cartilage, fusion of skull bones, and concomitant loss of the cosmine covering.

Ceratodontimorphs appear first in the Lower Triassic and are represented today by the freshwater order **Ceratodontiformes**, containing three families and six species of lungfishes in Australia (Ceratodontidae, one species), South America (Lepidosirenidae, one species), and Africa (Protopteridae, four species) (see Chapter 13). Modern lungfishes take the anatomical trends to the extreme, having eel-like, largely cartilaginous bodies, lacking any cosmine bony layers, and possessing diphycercal tails. The modern Australian lungfish is more similar to the heavier bodied dipnoans of the Paleozoic and Mesozoic. Although limited to fresh waters on three continents today, fossil ceratodontids occupied North and South America, Africa, and Madagascar, many in marine deposits.

Lungfishes underwent extensive diversification during the Devonian, evolving more than 60 genera and 100 species, 80% of which occurred during the Upper Devonian (Marshall 1987). Numbers diminished substantially during the Carboniferous. Many lungfish species are known only from fossilized toothplates, with toothplates and other structures found in fossilized lungfish burrows. These finds indicate that air breathing and **estivation** (entering torpor and burrowing in mud during drought) evolved as early as the Devonian, a fortuitous (for paleontologists) instance of fish waiting for rains that never came (Moy-Thomas & Miles 1971). Some ceratodontids were quite large; a North American Jurassic species, *Ceratodus robustus*, was 4 m long and may have weighed as much as 650 kg (Robbins 1991). The modern genus *Neoceratodus* occurs as early as the Upper Cretaceous in Australia. The lepidosirenid lungfishes of Africa and South America represent a family that goes back to the Late Carboniferous, but members of the two extant genera do not appear until the Eocene and Miocene, on the same continents where they occur today (Carroll 1988).

Much controversy has swirled around the ancestry of lungfishes, as well as a possible dipnoan ancestry for terrestrial vertebrates (see reviews in Carroll 1988; Pough et al. 1989). Some of this speculation originated with the early misidentification of lungfishes as amphibians (see Chapter 13). More recent arguments have focused on shared aspects of the lungs, limblike fins, and internal nostrils (e.g., Rosen et al. 1981). However, workers in this area have increasingly reached the conclusion that the ancestry of tetrapods is more closely linked to another group of sarcopterygians, the infraclass Elpistostegalia (see below and Box 11.1).

Tetrapodamorphs: tetrapod ancestors

Appearing in the Early Devonian with the dipnoans are the three clades referred to as tetrapodamorphs. First to appear were the **rhizodonts** (Rhizodontimorpha, order **Rhizodontiformes**, family **Rhizodontidae**), with at least seven genera. Next were the **osteolepidiforms** (Osteolepidomorpha, order Osteolepidiformes; osteolepiforms in Fig. 11.10), including five families. Finally, the infraclass **Elpistostegalia** appeared, with its important (to us as tetrapods) genera ***Elpistostege*** and ***Panderichthys*** (and *Tiktaalik*, see Box 11.1) in a family that is variously recognized as either Panderichthyidae or Elpistostegidae.

Tetrapodamorphs as a group were large, predatory fishes characterized by sarcopterygian traits such as two dorsal fins, cosmine covering of the bones and scales, kinetic (jointed) skulls, lobed fins, and replacement teeth on the jaw margins. They remained common throughout the latter half of the Paleozoic, and most forms disappeared by the end of the Permian. Some were large (up to 4 m long), cylindrically shaped predators that occurred primarily in shallow, freshwater habitats (Fig. 11.13). Evolutionary trends include reduction in dermal bone thickness, a change from diamond- to round-shaped scales, and an increasingly symmetrical tail. The latter trait is often considered indicative of a hydrostatic function for the gas bladder (Moy-Thomas & Miles 1971).

Of the three groups, we know most about the osteolepidiforms and especially the tristichopterid ***Eusthenopteron foordi*** because of exceedingly well-preserved material painstakingly prepared by E. Stensiö and associates (Fig. 11.13). One specimen alone required 6 years of serial grinding and many more years of analysis to characterize just the anatomy of the skull of this fish. Jarvik (1980) commented that we probably know more about the skeletal anatomy of *Eusthenopteron* than we do about most extant fishes. This knowledge is fundamental to our understanding of the anatomical transitions that occurred as sarcopterygians changed from purely aquatic forms capable of breathing atmospheric oxygen to semiterrestrial forms capable of movement on land and no longer dependent on gills (Fig.11.14).

Although osteolepidiforms possessed many homologies with later tetrapods, these fishes were unlikely to have been transitional forms to living on land, even temporarily. It is the elpistostegalians that are generally considered the most likely sister group of modern tetrapods. Focus has been placed on many apparent homologies, including eye position, skull roof bones, paired fins, dentition, and vertebral accessories (Pough et al. 1989, 2005; Forey 1998). Elpistostegalians and tetrapods both have eyes set close together on the top of the skull facing upwards, with eyebrowlike ridges. The median series of skull roof bones – frontals, parietals, and nasals – may be homologous, although not all workers agree on terminology. The paired fins of the osteolepidiforms and elpistostegalians are very similar to those of the stem non-amniote tetrapods of the Upper Devonian, such as *Ichthyostega* (Fig. 11.15). This fin type contains bones homologous to the proximal elements of tetrapod fore- and hindlimbs (humerus, radius, ulna; femur, tibia, fibula), unlike the

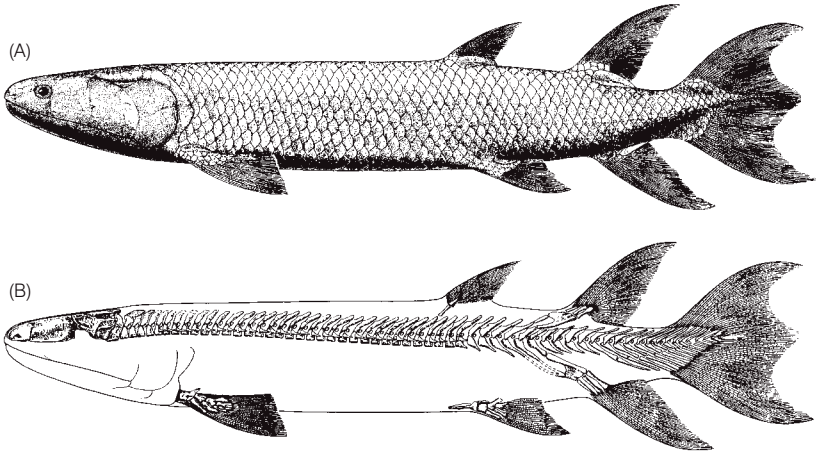


Figure 11.13
Eusthenopteron foordi, a well-known osteolepidiform and member of a lineage considered close to the direct ancestor to tetrapods. (A) The full restoration, and (B) the neurocranium, endoskeleton, and fin supports. Note the large mouth, large symmetrical tail, and posteriorly placed median fins, all characteristics of active predators. From Jarvik (1980), used with permission.

Figure 11.14

Presumed key traits that characterized the sarcopterygian ancestors of tetrapods, as evidenced by *Eusthenopteron*. Among the traits are (A) an intracranial joint in the skull roof associated with the profundus nerve foramen; (B) the arrangement of the dermal skull bones; (C) axial elements of the pectoral fin skeleton (e.g., humerus, ulna, ulnare); and (D) support skeleton of the second dorsal fin. After Ahlberg and Johanson (1998).

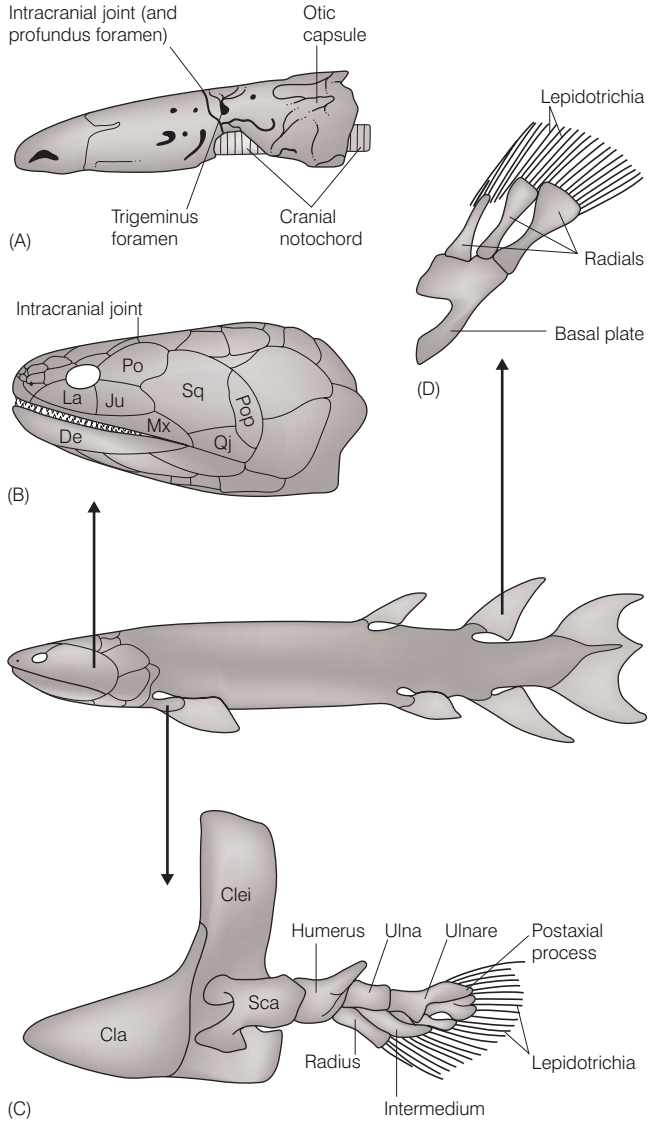
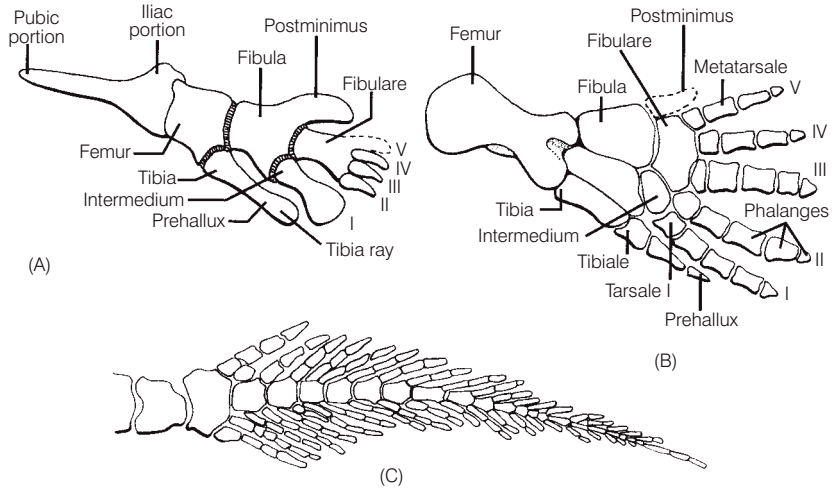


Figure 11.15

Comparative pelvic appendages of: (A) *Eusthenopteron*, a Devonian osteolepidiform fish; (B) *Ichthyostega*, a Devonian stem tetrapod; and (C) *Neoceratodus*, a modern lungfish. Note the apparent homologous bone series of the osteolepidiform and tetrapod limb, as compared with the less similar central axis and radials of the "archipterygial" lungfish fin. (A, B) from Jarvik (1980), used with permission; (C) from Semon (1898).



axially arranged, leaflike archipterygial fins of the dipnoans. The tetrapodomorph fin could provide improved body support for benthic locomotion, perhaps including movement across land. The dentition of both osteolepidimorphs and early tetrapods was very similar, consisting of conical teeth with numerous infoldings of the dentine, termed labyrinthodont dentition, although this may have been a convergent trait among large carnivorous vertebrates (see Pough et al. 2005). Both groups also had ossified neural spines that grew dorsally from ring-shaped, ossified, vertebral centra.

The search for the putative missing link between piscine sarcopterygians and early tetrapods (the latter no longer classified as amphibians) was greatly clarified with publication in 2006 of the description of *Tiktaalik roseae* and a discussion of its place in the vertebrate lineage (Box 11.1). Few fossil discoveries, aside from those involving hominid ancestors, have received as much media attention.

Class Actinopterygii

The primitive fish groups discussed so far are interesting for their antiquity and diversity, and for the effort required by paleontologists to slowly unearth and interpret features of their design. Yet these fishes bear little resemblance to most modern groups and are at most only distantly related to the familiar fishes of today. Speculation about the natural history, behavior, and ecology of extinct forms is based on scant information, much of it difficult to interpret. It is consequently challenging to "imagine" these animals as the living creatures that they were. These difficulties do not apply however to the ancestors of the Actinopterygii, the most successful of today's fishes. Although just as ancient as most of the other groups, primitive ray-finned fishes are similar in size and shape to many extant fishes, and many of their fossils are very well preserved. We can therefore equate many fossil and extant actinopterygians in terms of descendancy, form, and possibly function.

Subclass Cladistia

After a great deal of effort and no small amount of controversy (see Nelson 1994; Helfman et al. 1997), the weight of opinion has shifted to recognize the modern **polypteriforms** (bichirs and reedfish; see Chapter 13) as a separate subclass and the sister group of the other two subclasses of actinopterygians, the Chondrostei and Neopterygii. Also referred to as **brachiopterygians**, fossil cladistians are known only as far back as the Middle Cretaceous of Africa and Late Cretaceous of South America. This represents a dramatic gap in the fossil record for a group considered more primitive than other actinopterygians, which are known from the Devonian (cheirolepidiform and palaeonisciform chondrosteans) and the Triassic (semionotiform

Superclass Gnathostomata
- Grade Teleostomi
  - Subgrade Euteleostomi
    - Class Actinopterygii
      - Subclass Cladistia
        - Order Polypteriformes (bichirs, see Chapter 13)
      - Subclass Chondrostei
        - †Orders Cheirolepidiformes, Palaeonisciformes, Tarrasiiformes, Guildayichthyiformes, Phanerorhynchiformes, Saurichthyiformes, Ptycholepiformes, Pholidopleuriformes, Perleidiformes, Luganoiiformes
        - Order Acipenseriformes (sturgeons, paddlefishes, see Chapter 13)[a]
      - Subclass Neopterygii
        - †Orders Macrosemiiformes, Semionotiformes, Pycnodontiformes, Aspidorhynchiformes, Pachycormiformes
        - Order Lepisosteiformes (gars), Amiiformes (Bowfin)[b] (see Chapter 13)
      - Division Teleostei
        - †Order Pholidophoriformes, Leptolepidoformes, Tselfatiiformes
        - Subdivisions Osteoglossomorpha (two extinct and two living orders), Elopomorpha (one extinct and four living orders), Otocephala (one extinct and six living orders), Euteleostei (29 living orders) (see Chapters 14, 15)

[a] Acipenseriforms appear in the fossil record before some extinct chondrosteans but are separated here for simplicity.
[b] Fossil Bowfin and gar relatives appear in the fossil record before some extinct neopterygians but are separated here for simplicity.
† Extinct group.

Box 11.1

Tiktaalik the fishapod

The panderichthyids of the Middle Devonian diverged from the other tetrapodamorphs in many regards that were probable harbingers of eventual emergence onto land. *Panderichthys* for example lacked dorsal or anal fins, and both *Panderichthys* and the slightly more tetrapod-like *Elpistostege* had a broad head shape with low brow-crests above the eyes similar to those of early stem tetrapods in the genera *Acanthostega* and *Ichthyostega*. However, the panderichthyids still retained enough fishlike traits to eliminate them as a definitive link between fish and tetrapod. In addition to this anatomical "gap", an approximate 20-million-year period lay between *Panderichthys* (Middle Devonian, 385 mybp) and *Ichthyostega* (Late Devonian, 365 mybp) (Ahlberg & Clack 2006). Into this gap leaps *Tiktaalik roseae* (Fig. 11.16).

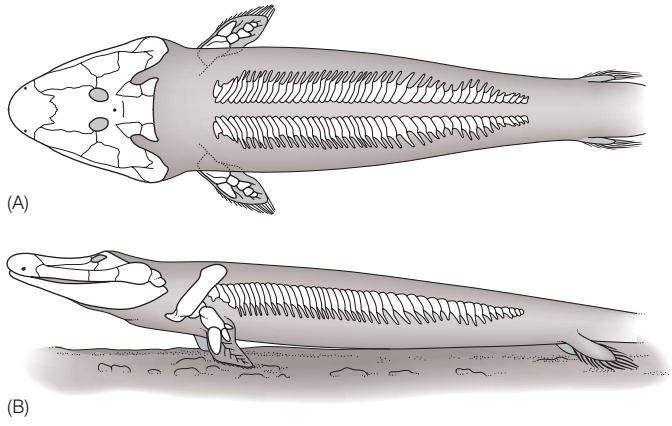
Discovered in mid 2005 in Nunavut Territory of Arctic Canada, *Tiktaalik* was announced to the world in early April 2006, with considerable fanfare (Daeschler et al. 2006; Shubin et al. 2006). *Tiktaalik* grew to almost 3 m and is identifiable as an elpistostegalian (= panderichthyid) tetrapodamorph because of a number of sarcopterygian, fishlike traits. It possessed the dorsally placed eyes, gill arches, scales, pectoral and pelvic fin rays, lower jaw, and palate of those advanced sarcopterygians. But it also possessed the shortened skull roof, otic skeleton, mobile neck, and most significantly, the functional wrist joint of the later appearing stem tetrapods such as *Acanthostega* and *Ichthyostega*.

Several other skeletal features are intermediate or more tetrapod-like (e.g., loss of opercular and subopercular bones; reduced fin rays; elongate, crocodilelike snout; stout, interlocking ribs suggestive of a lung cage; widened spiracle and broadened skull also suggestive of lung function). Equally important, *Tiktaalik* fossils come from Late Devonian strata 382–383 million years old, precisely between the fish and tetrapod groups. The fossils occurred in freshwater alluvial deposits typical of meandering stream systems. Other animals found in the same deposits included an antiarch placoderm, lungfish, porolepiforms, and osteolepidid and tristichopterid sarcopterygians.

Reconstructions of *Tiktaalik* indicate a heavy-bodied organism (termed a "fishapod" in the popular press) without dorsal fins but with teeth, neck, wrist, and digits; for example, these were ". . . large, flattish, predatory fishes with crocodile-like heads and strong limb-like pectoral fins that enabled them to haul themselves out of the water" (Ahlberg & Clack 2006, p. 748). The pectoral skeleton is especially striking in that it is clearly transitional between a fish fin and a tetrapod limb in terms of both structure and function (Shubin et al. 2006) (Fig. 11.17). Although still sporting fin rays, *Tiktaalik*'s distal fin structure includes transverse joints and digitlike elements (e.g., a primordial wrist and digits, ". . . transversely aligned and capable of flexion and extension" (Shubin et al. 2006, p. 768)). This structure would be capable of supporting the fish on its "fingertips", presumably to hold itself up above the water surface and perhaps support itself to some extent on land, actions unlikely among earlier sarcopterygians given their internal limb skeleton. The cladogram of relationships places *Tiktaalik* firmly between the lobefin fishes and stem tetrapods of the Late Devonian (Fig. 11.18).

Recognition of *Tiktaalik* as the sarcopterygian sister group of the stem tetrapods qualifies this exciting discovery as a true missing link, on par with *Archaeopteryx* in linking birds with ancestral reptiles.

Figure 11.16
Dorsal (A) and lateral (B) views of the reconstructed elpistostegalian fish, *Tiktaalik roseae*. Features evident are the lack of opercular bones, the tetrapod-like arrangement of elements in the pectoral fins/limbs, and the stout ribs forming a rib cage that may have protected the lungs. From Daeschler et al. (2006), used with permission.



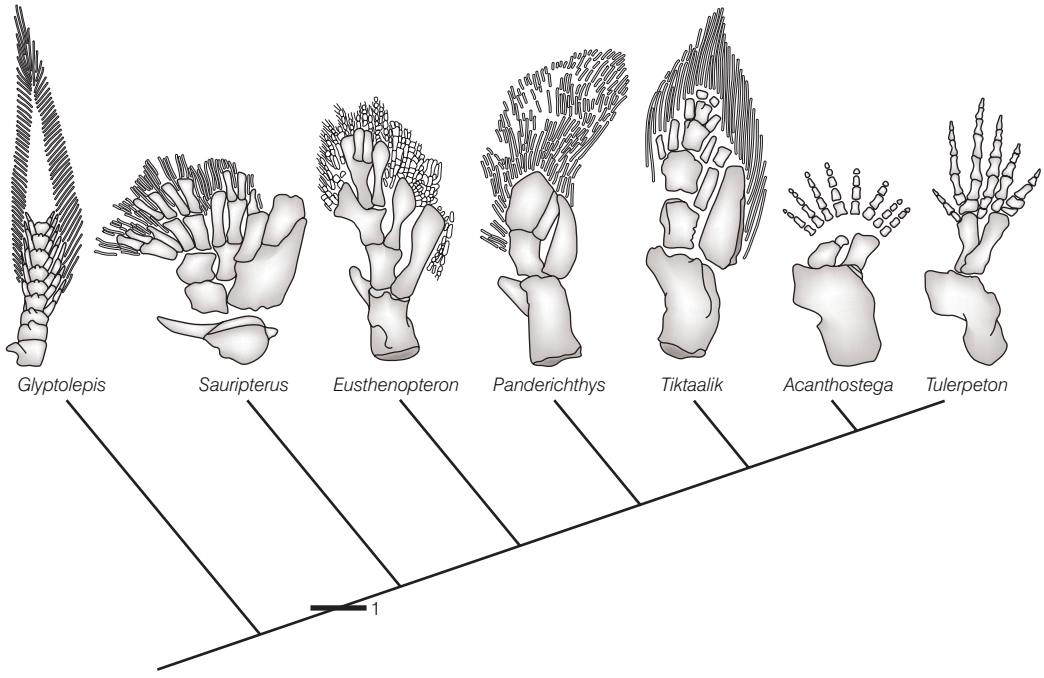


Figure 11.17

A cladogram of relationships among sarcopterygians and tetrapods, evidenced by changes in the pectoral fin and limb. *Tiktaalik* retains the central axis of enlarged endochrondral bones of more primitive sarcopterygians, but has fewer lepidotrichia (fin rays) and more radial elements than ancestral fishes. *Tiktaalik* is more advanced in its proliferation of transverse joints across the distal region of the fin, allowing for propping up and moving the body. *Glyptolepis* was a porolepiform dipnomorph related to lungfishes; its archipterygial fin is representative of the basal condition. From Shubin et al. (2006), used with permission.

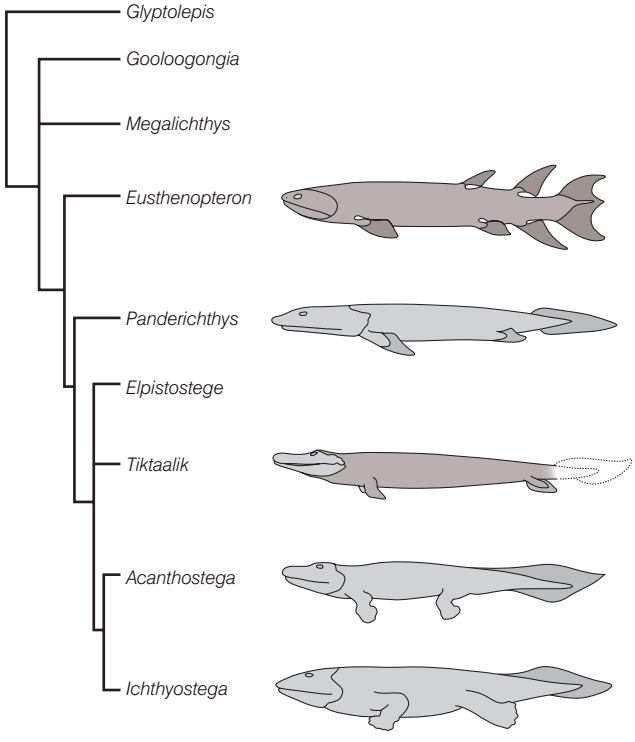


Figure 11.18

Cladogram (strict consensus tree) of relationships among sarcopterygians and tetrapods, showing *Tiktaalik*'s intermediate position as a sister group (with *Elpistostege*) to the early tetrapods *Acanthostega* and *Ichthyostega*. The cladogram was calculated from an analysis of 114 characters and nine taxa. After Daeschler et al. (2006).

neopterygians). The placement of "Polypteriformes(?)" on Fig. 11.23 within the Chondrostei is probably incorrect, but their mixture of primitive, advanced, and unique traits makes resolving their position within the Actinopterygii challenging.

Subclass Chondrostei

The origins of the Actinopterygii are once again obscure. Scale fragments appear in Late Silurian marine deposits, which may mean that the group is older than the sarcopterygians and as old as placoderms and elasmobranchs. Only the acanthodians among the bony, jawed fishes are of greater antiquity, supporting speculation of an acanthodian ancestry for modern bony fishes. However, complete fossil actinopterygians do not appear until the Mid to Late Devonian, when the group had expanded into a variety of marine, estuarine, and freshwater habitats. These early fishes, collectively known as **palaeoniscoids** (but see below) were relatively small (5–25 cm) and were distinguished from sarcopterygians by the presence of a single triangular dorsal fin, a forked heterocercal tail with no upper lobe above the unconstricted notochord, paired fins with narrow rather than fleshy bases, dermal bones lacking a cosmine layer, scales joined by a peg-and-socket arrangement and covered with ganoine ("ganoid" scales), relatively large eyes, and a blunt head (Fig. 11.19A, B). The term "ray-fin" refers to the parallel endoskeletal fin rays that were derived from scales. These rays supported the median and paired fins, which were moved by adjacent body musculature. In contrast, the fins of the Sarcopterygii had a thick, bony central axis and muscles contained in the fin itself (see Fig. 11.15C).

Chondrosteans include one extant and 10 extinct orders, with relationships obscure. The most primitive group, the Devonian cheirolepidiforms, includes a species with the distinction of possessing the largest number of pelvic fin rays known among fishes, living or otherwise. *Cheirolepis canadensis* had 124 such rays versus six or fewer in living teleosts. The most diverse order, the Palaeonisciformes, contained four suborders and 17 families of well-represented fishes that showed tremendous morphological diversity (Figs 11.19, 11.20). The other orders of early chondrosteans are often lumped together as "palaeoniscoids" despite taxonomic differences, and palaeoniscoids are then treated as ancestral to later neopterygians and therefore teleosts.

Among the other orders are the Carboniferous tarrasiiforms, which were remarkably convergent with many modern eel-like forms, possessing an elongate body, dorsal and anal fins continuous with the caudal fin (the latter being diphycercal in this group), and pelvic fins and scales reduced or absent (Fig. 11.20). Saurichthyiforms converged on a needlefish body shape and are thought to have been similarly predatory on small fishes, and phanerorhynchiforms bore a superficial resemblance to modern sturgeons.

An advanced order from the Late Triassic, the perleidiforms, included *Thoracopterus*, a genus with expanded paired fins thought capable of biplane gliding, as occurs in modern exocoetid flyingfishes (Tintori & Sassi 1992). *Thoracopterus* possessed the enlarged pectoral and pelvic fins, reinforced rays in the paired fins, asymmetrical caudal fin, expanded caudal neural spines for muscle insertion, posterior position of dorsal and anal fins, and head shape of

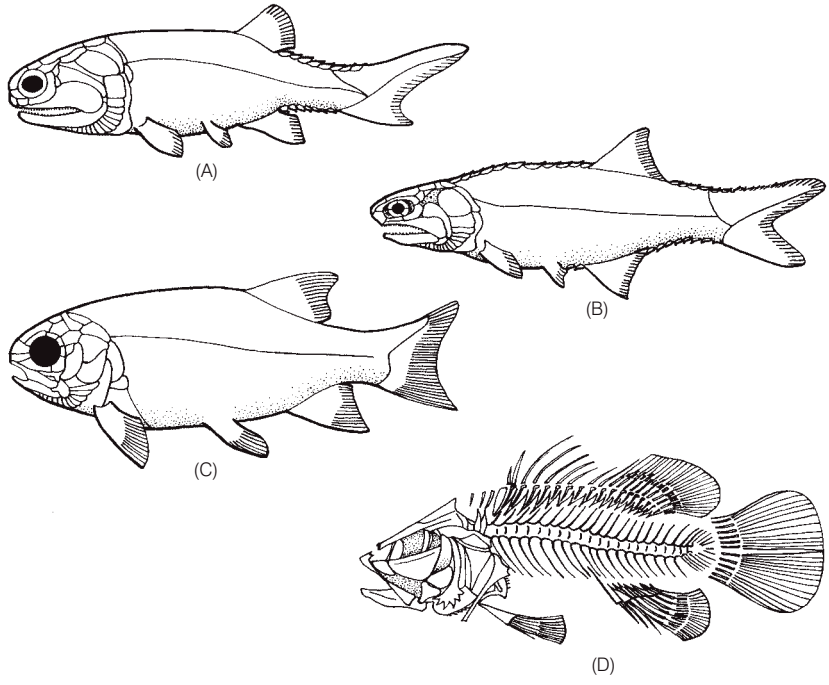


Figure 11.19

Actinopterygian fishes at different grades of development. (A) *Moythomasia* and (B) *Mimia*, two primitive palaeoniscoid fishes from the Upper Devonian, with thick rhomboidal scales extending onto the fins, broadly triangular dorsal and anal fins, fulcral (ridge) scales along the back, a long mouth, and an asymmetrical heterocercal tail. (C) *Parasemionotus*, a pre-teleostean neopterygian from the Triassic, showing more flexible fins, shorter mouth, and abbreviate heterocercal tail. (D) *Eolates*, an advanced euteleost from the Lower Eocene, with characteristic teleostean diversified dorsal and anal fins, shortened vertebral column, premaxillary dominated upper jaw, and homocercal tail. (A) after Jessen (1966); (B) after Gardiner (1984); (C) after Lehman (1966); (D) after Sorbini (1975).

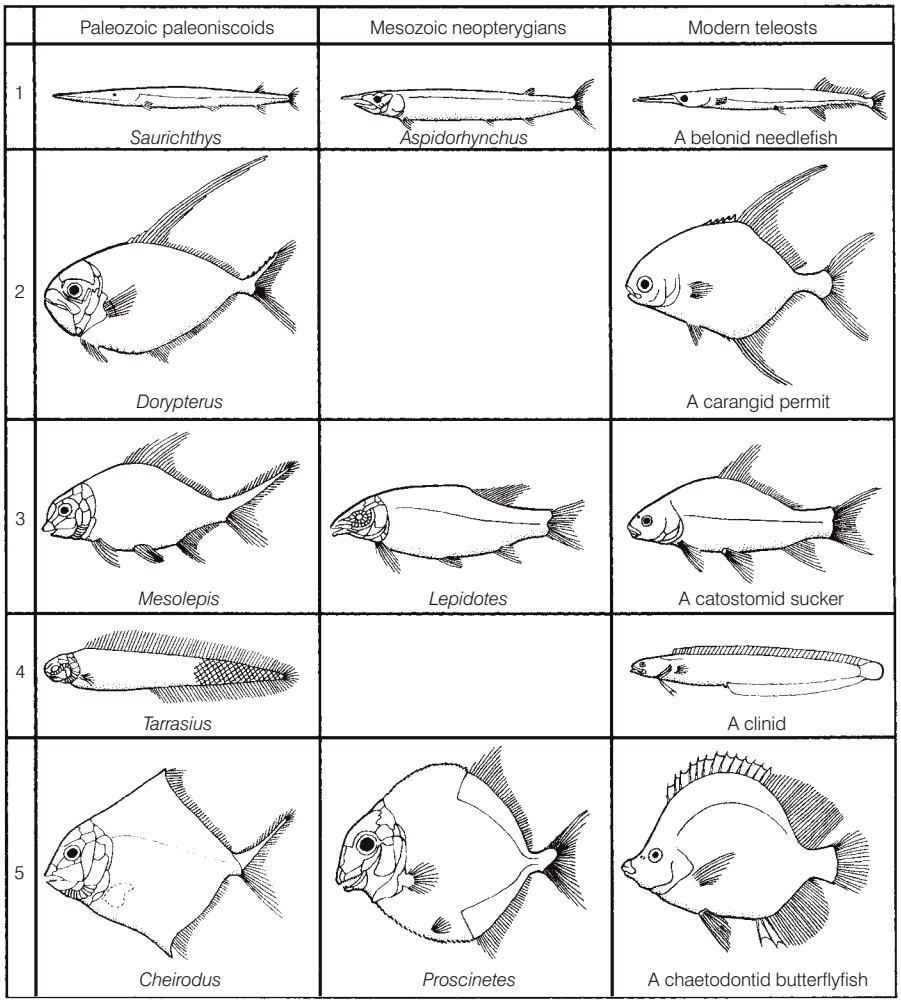


Figure 11.20

Morphological (and ecological) convergence in fish evolution. Palaeoniscoids were ancestral to early neopterygians, which were ancestral to modern teleosts. Certain body designs or plans have apparently been repeatedly favored in actinopterygians, leading to convergent designs among unrelated lineages. These striking convergences in body shape and presumably function are depicted for representative palaeoniscoids, early neopterygians, and teleosts. 1, Elongate piscivores with long, tooth-studded jaws and dorsal and anal fins placed posteriorly for rapid starts; 2, compressed-bodied, predatory, shallow water fishes with deeply forked tails and trailing fins; 3, broad-finned bottom feeders with subterminal mouths; 4, eel-like benthic forms; and 5, compressed, circular forms with large fins for maneuverability in shallow water habitats with abundant structure (see also Chapter 8). Gliding fishes such as the Triassic chondrostean *Thoracopterus* (Fig. 11.21) can also be equated with modern teleostean flyingfishes. Adapted from Pough et al. (1989), not drawn to scale.

modern gliding forms (Fig. 11.21; see Chapter 20, Evading pursuit). Such convergence, remarkable in itself, would have required substantial reduction in the otherwise heavy armoring characteristic of the early chondrosteans. Modern chondrosteans, the acipenseriform sturgeons and paddlefishes, have fossil representation in the Jurassic and Lower Cretaceous, respectively (see Chapter 13).

Palaeoniscoid trends

Palaeoniscoids flourished throughout the latter Paleozoic. Meanwhile, ostracoderms, acanthodians, and placoderms disappeared and sarcopterygians diminished in abundance. This correlation suggests ecological interaction among groups, and possible replacement of primitive jawed and jawless fishes with more advanced actinopterygian and chondrichthyan lineages. What innovations did the ray-finned fishes possess that might have given them ecological superiority? The available evidence strongly suggests that, once again, changes in jaw and fin structure leading to diversified feeding habits and increased mobility were critical to actinopterygian success and dominance.

Changes in the mechanics of jaw opening and closing during actinopterygian phylogeny have been the subject of intensive study (e.g., Lauder & Liem 1981; Lauder 1982; see also Carroll 1988, Pough et al. 2005 for reviews). The highly ossified braincase of the early actinopterygians makes it possible to determine the origins, insertions, and approximate sizes of the different muscle masses involved in jaw function, from which we can estimate the forces in operation.

During actinopterygian evolution, culminating in advanced teleosts, changes in the angles and connections between the skull case, dermal bones, muscles, and ligaments of the head and jaws have been most influential. In particular, the hyomandibula has been reoriented from oblique to vertical, the posterior end of the maxilla has been freed from the cheek bones, and the jaw musculature has increased in size and complexity. These changes increased the speed and strength of the bite. They also allowed for enlarging of the mouth both vertically and laterally. Hence when the mouth was opened, its volume increased and it assumed a more tubular shape. This changed the bite of a

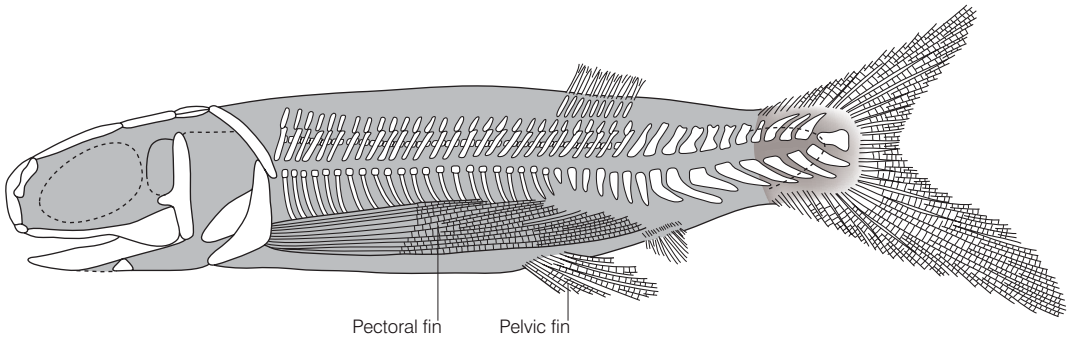


Figure 11.21

Thoracopterus magnificus, a 6 cm-long perleidiform chondrostean from the Triassic adapted to gliding. Most notable are the expanded pectoral and pelvic fins and asymmetrical caudal fin with its larger lower lobe. These and other traits are strongly convergent with features that allow modern exocoetid flyingfishes to engage in biplane gliding. From Tintori and Sassi (1992), used with permission.

fish from a simple scissorslike action to a suction action. In the modified condition, when the mouth is opened, water and prey are sucked in; when the mouth is closed, instead of water being pushed back out through the jaws, flow continues posteriorly through the gill slits, thereby trapping prey inside rather than pushing it back out of the mouth. Transport of water over the gills during breathing may also have been facilitated by these modifications.

Apparent improvements in other skeletal components are no less important. Palaeoniscoid *scales* changed from heavy, interlocking, diamond-shaped units to thinner, lighter, circular, cycloid structures. This reduction was accomplished by elimination of the dentine, vascular, and ganoine layers. Because palaeoniscoid fins consisted of jointed scales, reduction in scale thickness meant increased flexibility in fins; fins became mobile structures composed of **dermal fin rays** that could be erected or lowered and also moved laterally. Associated with scale reduction was increased ossification of the **vertebral column**, leading to recognizable centra with dorsal and ventral accessory structures (neural and haemal arches). These accessory structures are closely related to modifications in the **caudal region**, where a major trend has been toward an increasingly symmetrical, homocercal tail (see Fig. 11.19). Caudal fin rays became supported by a series of ventral accessory, hypural bones.

All these changes during palaeoniscoid phylogeny imply increased reliance on locomotion, integrated in both escape and prey capture. Heavy ganoid scales offer passive protection against predators but do not function until a predator has already captured a prey individual, a risky event that most potential prey would undoubtedly rather avoid. Lighter scales mean a lighter, more flexible body, capable of more rapid swimming and quicker turns. Greater reliance on a gas bladder for attaining neutral buoyancy has also been suggested, which also frees fins to provide propulsion and maneuverability. Weight reduction of fins allows them to better serve as propellants, or as brakes and flaps for swimming, stopping, and turning (and gliding?). The correlation between dermal armor reduction and increased vertebral ossification may indicate a shift from reliance on an external elastic/hydrostatic skeleton to an internal, muscular/tendonous system (see Chapter 8, Locomotion: movement and shape). Increased speed and mobility, combined with the already mentioned improvements in mouth structure, would mean that more advanced actinopterygians would not only be better at avoiding predators but also at capturing prey. These trends in palaeoniscoid evolution reoccur later in more advanced actinopterygian lineages (see Fig. 11.20).

Subclass Neopterygii

"In their great numbers and degree of anatomical diversity, the modern ray-finned fishes may be considered the most successful of all vertebrates" (Carroll 1988, p. 136). Just as improvements in feeding and locomotion may have created competitively superior, primitive actinopterygians, continued evolution of these same traits probably led to the replacement of early actinopterygians by more advanced forms. These descendants, termed **Neopterygii** ("new fins"), first appear in the fossil record during the Upper Permian. They underwent an initial radiation in the Triassic and Jurassic and then expanded more extensively in the Late Cretaceous. Many of the orders of modern teleostean fishes, the dominant group of bony fishes alive today, are represented in this late Mesozoic radiation. In fact, of the 40 recognized living orders of teleosts, half have fossil records that date back to the Cretaceous, with only about seven orders arising more recently than the Eocene (i.e., are younger than 50 million years old).

Pre-teleostean neopterygians include seven orders, five of which are extinct. Jurassic **semionotiforms** were quite diverse, radiating into species flocks in eastern North America (see Fig. 15.17); some analyses place this order on a direct line to modern gars (Lepisosteiformes). **Pycnodon-**

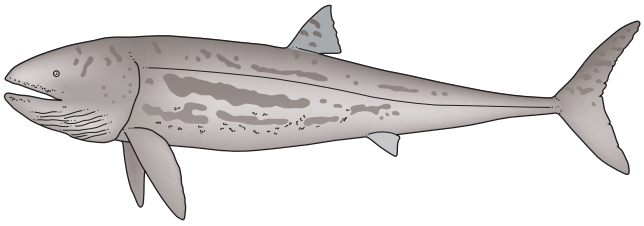


Figure 11.22
Leedsichthys problematicus, perhaps the world's largest fish ever. This 15 m+ zooplanktivorous pachycormid is known from fragments and several partial skeletons discovered in clay deposits from the Middle–Upper Jurassic. After Paul Vecsei, based on an illustration by Bob Nicholls, www.paleocreations.com.

tiforms were another diverse group of shallow water marine forms in at least eight families. **Aspidorhynchiforms** converged on a needlefishlike body form, as did the saurichthyiform palaeoniscoids before them (see Fig. 11.20). The **Pachycormiformes**, with one family and eight orders of Jurassic to Late Cretaceous fishes, are considered by some to be a sister group to early teleosts. A giant pachycormid, *Leedsichthys problematicus*, has been discovered in Middle to Upper Jurassic marine deposits in what is now England, western Europe, and Chile (Fig. 11.22). Reconstructions suggest a total length in excess of 15 m, making it the largest bony fish, and perhaps the largest fish, to ever exist (Martill 1988; Liston 2004; see also www.big-dead-fish.com). Anatomical features indicate that – like the modern Whale, Basking, and Megamouth sharks – *Leedsichthys* was planktivorous, another example of convergence of form and function across taxa and time (e.g., Fig. 11.20).

The two extant pre-teleostean, neopterygian groups, the **lepisosteiform** gars and **amiiform** Bowfin (see Chapter 13), are intermediate between palaeoniscoids and teleosts in a number of structures: gars retain the ganoidlike scales of primitive neopterygians, Bowfin have a primitive gular plate under the head, and both groups have identifiably heterocercal tail elements. In most other respects they are quite specialized, as would be expected for fishes that have existed as recognizable taxa since the Mesozoic. They differ sufficiently in derived traits to generally justify their placement in separate orders, although some analyses indicate that similarities among gars, Bowfin, and their fossil relatives justify their placement together in a separate group, sometimes referred to as the division **Holostei** (e.g., Olsen & McCune 1991). Neither gars nor Bowfin are considered to be on a direct line to the teleosts.

Division Teleostei

Teleosts ("perfect bone") far outnumber all other living fish groups, accounting for more than 26,000 species – more species than in all other vertebrate classes combined. Because Chapters 14 and 15 are devoted to characterizing different teleostean groups, they will only be briefly described here. For the present discussion, it is important to realize that teleostean evolution largely repeats and extends trends that originated with the ancestral palaeoniscoids and were continued in early neopterygians. Refinements in the structure and function of mouths and fins appear to explain much of the success of the group. Evidence of these trends is preserved both in the fossil record and in the ancestral traits retained by recognizably primitive teleostean taxa. These trends are detailed in Fig. 11.23 and summarized below.

Teleosts, despite their incredible diversity, form a definable group with a recognizable ancestry. On cladistic grounds, at least 27 anatomical synapomorphies support the contention that teleosts constitute a monophyletic group. Chief among these are ural neural arches elongated to form the **uroneurals** of the tail support, unpaired **basibranchial toothplates**, a distinctive **urohyal**, and the prevalence of a **mobile premaxilla** (Nelson 2006) (Fig. 11.23).

Teleosts arose in the Middle or Late Triassic (215 mybp), followed by major diversification into modern groups in the Cretaceous. Teleostean evolution apparently involved four major radiations, three that each gave rise to distinct, primitive subdivisions, and a fourth that produced the major advanced groups alive today (between three and six other radiations died out during the Mesozoic). Multiple radiations imply that modern teleosts as a group could be polyphyletic, more a developmental grade than a single clade. Yet shared traits among the modern groups imply a monophyletic clade (Lauder & Liem 1983).

Separate ancestors are postulated for the different radiations, but all may have been derived from the **pholidophoriforms**, an early mainstem teleost group, now extinct. Five families of pholidophoriforms are recognized. Two other poorly understood teleostean Mesozoic orders are the **leptolepidiforms** and **tselfatiiforms**.

The first three major radiations of modern teleosts produced the **osteoglossomorphs** (bony tongues), **elopomorphs** (tarpons and true eels), and **otocephalans** or **ostarioclupeomorphs** (herrings and minnow relatives). These groups stand separately as subdivisions of the Teleostei, apart from the larger, more advanced, fourth radiation, the subdivision **Euteleostei**. Osteoglossomorphs include two living orders (see Chapter 14) and possibly two extinct Jurassic and Cretaceous orders, the highly predatory **ichthyodectiforms** (with five families and including the 4 m *Xiphactinus*) and the **lycopteriforms**. Elopomorph eels and tarpons are contained in four orders, all extant. The subdivision Otocephala is divided into two superorders. The **Clupeomorpha** (herrings and anchovies) contain one living order, the **Clupeiformes**, and one extinct order, the Cretaceous to Eocene **Ellimmichthyiformes**. The other otocephalan superorder **Ostariophysi** contains five orders, all living. Euteleosts include the advanced, living, bony fishes, divided into seven (or nine) superorders, 28 (or 29) orders, 346 families,

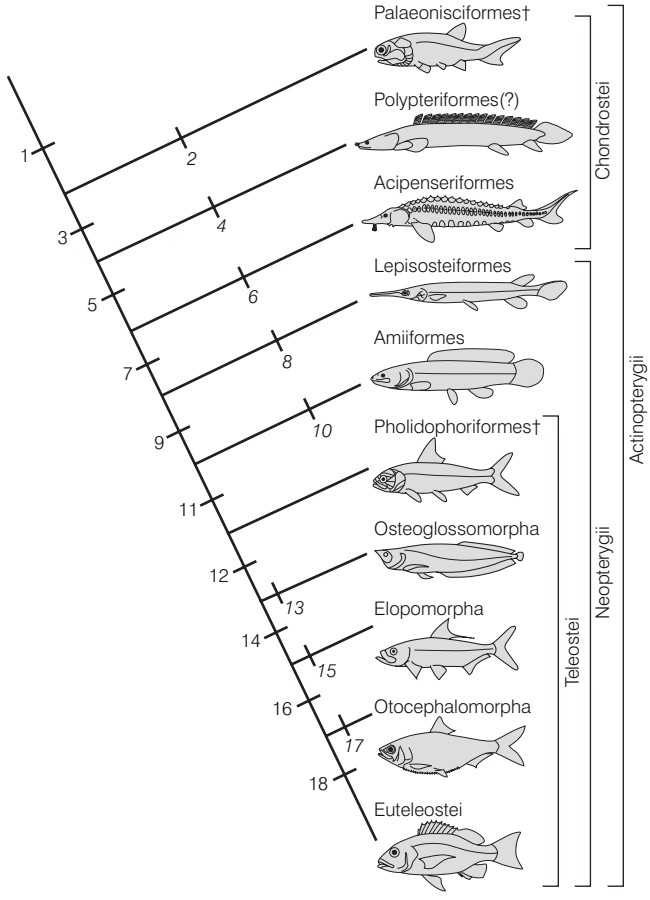


Figure 11.23

Phylogenetic relationships among actinopterygian fishes. The numbered characteristics defining the branching points (synapomorphies) are selected from a much larger list; groups after a branch point share the traits (although traits may be secondarily lost), groups before the branch do not share the trait. Italicized numbers are unique derived traits (autapomorphies) particular to a group and not shared by other taxa. Pholidophoriforms are one of several possible groups ancestral to modern teleosts. Daggers indicate extinct groups. Additional details can be found in Lauder and Liem (1983), Pough et al. (1989, 2005), Nelson (1994, 2006), and papers cited in those publications.

1, single dorsal fin; ganoin in scales, which have an anterior peglike process; pectoral fin with enlarged basal elements ("propterygium"); *2*, fully ossified, sutureless adult braincase; 3, dentinous tooth cap; basal elements of pelvic fin fused; modifications to jaw and gill arch muscles; *4*, dorsal fin spines uniquely flaglike; pectoral fin base platelike; 5, modifications to dermal elements of skull, pectoral girdle, and fins; spiracle penetrates postorbital process of skull; fins preceded by specialized scales ("fulcra"); *6*, upper jaw bones fused; 7, number of endoskeletal elements supporting rays of median fins reduced to a 1 : 1 correspondence; caudal fin more symmetrical, with reduction in upper lobe; dentition of upper pharyngeal consolidated into a tooth-bearing plate; clavicle reduced or lost; *8*, vertebral centra convex anteriorly and concave posteriorly ("opisthocoelus" condition); elongate upper jaw largely constructed from infraorbital bones; 9, maxilla mobile; interopercle and median neural spines present; *10*, jaw articulation involves quadrate and symplectic bones; gular plate present; 11, mobile premaxilla; posterior neural arches (uroneurals) elongate; ventral pharyngeal toothplates unpaired; 12, particular combination of skull bones present (basihyal, four pharyngobranchials, three hypobranchials); *13*, toothplate on tongue bites against roof of mouth; intestine lies to the left of stomach; 14, two uroneural bones extend over the second tail centrum; epipleural intermuscular bones abundant in abdominal and caudal region; *15*, ribbon-shaped (leptocephalus) larva; 16, neural arch of first tail vertebra reduced or missing; upper pharyngeal jaws fused to gill arch elements; jaw joint with unique articulation and ossification; *17*, specialized ear to gas bladder connection; 18, dorsal adipose fin and nuptial tubercles on head and body; first uroneural bones of tail have paired anterior membranous outgrowth. Additional characteristics of modern teleosts are given in Chapters 14 and 15.

and more than 17,000 species (see Chapters 14, 15 and Fig. 14.1). Most groups are well represented in early Cenozoic deposits, such as the famous Eocene sites in Green River, Wyoming, and Monte Bolca, northern Italy (see Frickhinger 1995; Long 1995; Maisey 1996).

Trends during teleostean phylogeny

Although numerous derived traits characterize teleostean groups (Fig. 11.23), trends in five areas can be readily linked to functional improvements that contributed to teleostean success. These trends include reduction in bony elements, repositioning and elaboration of the dorsal fin, change in placement and function of paired fins, structural modifications to and interaction between the caudal fin and gas bladder, and jaw improvements.

Reduction of bony elements Teleosts show a general reduction in bony elements as compared to pre-teleostean groups (see Nelson 1994, 2006). This reduction occurred through fusion or actual loss of bones. For example, higher teleosts have the following features.

1. There are fewer, more ossified vertebrae (in general 60–80 in many elopomorphs and clupeomorphs, 30–40 in ostariophysans, 30–70 in protacanthopterygians, 20–35 in paracanthopterygians, and 20–30 in most percomorphs). A shorter, more ossified axial skeleton would allow for attachment of stronger trunk musculature, thus enhancing locomotion.
2. There are fewer vertebral accessories, such as intermuscular bones and ribs, and the replacement of numerous small intermuscular bones with fewer, thicker zygopophyses (compare the "boniness" of fillets from a herring or trout with that from a tuna or flatfish).
3. There are fewer bones in the skull (e.g., the orbitosphenoid is missing in perciforms; there are 10–20 branchiostegals in osteoglossomorphs, elopomorphs, and clupeomorphs, 5–20 in ostariophysans and protacanthopterygians, and 4–8 in paracanthopterygians and acanthopterygians).
4. There is a reorganization and reduction in the number of bones of the tail, including fusion of the supporting

Table 11.1

Repeated trends in fish evolution. Although fishes represent diverse and heterogeneous assemblages assigned to at least five different classes, certain repeated trends have characterized the evolution of these groups or of major, successful taxa within them. The following list summarizes traits or characteristics common to the evolution of several groups.

1 *Origin in oceans, radiation into fresh water*: thelodonts, pteraspidiforms, cephalaspidiforms, anaspids, placoderms, dipnoans, actinopterygians, teleosts, elasmobranchs
2 *Feeding and locomotion improvements*:
   A. Diversification of dentition: acanthodians, placoderms, dipnoans, palaeoniscoids, teleosts, elasmobranchs
   B. Improved inertial suction feeding: elasmobranchs, chondrosteans, neopterygians, teleosts
   C. Increased caudal symmetry: dipnoans, osteolepidimorphs, coelacanthimorphs, palaeoniscoids, teleosts (reversed in pteraspidiforms and elasmobranchs)
   D. Decreased external armor: pteraspidiforms, acanthodians, placoderms, dipnoans, osteolepidiforms, palaeoniscoids, teleosts
3 *Bases of spines become embedded in body musculature*: acanthodians, elasmobranchs
4 *Fusion of skull bones*: pteraspidiforms, acanthodians, placoderms, dipnoans, teleosts
5 *Bone preceded cartilage as skeletal support*: cephalaspidiforms (if ancestral to lampreys), dipnoans, acipenseriforms
6 *Electroreceptive ability*: pteraspidiforms, cephalaspidiforms, acanthodians, placoderms, dipnoans, actinistians, cladistians, chondrosteans, teleosts, elasmobranchs (for extinct groups, based largely on morphology of pits and canals in head and body; reinvented in modern teleosts) (see Pough et al. 1989; Chapters 6, 13)

bones (epurals, hypurals, centra) and a reduction of the number of fin rays in the tail (most lower teleosts have 18 or 19 principal fin rays, never more than 17 in perciforms; see also below).

5 There is a reduction of the number of biting bones in the upper jaw from two to one. The maxilla becomes *excluded from the gape* in paracanthopterygians and acanthopterygians. In more primitive groups, it is a tooth-bearing bone, whereas in the two spiny superorders, it pivots with the elongate premaxilla to create a tubular mouth (see below).

6 There is a reduction in the number of fin rays in paired fins (six or more soft pelvic rays in most lower teleosts, six or fewer in most paracanthopterygians, and one spine with five or fewer rays in most acanthopterygians).

7 There is a reduction in the amount of bone in the scales (compare the heavy cycloid scale of a tarpon, Megalopidae, or arapaima, Osteoglossidae, with the thin ctenoid scales of most paracanthopterygians and acanthopterygians). A trend toward reduction in armor is familiar by now, as it also occurred during the evolution of several groups (Table 11.1). One possible interpretation is that mechanical protection against predators was of paramount importance when several of these taxa arose, but a premium on mobility soon developed because lighter, quicker fishes with improvements in both predator avoidance and food getting were favored.

Shifts in position and use of the dorsal fin The dorsal fin in primitive teleosts is a simple, spineless, fixed, single, midbody keel that prevents rolling and serves as a pivot point for fishes that typically swim in open water situations (e.g., Mooneye, tarpon, bonefish, herrings, minnows, trouts) (Fig. 11.24). In higher teleosts, the trend is for the dorsal fin to become elongate and diversified. This is usually manifested as two fins, the anterior portion spinous and the posterior portion soft-rayed. Diversification of a fin into an anterior, hardened spinous portion and posterior, flexible portion maintains the protective function of the fin without sacrificing its role in maneuverability. Stability is still provided when the fin is erect, but many other functions can be served. The erected spiny dorsal provides protection from predators by increasing the body dimensions of the fish; folding the spinous dorsal against the body enhances streamlining. Rapid raising and lowering of the dorsal serves as a social signal in many fishes (similar diversification and actions in the anal fin serve the same purposes). The soft dorsal, through its flexibility, can function as a rudder when slightly curved and as a brake when greatly curved. It can also provide mobility if sinusoidal waves are passed down its length (various knifefishes) or if it is flapped in conjunction with the anal fin (triggerfishes, ocean sunfish) (see Chapter 8, Locomotory types).

Truly bizarre modifications of the dorsal fin are seen in many higher teleosts. In paracanthopterygian anglerfishes (see Chapter 14), the first spiny ray is modified into an elongate, ornamented lure to attract prey, whereas filaments and fleshy growths increase the resemblance that some fishes show to seaweed or other structures (e.g., Sargassumfish, Antennariidae). Scorpionfishes (Acanthopterygii) use the spiny dorsal as a venom delivery system for protection against predators. Long, trailing filaments of probable social function (mate attraction, school maintenance) characterize many acanthopterygian fishes (e.g., carangids, angelfishes, cichlids). The familiar suction disk of the sharksucker, another acanthopterygian, is derived from the first dorsal fin.

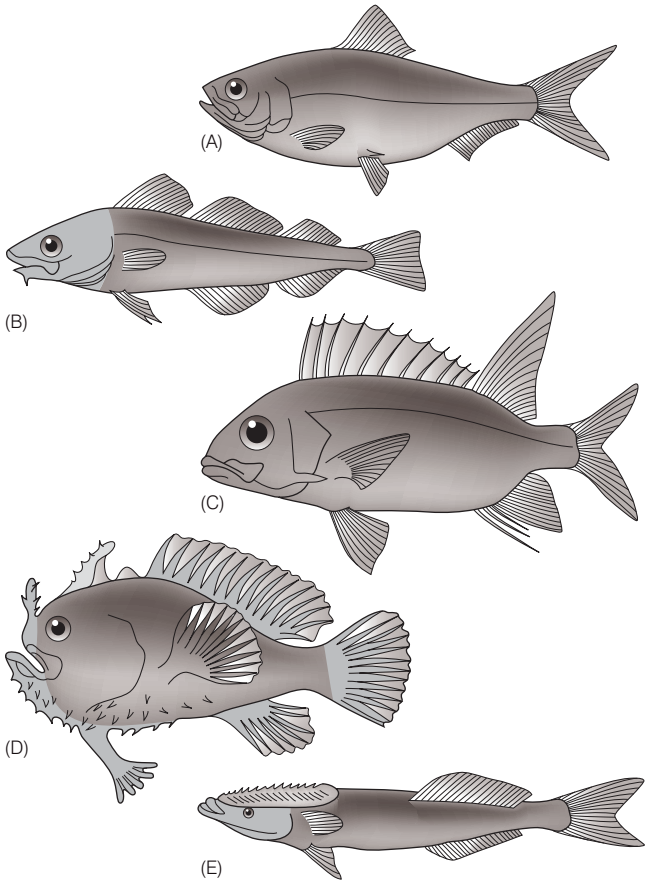


Figure 11.24

Diversification of the dorsal fin in modern teleosts. (A) Primitively, the dorsal fin is a single, spineless, subtriangular structure that serves as an antiroll device and pivot point during swimming, such as in the herrings (Clupeidae). However, this simple fin has been greatly modified in more advanced groups and can serve in locomotion, predator protection, and a variety of other functions. (B) In cods (Gadidae), three dorsal fins exist. (C) More commonly, a spiny anterior and soft-rayed posterior separation occurs, as in the squirrelfishes (Holocentridae). (D) In frogfishes (Antenariidae), modified dorsal spines serve as lures and as camouflage. (E) The sucking disk of the sharksucker (Echeneidae) is derived embryologically from the spiny dorsal fin. After Nelson (2006).

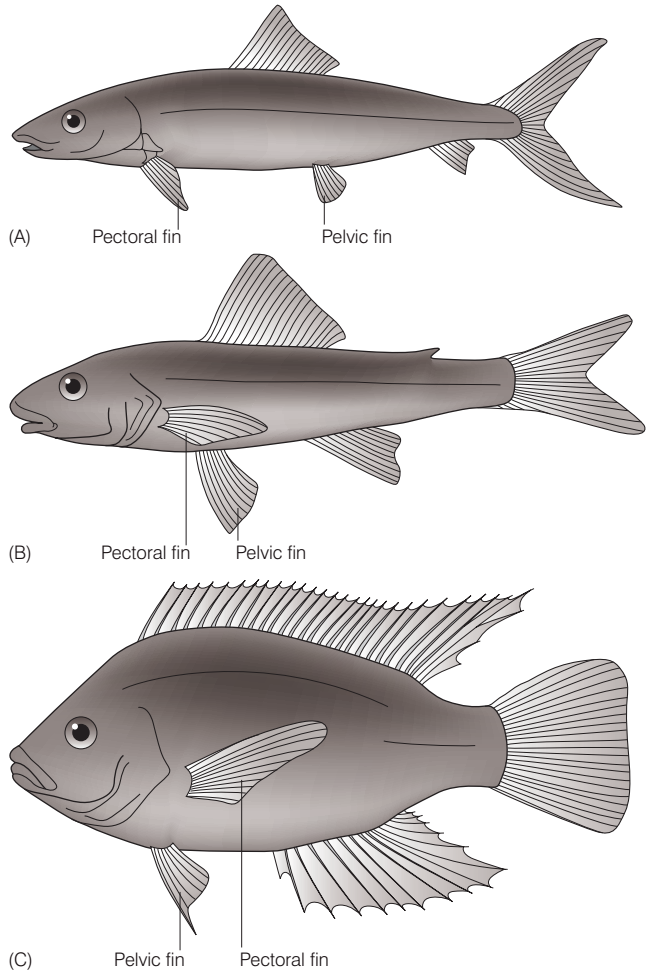


Figure 11.25

The phylogeny of paired fin locations in teleosts. The locations and functions of the pectoral and pelvic girdles have changed during evolution of the Teleostei. Pectoral fins move from a ventral to a lateral position and the pectoral fin base changes its orientation from horizontal to vertical. Pelvic fins move from abdominal to thoracic and even jugular locations. Extant representatives of phases in this observed trend are represented by (A) an elopomorph (bonefish, Albulidae), (B) a primitive paracanthopterygian (Troutperch, Percopsidae), and (C) a generalized acanthopterygian (cichlid, Cichlidae). This trend is by no means absolute: many specialized, relatively primitive teleosts have laterally placed pectorals (e.g., catfishes) and advanced teleosts may have pelvics in abdominal positions (e.g., atherinomorphs), but overall the trends describe a progressive change during teleostean phylogeny. After Nelson (2006).

Placement and function of paired fins In basal teleosts, pectoral fins are oriented horizontally and located in the **thoracic** position, below the edge of the gill cover; pelvic fins occur at mid-body in an **abdominal** location (Fig. 11.25). In this configuration, both fins act primarily as planes that help stabilize movement up and down (pitch) or from side to side (roll), as well as providing some braking force. During teleostean phylogeny, pectoral fins move up onto the sides of the body and their base assumes a vertical orientation; pelvic fins move into **thoracic** or even **jugular** (throat) position. These relocations have several apparent functions (see Webb 1982). Pectorals on the side can be sculled for fine movement and positioning, such as slow swimming, and hovering and backing in midwater. As these fins are often transparent, their use in locomotion might be less obvious to a potential prey animal than would be lateral undulations of the body. Placement of the pelvics forward helps in braking and reduces pitching; their location under the spinous dorsal, in combination with spinous armament, increases the effective body depth of a fish at the point at which it is most likely to be attacked by a predator (Webb & Skadsen 1980).

Caudal fin and gas bladder modifications Actinopterygian evolution is characterized by a progressive increase in symmetry of the tail fin (see Fig. 11.19). Tail fins became externally and functionally homocercal fairly early in the group's history. Fossil impressions of the tails of late Paleozoic palaeoniscoids show that the upper and lower lobes were equal, in contrast to the heterocercal and abbreviate heterocercal tails of earlier palaeoniscoids. Symmetry becomes more pronounced in the teleosts, reflecting the internal modifications that followed. These internal changes include notochord and body shortening and the reworking of large bones and sets of bones that support the caudal fin rays. In particular, teleosts developed a series of **hypural bones** from several haemal arches. Some of these bones fused to form a ventral **hypural plate**, continuing a trend evident in palaeonisciforms. Fusion and reduction of number of vertebrae, reduction of intermuscular bones, and increased tail symmetry all correlate with a greater role of the caudal region in locomotion. The trend is toward an increased dependence on high power caudal swimming, culminating in steadily swimming fishes with lunate tails, such as jacks (Carangidae), tunas (Scombridae), and billfishes (Istiophoridae) (Webb 1982). Primitive teleosts used sequential contraction of trunk musculature throughout the body, producing a wave of contraction from head to tail (see Chapter 8). By focusing muscle contraction on the tail and its supporting structures, advanced teleosts could swim faster and more efficiently than more primitive teleosts that depended on sinusoidal movement of the body (Carroll 1988; Lauder 2000). Hydrodynamic attributes and implications of heterocercal and homocercal tails are discussed in Chapter 8 (Locomotion: movement and shape).

In apparent conjunction with tail and paired fin modifications, an additional teleostean trend is added control over **gas bladder function**. It can be debated whether gas bladders arose initially as breathing or buoyancy control structures (see Chapter 5, Buoyancy regulation), but the latter function has taken precedence in teleosts. Living pre-teleosteans and primitive teleosteans have a **physostomous** gas bladder, in which a pneumatic duct connects the gas bladder with the gut and ultimately the mouth (see Chapters 4, 5). The gas bladder is filled with gas by gulping air; gas is expelled largely via the same route. Fine adjustments are difficult in this system, and the fish is somewhat dependent on access to the surface. More advanced teleosts (paracanthopterygians, acanthopterygians) are **physoclistous**, having lost the pneumatic duct and the link to atmospheric air. They instead rely more on internally generated and absorbed gases to fill and empty the gas bladder and are capable of finer control of buoyancy (physostomous fishes have gas secretion capabilities, but are usually not as refined as in physoclists; see Fig. 5.8).

Although gas bladders do not normally fossilize, the co-development of a gas-filled, internally controlled gas bladder, a homocercal tail, and paired, multifunctional, flexible fins is taken as a strong indication that they evolved as a suite of characters. A gas bladder makes an otherwise dense fish neutrally buoyant, which means that small, precise adjustments in body orientation and movement will not be counteracted by continuous sinking. Thus a fish can remain at a fixed point in the water column and turn on its body axis without moving forward. This trend toward a combination of a functionally homocercal tail and some sort of internal hydrostatic organ was previously evident in the three major sarcopterygian groups. Lungfishes, osteolepidimorphs/elpistostegalians, and coelacanths evolved symmetrical, diphycercal tails. The first two groups had functional gas bladders (lungs), and early coelacanths possessed a gas bladder (Lund & Lund 1985), although it is small and fat-filled in the living coelacanths. Interestingly, the feeding mode of the living coelacanths involves hovering relatively still in open water by a combination of paired fin movements and buoyancy control (Fricke et al. 1987).

Feeding apparatus modifications Two major changes have characterized the anatomy of foraging in teleosts.

1. Teleosts continue a trend seen in neopterygians with respect to increasing suction capabilities. Teleosts developed a protrusible **pipette mouth**, capable of generating powerful, directed, negative pressures (see Figs 8.4, 8.5). The pipette mouth results from enlargement of the muscles and modifications to the bones in the jaw apparatus, most notably the maxilla and hyomandibula, but also involves connections with the mandibular, opercular, and pectoral bone series. Early in teleostean evolution, the rear portion of the maxilla was freed from its connection with other cheek bones, allowing it to swing forward and allowing the reoriented hyomandibula to move outward, thus increasing mouth volume. Skin folds developed along the lateral margins of the jaw bones, creating a hole-free tubular apparatus that prevents lateral escape by small prey. In the more advanced groups (Paracanthopterygii and particularly the Acanthopterygii), the premaxilla develops an **ascending process** which is basically a vertical extension at its anterior tip that slides along the front of the skull, thus allowing the premaxilla to shoot forward at prey as the mouth is opened (see Chapter 8, Jaw protrusion: the great leap forward).

   The end product of action in this complex of bones, muscles, ligaments, and pivot points is very rapid expansion of the orobranchial chamber. In paracanthopterygian anglerfishes, mouth volume can increase 13-fold over the course of 7 ms (7/1000 of a second) (Pietsch & Grobecker 1987). Maximal expansion of the gape is one direction these changes take, particularly in predators on other fishes. In feeders on zooplankton and other small prey, many

advanced teleosts have, if anything, reduced gape width to increase suction power. And some groups have maximized the speed of mouth extension without suction. For example, zooplanktivorous *Chromis* damselfish (Pomacentridae) can fully protrude their jaws in as little as 6 ms to capture evasive copepods (Coughlin & Strickler 1990). During jaw protrusion in the pikehead, *Luciocephalus pulcher* (Luciocephalidae), head length is increased by one-third at a rate of 51 cm/s, thus increasing the speed of attack by almost 40%, with no appreciable suction force generated; velocity increases of up to 89% have been recorded in Largemouth Bass (Nyberg 1971; Lauder & Liem 1981). Observations of mouth extension without suction have fueled a debate as to whether the pipette mouth developed primarily to generate suction power for inhaling prey or to rapidly extend the anterior portion of the body to overtake prey (Lauder & Liem 1981; Lauder 1982). Regardless, the primary selection pressure driving these modifications in the jaw was undoubtedly facilitation of prey capture.

2 Once prey are captured, they are passed back into the mouth to be manipulated. For soft-bodied prey, including most small fishes, manipulation primarily involves positioning the prey to facilitate head-first swallowing, thus avoiding the improved teleostean fin spines that might cause choking or blockage if prey are swallowed tail first. Later digestion of fish prey requires little more than chemical breakdown in the gut. However, many potential prey have extremely effective physical defenses that are relatively impervious to gut chemistry. The hard, calcareous shells of mollusks, the chitinous exoskeletons of crustaceans, and the cell walls of plants all require mechanical rupturing before digestive enzymes can have much effect. A protrusible mouth is effective for initial capture of prey, but, because of the emphasis on fore–aft movement, protrusibility evolved at a sacrifice in up-and-down chewing motion. Therefore mechanical rupturing must occur elsewhere. In teleosts, it has been the dentition and musculature of the **pharyngeal** "**jaws**" that have diversified to serve this chewing, crushing, and grinding function (Lauder 1982).

Pharyngeal **pads** lie posterior to the marginal jaws, just anterior to the esophagus (see Fig. 3.11), and are derived from dermal tooth plates in the pharynx. During teleostean phylogeny, the function of these pads has elaborated from simple holding of prey prior to swallowing to manipulation and preparation that facilitates digestion. The pads have become armed with a variety of dentition types and have fused to dorsal and ventral elements of the gill arches. The branchial musculature has been reworked and a new muscular connection from the anterior vertebral column has been made, to bring upper and lower plates together in complex, powerful movements. Hence in acanthopterygian groups with this **pharyngognathous** condition, we find the mollusk-feeding croakers and drums (Sciaenidae) with molariform dentition, parrotfishes (Scaridae) with pharyngeal jaws capable of grinding up coral rock to expose the algae contained therein, and the highly successful cichlids with a variety of pharyngeal tooth and jaw arrangements that allow their food to be "crushed, triturated, macerated, compacted or in other ways prepared" (Liem & Greenwood 1981, p. 93; see Chapters 8, 15). The development and diversification of pharyngeal jaws and dentition has undoubtedly broadened the diet of teleosts to include hard-bodied prey and, more importantly, plant material; herbivory is essentially unknown in non-teleostean fishes. This diversification probably extended teleost foraging capabilities far beyond what was possible with the early actinopterygian dependence on more anterior jaw elements. It is more than coincidence that several of the most successful modern teleostean families (cyprinids, cichlids, labrids) have both highly protrusible front jaws and diversified pharyngeal jaws.

Although our emphasis above has been on identifying five general areas that changed during teleostean phylogeny, it is important to remember that these traits changed in concert, that anatomical trends during teleostean phylogeny represent a suite of adaptations. Modification of one trait probably enhanced the effectiveness of and was affected by the other traits. The greatest manifestation of the trends is evident in the acanthopterygian fishes, with their ctenoid scales, diversified yet spiny fins, symmetrical tails, fine maneuverability via pectoral fin sculling, physoclistous gas bladders, greatly expandable mouth volumes, and effective pharyngeal teeth. The end result "has been increased swimming speed combined with maneuverability . . . without significant loss of defensive structures" (Gosline 1971, p. 152). In other words, higher teleosts represent quick, spiny fish with a highly efficient feeding apparatus that can catch and eat small, hard prey items.

Also note that these trends generally describe different taxonomic groups but in no way preclude the possibility of a primitive group deriving specializations characteristic of a more advanced taxon. For example, true eels (a relatively primitive teleostean order) as well as other eel-like fishes, regardless of taxonomic position, have expanded dorsal and anal fins, greatly reduced or absent scales, and missing pelvic and even pectoral fins. Elaborate median fins are not found solely in advanced superorders. Many osteoglossomorphs are highly derived, specialized fishes that use their own electrical output to locate objects and locomote via an elongate dorsal (gymnarchids) or anal (gymnotids) fin (see

Chapter 14). Many adult deepsea fishes (Stenopterygii, Cyclosquamata, Scopelomorpha), although belonging to relatively primitive superorders that should be characterized by physostomous gas bladders, are instead secondarily physoclistous, probably to prevent gas loss via the gut and because they never go to the surface to gulp air. Elaborate pharyngeal dentition, a hallmark of the Acanthopterygii, is used widely in the relatively primitive minnows and suckers (Ostariophysi). A protrusible mouth – brought on by an ascending, sliding premaxillary process – characterizes acanthopterygians and the closely related paracanthopterygians, but was evolved independently and differently in a more primitive group, the ostariophysan cypriniforms, as well as in elasmobranchs and sturgeons. Environmental conditions determine the selection pressures operating on a lineage; groups that evolve more effective adaptations will be favored whether or not they are "breaking the rules" of teleostean phylogeny.

Advanced jawed fishes II: Chondrichthyes

The lineages of bony fishes can be traced with fair certainty back to the Silurian. Their success is evidenced by the diversity of forms found throughout the late Paleozoic and Mesozoic, and because of the overwhelming dominance of teleosts today. However, another group of fishes also arose during the early Paleozoic that followed a very different course of development and that also radiated in the Mesozoic and is well represented today. These are the **Chondrichthyes** ("cartilaginous fishes"), a group that rapidly specialized as marine predators. By the Carboniferous, sharks made up as much as 60% of the species of fishes in some shallow tropical habitats (Lund 1990).

Although traditionally thought of as "primitive" because of their cartilaginous skeleton, it turns out that many of the characters of modern Chondrichthyes are secondarily derived and represent specializations for a very different, parallel mode of life in water. As with the sarcopterygian and actinopterygian divergence among the bony fishes, two major subclasses of chondrichthyans – the Holocephali and the Elasmobranchii – also developed. The two groups are united by several synapomorphies, chief among which are a prismatic type of **calcification of endoskeletal cartilage** and the presence of **pelvic claspers** in males (Grogan & Lund 2004).

The common ancestor of the two groups remains to be discovered, and many "sharklike" fossils do not fit well into known groups, or are the subject of debate. Our knowledge of chondrichthyan phylogeny is constrained by

Superclass Gnathostomata
- Grade Chondrichthiomorphi
  - Class Chondrichthyes
    - Subclass Elasmobranchii
      - †Infraclass Cladoselachimorpha
        - Order Cladoselachiformes
      - †Infraclass Xenacanthimorpha
        - Order Xenacanthiformes
      - Infraclass Euselachii
        - †Order Ctenacanthiformes
        - †Division Hybodonta
          - Order Hybodontiformes
        - Division Neoselachii (modern sharks and rays)
          - Subdivision Selachii (sharks: three superorders, 13 orders; see Chapter 12)
          - Subdivision Batoidea (rays: four orders; see Chapter 12)
    - Subclass Holocephali
      - †Superorder Paraselachimorpha
        - Orders Orodontiformes, Petalodontiformes, Helodontiformes, Iniopterygiformes, Debeeriiformes, Eugeneodontiformes
      - Superorder Holocephalimorpha
        - †Orders Psammodontiformes, Copodontiformes, Squalorajiformes, Chondrenchelyiformes, Menaspiformes, Cochliodontiformes
        - Order Chimaeriformes (chimaeras)

† Extinct group.

the availability of fossil skeletal material; by its nature, cartilage does not fossilize readily and hence our ideas concerning many basal groups rest on incomplete specimens. Accordingly, interrelationships among the Chondrichthyes are, once again, the subject of considerable discussion. Fortunately, the last few decades have seen an upsurge in discoveries, clarifying if not solving many earlier points of contention but leaving others unresolved (again, see Nelson 2006 for a review).

Subclass Elasmobranchii

Definitive sharklike fossils first appear in the Early Devonian, involving teeth (418 mybp) and an intact shark fossil (409 mybp); scales or dermal denticles are known from the Late Ordovician (455 mybp). The **elasmobranchs** ("plate or strap gills") have undergone several major radiations, with much controversy surrounding interrelationships. At least eight orders of elasmobranchs with origins in the Paleozoic arose and disappeared by the Triassic (Compagno 1990b). Identification of the various lineages is based largely on tooth, scale, and spine morphology, and the fossil evidence indicates that, as with bony fishes, foraging and locomotor improvements characterize successive groups.

Elasmobranchs are divided into three infraclasses, the extinct cladoselachimorphs and xenacanthimorphs, and the euselachians, which include modern forms and their extinct relatives. **Cladoselachimorphs** contained one family, the **Cladoselachidae** (Fig. 11.26A). Cladoselachids had five gill slits and a terminal mouth. Their dentition, referred to as **cladodont**, consisted of multicuspid teeth in which the central cusp was usually larger. The teeth were made of enamel-covered dentine and were homologous with scales. These elasmobranchs were often large (2 m), pelagic, marine predators with an unconstricted notochord protected by calcified cartilaginous neural arches, and with small precaudal, lateral keels analogous to those found in modern pelagic sharks (Moy-Thomas & Miles 1971). The dorsal fins were often preceded by a spine that may have been supportive or protective in function. Caudal morphology was functionally symmetrical, although the notochord extended into the dorsal lobe of the fin (Fig. 11.26A). Cladoselachids were recognizably sharklike in appearance.

Another mainstem elasmobranch infraclass, the **xenacanthomorphs**, were common in tropical waters from the Lower Devonian into the Triassic. Recognized families include xenacanthids, lebachacanthids, and diplodoselachids. Xenacanths had a tooth type different from the cladoselchids termed **pleuracanth**, in which the two lateral cusps were large and the median cusp was smaller. Xenacanthids invaded fresh water and assumed an eel-like morphology (Fig. 11.26B). Some xenacanthid sharks had pectoral fins reminiscent of the archipterygium of the dipnoans and may have been bottom dwellers. Xenacanthids also were unusual in possessing two distinct anal fins.

The earliest **euselachians** were the **Ctenacanthiformes** of the Middle Devonian to the Upper Triassic. **Ctenacanthids** had two dorsal fins with prominent spines, an anal fin set far back on the body, and a slightly overhanging snout along with a terminal mouth (Fig. 11.27A). **Hybodontiformes** of the Triassic and Jurassic are placed in their own division, the **Hybodonta**, because they are considered the sister group of the modern sharks of the division **Neoselachii**. However, unlike modern neoselachians, hybodonts retained the terminal mouth of the ctenacanth sharks, rather than the subterminal mouth evolved by neoselachians in the Jurassic (Fig. 11.27B). Hybodont teeth represented an innovation over more primitive sharks in that hybodonts had **multicuspid** teeth that were often differentiated into

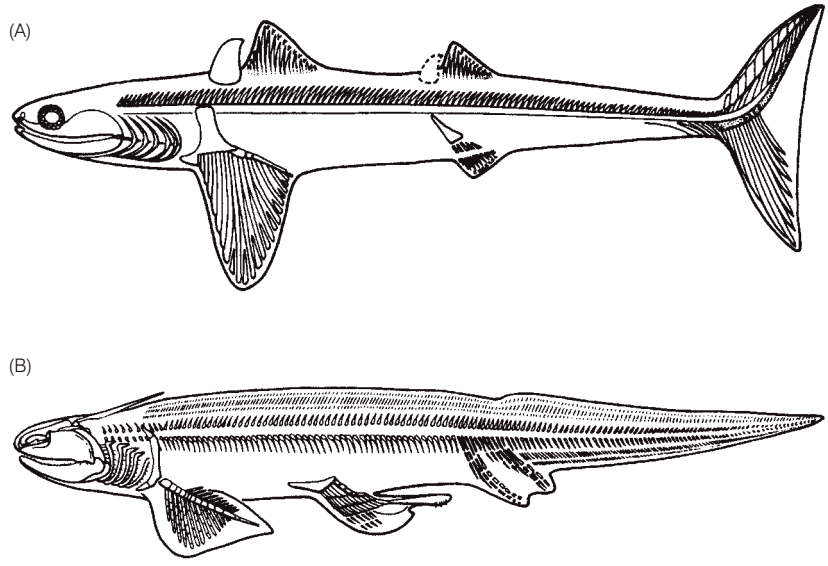


Figure 11.26
Diversity in the body form of Paleozoic sharks from the two extinct infraclasses. (A) *Cladoselache*, a cladoselachid (Cladoselachimorpha); (B) *Xenacanthus*, a freshwater xenacanthid (Xenacanthiimorpha). (A) from Schaeffer (1967); (B) from Schaeffer and Williams (1977), used with permission.

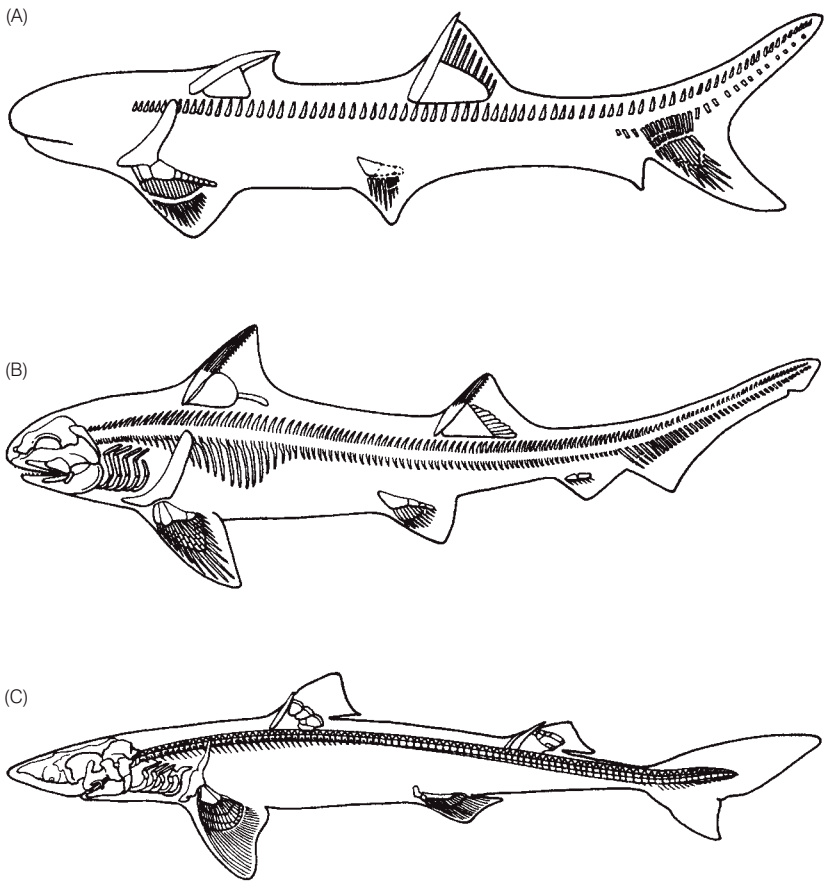


Figure 11.27
Sharks allied with the infraclass Euselachii. (A) *Ctenacanthus*, an Upper Devonian ctenacanthid (Ctenacanthiformes); (b) *Hybodus*, a hybodontid, representative of the order Hybodontiformes, the most diverse elasmobranch group in the Triassic and Jurassic; and (C) *Squalus*, a modern squaliform shark in the division Neoselachii. From Schaeffer and Williams (1977), used with permission.

anterior grasping and posterior crushing types, functionally analogous to the marginal and pharyngeal teeth of modern teleosts (and such modern forms as the heterodontid bullhead sharks; see Fig. 8.8). Hybodontoid paired fins were flexible and mobile, probably giving them a maneuverability that was not possible with the stiffer appendages of the earlier sharks. Caudal fins became increasingly heterocercal, a reverse of the trend seen in bony fishes. Paralleling a trend seen during acanthodian phylogeny, the spines that precede the dorsal fins became more deeply embedded in the body musculature.

Although hybodonts were notably diverse during the Triassic and Jurassic, occupying perhaps as many adaptive zones as modern sharks, neither they nor any of the earlier shark groups survived beyond the Mesozoic. They were replaced by neoselechian modern sharks in marine habitats and by neopterygians in freshwater regions. **Neoselachians** first appear in the Lower Triassic, contemporaneous with the hybodonts. By the Early Jurassic, recognizably modern sharks are found (Fig. 11.27C). One major distinction between modern and earlier sharks is the characteristic overhanging snout of neoselachians, producing a ventral rather than terminal mouth. The overhanging snout results from an enlarged rostral area that encases a larger olfactory system. Modifications in jaw suspension, jaw–pectoral girdle linkage, and jaw-opening muscles create a protrusible upper jaw and the generation of suction forces, paralleling the trend seen in teleosts. **Calcified vertebral centra** largely replaced the unconstricted notochord of earlier groups, and fin supports changed from multiple basal cartilages with cartilage radiating out to the fin margins to smaller, fused basal supports (usually three) and flexible, horny rays termed **ceratotrichia** supporting the web of the fin. This combination of vertebral and fin modifications should have provided for faster swimming and greater maneuverability.

Regardless of the radiation in question, several elasmobranch innovations probably gave them a selective advantage over the other early gnathostomes present at the time. In contrast to the placoderms and most acanthodians, sharks quickly evolved a **tooth replacement** mechanism. Teeth grew in whorls or spiral bands (Fig. 11.28), with the functional, exposed tooth backed up by several replacement teeth embedded in the jaw cartilage. As embedded teeth grew, they moved along the whorl until they erupted at the jaw periphery, only to be later replaced by younger teeth. Dentition replacement patterns differ among different lineages of modern sharks (see Chapter 12), but in all

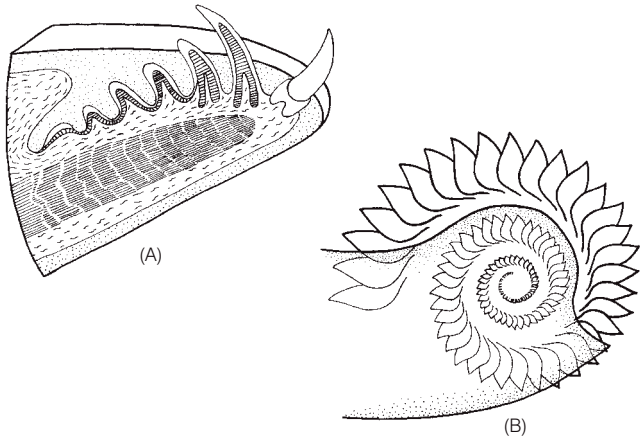


Figure 11.28

Tooth replacement in chondrichthyans. (A) Cross-section through the jaw of a modern shark, showing a functional tooth backed by rows of developing replacement teeth. Variations on this mechanism are found in many fossil groups. (B) Symphysial (middle) portion of the lower jaw of the late Paleozoic edestoid *Helicoprion*, thought to be a holocephalan, showing its spiral replacement tooth whorl. After Carroll (1988) and Pough et al. (1989).

likelihood teeth were regularly shed and replaced spontaneously in primitive groups, as happens in modern elasmobranchs. This arrangement took on some relatively bizarre forms, as in the Permian edestoid holocephalan, *Helicoprion* (Fig. 11.28B).

Other characteristics of modern sharks undoubtedly had their origins in late Paleozoic groups. Sexually dimorphic males had pelvic fins modified as intromittent organs for sperm deposition, indicating that **internal fertilization** evolved early in chondrichthyans (see Fig. 11.26B). A strong dependence on electroreception, highly acute olfactory capabilities (associated with the longer snout that houses the nasal capsules), increased buoyancy through oil accumulation in the liver (paralleling gas bladder evolution in bony fishes), and large brain and body size have all contributed to the position of modern elasmobranchs among the top predators in marine habitats (see Chapter 12).

Subclass Holocephali

A calcified cartilaginous skeleton and internal fertilization, among other traits, link the **Holocephali** ("whole heads") with the elasmobranchs (see Chapter 12). Holocephalans arguably date back to at least the Late Devonian (Fig. 11.29). Holocephalans and elasmobranchs are considered to form a monophyletic unit with the shared, derived traits of prismatic endoskeletal calcification and pelvic claspers. The stem group is debated, but a Middle Devonian braincase from Bolivia of an animal named *Pucapampella* has been proposed as ancestral.

Regardless, holocephalans differ in many respects from elasmobranchs. Most notable is the position and structure of the gill chamber, which is located further forward than in sharks and has a **single opercular opening** covering four gill openings. Holocephalans have non-protrusible jaws because the palatoquadrate (upper jaw) is fused to the braincase (= **autostylic suspension**); in modern elasmobranchs the upper jaw gains mobility via a posterior hyomandibula and an anterior ligamentous connection to the chondrocranium (= **hyostylic suspension**). Most fossil and all modern chimaeras and ratfishes have **tooth plates** on the jaw margins that continue to grow during ontogeny; iniopterygians and eugeneodontiforms had replacement dentition. Tail form in holocephalans is variable but often of a diphycercal nature, hence the "ratfish" designation for extant chimaeras.

Chimaeras are a truly ancient group of fishes, the living members of which represent a very small subset of a previously diverse clade. Recent work has identified (with contention) two superorders and 13 orders of holocephalans, 12 of which are extinct. Even two of the three suborders of Chimaeriformes, the order containing all modern forms, are extinct. None of the extinct forms existed into the Cenozoic, and all three modern holocephalan families have fossil records dating back to the Jurassic and Cretaceous. Early holocephalans showed a tremendous diversity of form, including orodontids that reached 4 m in length and debeeriids that did not exceed 10 cm in length. Some petalodontiforms such as *Janassa* were skatelike in morphology and others such as *Belantsea* were globose and almost pufferfishlike in shape. *Chondrenchelys* was eel-like (Fig. 11.29C). A chimaera in Greek mythology was an imaginary monster constructed of incongruous parts.

The past few decades have seen an impressive increase in discoveries of fossil holocephalans, largely through the untiring efforts of Eileen Grogan and Richard Lund (see www.sju.edu/research/bear_gulch). In our 1997 edition, we anticipated "fossil discoveries [that would help] develop a more meaningful synthesis" of relationships among holocephalans. This synthesis is now underway, but interpretations of the new findings have proliferated (e.g., Grogan and Lund (2004) refer to two subclasses, the Euchondrocephali, recognized here as subclass Holocephali, and the Holocephali, recognized here as the superorder Holocephalimorpha). We have chosen to follow the more traditional terminology and organization laid out in Nelson (2006) until workers in this dynamic area approach a consensus.

A history of fishes: summary and overview

As should be obvious, the gaps in our knowledge about fossil fishes and their relationships to one another and to modern groups are large and plentiful. Such gaps are the

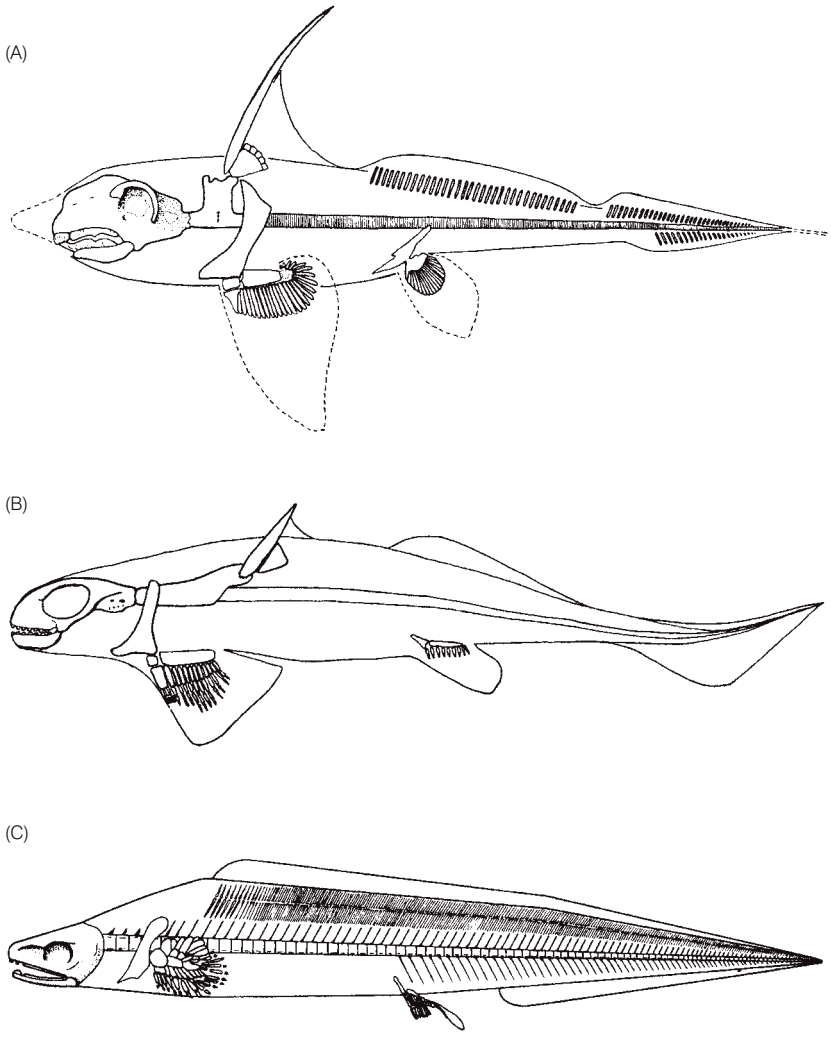


Figure 11.29

Extinct holocephalans. (A) *Ischyodus*, a Jurassic callorhinchid in the same family as modern plownose chimaeras; (B) *Helodus*, an Upper Devonian helodontiform; and (C) *Chondrenchelys*, a Lower Carboniferous chondrenchelyiform. Note the convergence in body form between *Chondrenchelys* and the actinopterygian *Tarrasius* and the clinid in Fig. 11.20. From Patterson (1965), used with permission.

initiation points for future research. For starters, three topics arise from these unanswered questions and deserve some exploration.

The diversity of fossil fishes

We speak of the success of different ancient groups and compare among them and between modern teleosts and extinct forms. All of the preceding discussion is totally dependent on the fossil record. But how accurately does the fossil record represent the diversity of fossil fishes? How many fishes would we estimate are alive today if we were forced to rely on fossils? As of 1988, approximately 333, or about 8% of modern teleostean genera, are represented by Recent fossils (Carroll 1988; Nelson 1994). Significantly, the number of fossils available for study decreases with time because geological processes tend to destroy fossilized material. Therefore, the fossil record of Recent fishes is at best an optimistic underestimator of the accuracy with which earlier groups are represented.

Fossilization is a chance procedure, compounded by the relatively small surface of the earth available for paleontological discovery. Inadequacy of sampling is obvious when we realize that most fossils are recovered from only the top few meters of rock, and much of the surface land of the Mesozoic and early Cenozoic has been subducted by tectonic processes (see Chapter 16). Our limited sample size is aggravated by inaccessibility of major areas of the earth's surface; recall that 70% of our planet is under water, where very little paleontological exploration occurs. Significantly, about 2400 species, or 10%, of living fishes occur in water deeper than 200 m (Cohen 1970), yet few of the recognized pre-teleostean groups are postulated as having occupied the deep sea. Deepsea fishes, regardless of taxon, are highly convergent in body form and structure (see Chapter 18); such adaptations should be obvious in fossils and such fishes should be assignable to the deepsea habitat. However, the fossil record for living deepsea groups is understandably limited. For example, stomiiforms are among the most abundant of the deepsea orders, with >50 recognized

genera, but only five of these, or about 10%, have a fossil record (Nelson 1984; Carroll 1988) (fossil rarity may also reflect convergence on the trait of reduced ossification, reducing further the likelihood of fossilization). The deep sea is one of the most stable aquatic habitats on earth and it seems unlikely that living in the deep sea is a teleostean innovation. Pre-teleostean diversity in deepsea habitats is obviously underestimated.

Compound these problems further with the realization that many fossil species are described based on a single, often fragmentary, specimen. How many of these fragments remain undiscovered and, more importantly, how many rare species never fossilized? In our search for antecedents of modern groups, how does this selective preservation of forms affect our interpretations of lines of descent, particularly if there exists at best a one-in-10 chance that an ancestor will fossilize? Our optimistic hope is that the fossil record is somehow a proportional and representative subsample of reality, that we accept that we have grossly underestimated the diversity of primitive fishes, and that many more future researchers will take up the challenges of paleontology.

The tangled web of early vertebrate relationships: primitive does not necessarily denote ancestral

It is intellectually frustrating to have major living taxa, e.g. modern agnathans, jawed fishes, and gnathostomes in general, for which we can find no clear ancestral lineages. Such phylogenetic problems beg for solution. As a result, considerable effort has been extended attempting to link modern agnathan groups with Paleozoic forebears, and for that matter, modern gnathostomes with ancestors among the diversity of fishes that proliferated during the Devonian.

Plausible alternative explanations exist. First, the ancestors of modern groups may have died out without leaving fossil remains, at least none that we have found so far. Second, Paleozoic lineages were extinguished, period. Hence similarities between ancient and extant groups result from convergence and perhaps some retention of primitive characteristics derived from a common, distant (unfossilized) ancestor. The latter scenario is perfectly reasonable given the rather advanced condition of bones in the agnathous fishes and of jaws and other supporting bony elements in the early gnathostomes when they first appear in the fossil record. Groups ancestral to these early lineages must have existed for millions of years but lacked the necessary mineralized structures to fossilize. Extinction is a universal characteristic of species; it has been estimated that the average "life span" of a species is around 10 million years (Raup 1988). The mass extinctions that have occurred during the history of life (e.g., the Burgess Shale fauna in the Precambrian, and the Permo-Triassic and Cretaceous–Tertiary extinction events) have been particularly disastrous for shallow marine faunas, wiping out 50–100% of the species in existence at the time (Raup 1988). It seems reasonable to assume that fish lineages were as susceptible to mass extinctions as were contemporaneous invertebrate groups; declines in diversity of actinistians, amiiforms, hybodonts, holocephalans, and perhaps neopterygians at the end of the Cretaceous may attest to the vulnerability of fish groups to mass extinction.

Continuity in fish evolution

This chapter focuses on the antecedents of modern fishes. Implied in the organizational approach we have taken here is that fossil fishes should be dealt with separately from living forms. This separation is, however, arbitrary and superficial. It is more of a stylistic convenience for organizing a textbook than a statement of philosophy. Students of fish evolution should quickly recognize that modern fishes are extensions of fossil groups. As was pointed out earlier, the majority of modern fish families already existed in the Mesozoic if not earlier (see Fig. 11.1). Although some primitive groups that are unrepresented today (e.g., "ostracoderms", placoderms, acanthodians, osteolepidiforms, palaeoniscoids) probably deserve separate treatment from modern forms, it makes just as much sense to treat truly ancestral forms, such as primitive dipnoans, actinistians, neopterygians, and chondrichthyans, together with their modern derivatives. To paraphrase paleontologist A. R. McCune, why should mode of preservation – in rocks or in alcohol – be the primary determinant of how we deal with a taxonomic group? If modern, "primitive" species (e.g., the living coelacanths) were to become extinct through human neglect, would they immediately have to be placed only in a discussion of extinct fishes? It is our hope that students of ichthyology will recognize the continuity that exists between primitive and advanced groups and not view them as separate entities but rather as a continuum of organic change within lineages.

The following chapters on chondrichthyans and living representatives of primitive taxa focus on species that have strong, direct ties to the extinct (we think) groups discussed above. Where one lineage grades into another is in reality an undefined segment in a line drawn in geological time.

Summary

SUMMARY

1 Fishes have an ancestry that goes back at least 500 million years. Some fossil groups can be linked with extant taxa, some extant taxa lack obvious fossil antecedents, and numerous groups arose, prospered, and were extinguished.

2 The first fishes to fossilize occurred during the Early Cambrian and lived into the Devonian. They lacked jaws but possessed bony armor and had a muscular feeding pump. Five superclasses of diverse jawless vertebrate craniates are recognized: conodonts, pteraspidomorphs, anaspids, thelodonts, and osteostracomorphs. The latter four groups are frequently referred to as "ostracoderms" in reference to a bony shield that covered the head and thorax. Most ostracoderms lived in both marine and fresh water.

3 Conodonts were well known from toothlike structures that fossilized abundantly during Precambrian and later times but could not be linked to any particular body form. Four centimeter long body outlines containing the conodont tooth apparatus were finally discovered in Scotland and Wisconsin in the 1980s.

4 The development of jaws was a critical step in the advancement of fishes. However, the ancestry of jawed fishes is unclear because no intermediate fossils between jawed and jawless forms have been found. Placoderms were early jawed fishes that arose in the Silurian, disappeared by the Early Carboniferous, and left no apparent modern descendants. They had a bony, ornamented, platelike skin. Many were predators and achieved monstrous size. Many placoderms had a hinge at the back top of the head that allowed for greater opening of the mouth. Placoderm teeth consisted of dermal bony plates attached to jaw cartilage and could not be repaired or replaced.

5 The first advanced jawed fishes were the acanthodians or spiny sharks, which are unrelated to modern sharks. Acanthodians were water column swimmers. Many of their traits suggest they share a common ancestry with modern bony fishes, and they are often placed with sarcopterygians and actinopterygians in the grade Teleostomi.

6 Two classes form the euteleostomes, the Sarcopterygii and the Actinopterygii. These classes arose during the Silurian and Devonian and gave rise to modern bony fishes. Sarcopterygians diversified into three subclasses, the coelacanthimorphs (coelacanths), dipnoans (several superorders that include lungfishes, osteolepidomorphs, and elpistostegalians), and tetrapods (stem tetrapods, amphibians, reptiles, birds, and mammals). Elpistostegalians are the most likely ancestors of tetrapods, in that they share skull and neck characteristics and fin patterns with stem tetrapods. Actinopterygians diversified into cladistians (bichirs), chondrosteans (palaeoniscoids, sturgeons, and paddlefishes) and neopterygians (semionotoids, gars, Bowfin, and teleosts).

7 Actinopterygians arose during the Silurian. An early, successful group was the palaeoniscoids, which had a triangular dorsal fin, heterocercal tail, paired ray-supported fins with narrow bases, and ganoid scales. Important structural changes occurred in the jaw apparatus that strengthened the bite, increased the gape, and created suction forces. Mobility also improved with lightened scales, vertebral ossification, and an increasingly symmetrical tail. Palaeoniscoids may be ancestral to modern chondrosteans.

9 Neopterygian, or modern ray-finned, fishes are the most successful of all vertebrates. They first appeared in Late Permian times and radiated extensively during the Mesozoic. Two extant pre-teleostean groups are the lepisosteiforms (gars) and amiiforms (Bowfin). Teleostean evolution largely repeats and extends trends that originated with the ancestral palaeoniscoids, particularly with respect to advances in jaw and fin structure and function. Convergence in body form and presumably ecological function is striking across palaeoniscoid, neopterygian, and teleostean lineages.

10 The earliest teleosts were the pholidophoriforms. Four distinct lineages arose from these ancestors: the bony tongue osteoglossomorphs, the tarpon and true eel elopomorphs, the herringlike and minnowlike otocephalans, and the euteleosts, which contain most modern bony fishes. Five major trends characterize teleostean evolution: reduction of bony elements, shifts in position and function of the dorsal fin, placement and function of paired fins, caudal fin and gas bladder modifications, and improvements to the feeding apparatus.

11 Chondrichthyans (cartilaginous fishes) include two subclasses, the elasmobranchs (sharklike fishes) and

the holocephalans (chimaeras). Sharklike elasmobranchs first appeared in the Late Ordovician, underwent tremendous diversification, and are represented today by a comparatively depauperate group of specialized neoselachian sharks and rays. Earlier successful radiations included the cladoselachimorphs and xenacanthimorphs, the latter a largely freshwater infraclass. The third infraclass of elasmobranchs is the Euselachii, which includes the extinct ctenacanths and hybodonts, the latter probably ancestral to modern sharks. Modern neoselachian sharks arose during the Mesozoic, showing improvements in jaws, dentition, vertebrae, and fins that paralleled locomotory and feeding changes in bony fishes.

12 Holocephalans may date back to the Devonian. They share with elasmobranchs a calcified skeleton and pelvic fin claspers but differ by having non-protrusible jaws in which the upper jaw is fused to the braincase, and by a single opercular opening. Holocephalans, whose exact relationships remain a matter of debate, were tremendously successful and diverse through the Mesozoic but are represented today by a small subset of chimaeras.

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Chapter 12

Chondrichthyes: sharks, skates, rays, and chimaeras

Chapter contents

CHAPTER CONTENTS

Subclass Elasmobranchii

Although often portrayed as "primitive fishes", modern sharks, skates, and rays are highly derived, specialized fishes that differ dramatically from the abundant, diverse elasmobranchs that dominated marine and even freshwater habitats through much of the Mesozoic (see Chapter 11). Many traits that characterize elasmobranchs – such as a cartilaginous skeleton, placoid scales, internal fertilization, replacement dentition, and multiple gill slits – appeared early in the 400+ million year history of the group. However, modern sharks, skates, and rays exhibit tremendous variation in these and other characteristics, and have developed additional anatomical, life history, and behavioral adaptations that set them apart from bony fishes and make them surprisingly vulnerable to human exploitation. Only in recent years has the uniqueness and vulnerability of elasmobranchs received recognition and adequate attention.

Definition of the group

Modern elasmobranchs are generally large (>1 m) predatory fishes with a calcified but seldom ossified skeleton, including distinctive **calcified vertebral centra**. They differ from bony fishes in that the skull lacks sutures and their teeth are not fused to the jaws but are instead embedded in the connective tissue of the jaws. **Teeth**, which have the same embryonic origin as and may be derived from **placoid scales** (see Chapter 3, Modifications of scales), are replaced serially; such replacement is less common in osteichthyans. The biting edge of the upper jaw is formed by the **palatoquadrate cartilage**, rather than by the maxillary or premaxillary bones. The palatoquadrate is free from the braincase, creating a protrusible upper jaw during feeding. The mouth is subterminal (= ventral). Nasal openings are ventral and incompletely divided by a flap into incurrent and excurrent portions; bony fishes generally have completely separated, dorsally positioned nasal openings. Fin rays in elasmobranchs are soft, horny, unsegmented **ceratotrichia**.

Typical sharks, skates, and rays usually have five, and sometimes six or seven, external gill slits on each side. The first gill slit of elasmobranchs is often modified as a **spiracle**, supported by the hyoid arch and first functional gill arch. Elasmobranchs lack lungs and gas bladders, but possess large, buoyant livers and spiral valve intestines. Internal fertilization is universal to the group; males possess pelvic fin-derived intromittent organs (**myxopterygia** or **claspers**) and females either lay eggs or nourish embryos internally for several months before giving birth. Chloride ions and metabolic waste products in the form of urea and trimethyl-amine oxide (TMAO, an ammonia derivative) are concentrated in the blood and serve in osmotic regulation. A single **cloaca** serves as an anal and urogenital opening.

Historical patterns

Most orders of living chondrichthyans appeared by the Upper Jurassic, and all orders appeared by the end of the

Class Chondrichthyes (cartilaginous fishes)[a]
- Subclass Elasmobranchii (sharklike fishes)
  - Infraclass Euselachii (sharks and rays)
    - Division Neoselachii
      - Subdivision Selachii (sharks)
        - Superorder Galeomorphi
          - Order Heterodontiformes (eight species, marine): Heterodontidae (bullhead, horn sharks)
          - Order Orectolobiformes (32 species, marine): Parascyllidae (collared carpet sharks), Brachaeluridae (blind sharks), Orectolobidae (wobbegongs), Hemiscylliidae (bamboo sharks), Stegostomatidae (zebra sharks), Ginglymostomatidae (nurse sharks), Rhincodontidae (Whale Shark)
          - Order Lamniformes (15 species, marine): Odontaspididae (sand tiger sharks), Mitsukurinidae (goblin sharks), Pseudocarchariidae (crocodile sharks), Megachasmidae (Megamouth Shark), Alopiidae (thresher sharks), Cetorhinidae (basking sharks), Lamnidae (mackerel sharks)
          - Order Carcharhiniformes (224 species, mostly marine): Scyliorhinidae (cat sharks), Proscylliidae (finback cat sharks), Pseudotriakidae (false cat sharks), Leptochariidae (barbeled hound sharks), Triakidae (houndsharks), Hemigaleidae (weasel sharks), Carcharhinidae (requiem sharks), Sphyrnidae (hammerhead sharks)
        - Superorder Squalomorphi
          - Order Hexanchiformes (five species, marine): Chlamydoselachidae (frill sharks), Hexanchidae (cow sharks)
          - Order Echinorhiniformes (two species, marine): Echinorhinidae (bramble sharks)
          - Order Squaliformes (97 species, marine): Squalidae (dogfish sharks), Centrophoridae (gulper sharks), Etmopteridae (lantern sharks), Somniosidae (sleeper sharks), Oxynotidae (rough sharks), Dalatiidae (kitefin sharks)
          - Order Squatiniformes (15 species, marine): Squatinidae (angel sharks)
          - Order Pristiophoriformes (five species, marine): Pristiophoridae (saw sharks)
      - Subdivision Batoidea (skates and rays)
          - Order Torpediniformes (59 species, marine): Torpedinidae (torpedo electric rays), Narcinidae (numbfishes)
          - Order Pristiformes (seven species, marine and freshwater): Pristidae (sawfishes)
          - Order Rajiformes (285 species, marine): Rhinidae (bowmouth guitarfishes), Rhynchobatidae (wedgefishes), Rhinobatidae (guitarfishes), Rajidae (skates)
          - Order Myliobatiformes (183 species, marine and freshwater): Platyrhinidae (thornbacks), Zanobatidae (panrays), Hexatrygonidae (sixgill stingrays), Plesiobatidae (deepwater stingrays), Urolophidae (round stingrays), Urotrygonidae (American round stingrays), Dasyatidae (whiptail stingrays), Potamotrygonidae (river stingrays), Gymnuridae (butterfly rays), Myliobatidae (eagle rays)

[a] Classification after Nelson (2006).

Cretaceous. Some extant genera have been found in Upper Cretaceous deposits, with little change in some species since the Miocene (Compagno 1990a). Most extant groups have evolutionary histories much younger than actinopterygian and neopterygian fishes (see Chapter 11, Advanced jawed fishes II: Chondrichthyes). All non-euselachian elasmobranchs are extinct: cladoselachians died out by the Permo-Triassic transition and xenacanths died out during the Triassic. Ancestral groups such as ctenacanths and hybodonts disappeared during the Mesozoic.

Although some living sharks have morphologies similar to ancestral Paleozoic and Mesozoic species, these similarities reflect convergent design. The modern groups are very different with respect to features of the cranium, vertebral column, fin skeletons, tooth structure, and squamation. The greatest departure from a generalized body form exists in the highly successful batoids, the most advanced of which are the large-brained, filter-feeding manta and devil rays (Mobulinae). Among the sharklike elasmobranchs, the most derived species include the hammerhead sharks (Sphyrnidae), angel sharks (Squatinidae), and saw sharks (Pristiophoridae) (Compagno 2001; Compagno et al. 2005a, 2005b). Shark systematics is an active field and relationships among most groups are well established, although some groups remain unresolved and await further study (de Carvalho 1996; McEachran et al. 1996) (Fig. 12.1).

Modern neoselachian diversity

Nearly 950 species of neoselachians exist today, including 403 described sharklike species and 534 skates and rays

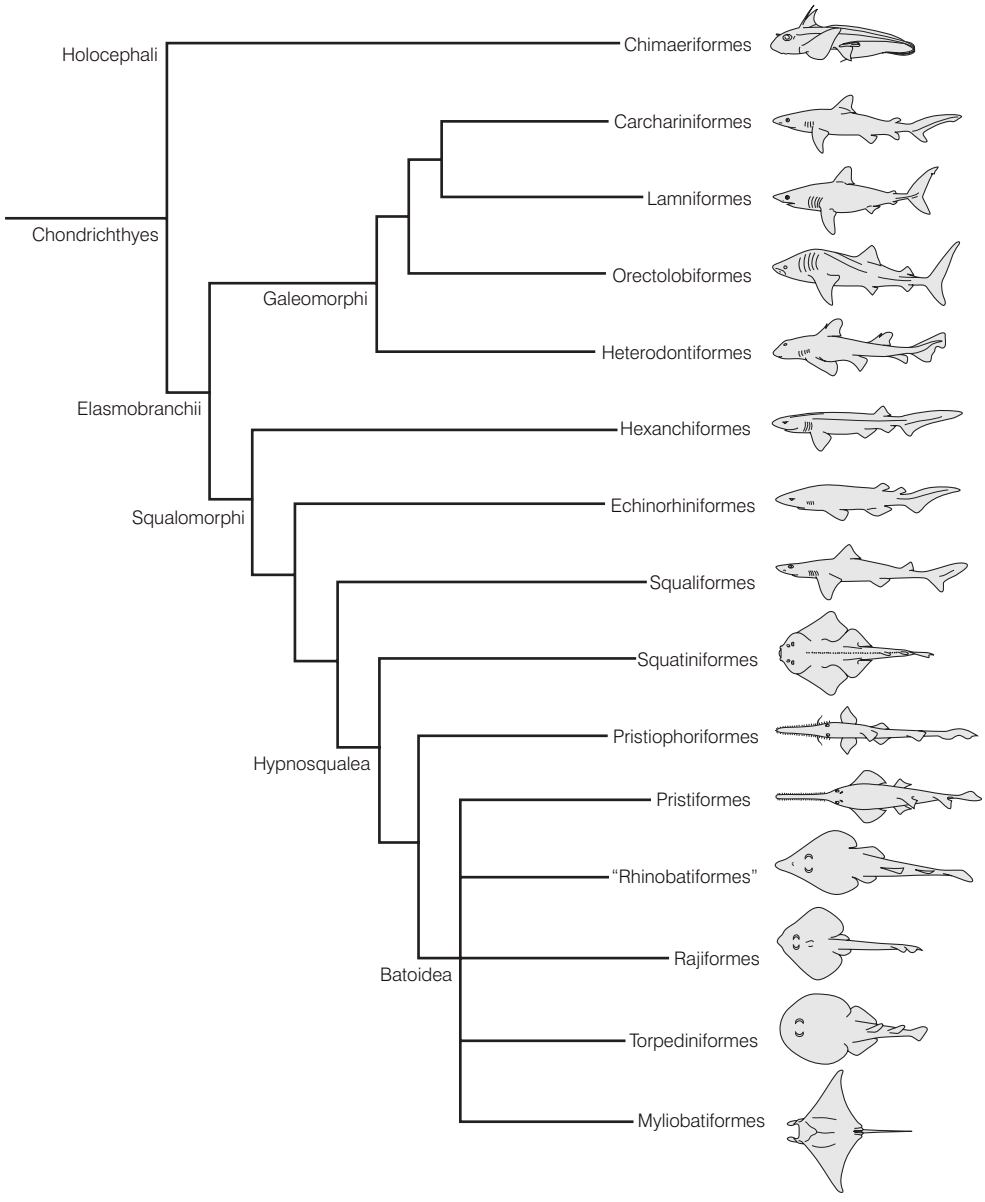

Figure 12.1
Phylogenetic relationships among living chondrichthyans. Relationships among the batoid rays remain a matter of debate, including discussion of whether the rhinobatiform guitarfishes are in fact monophyletic. From Stiassny et al. (2004), used with permission.

(Nelson 2006) (Fig. 12.2). Sharks (subdivision **Selachii**) can generally be distinguished from rays (subdivision **Batoidea**) by the following features. Sharks have: (i) gill openings on the sides of the body; (ii) the anterior edge of the pectoral fin not attached to the side of the head; (iii) the anal fin present in galeomorphs but absent in squalomorphs (except for the five species of hexanchiforms); and (iv) small lateral spiracles compared with large dorsal spiracles in rays. Rays in contrast have: (i) ventral gill openings; (ii) the anterior edge of the enlarged pectoral fin attached to the side of the head; (iii) the anal fin absent; and (iv) the intake of water for breathing chiefly through an enlarged dorsal spiracle (except in water column species).

Among the sharks, the **requiem** or ground sharks (Carcharhiniformes) make up more than half the species and are particularly diverse in tropical and subtropical, nearshore habitats. Offshore, pelagic sharks include **lamniform** species such as mako, White, thresher, and Basking sharks, whereas the **squaliform** dogfishes are particularly successful in the North Atlantic, North Pacific, and deepsea regions. The **batoids** are concentrated in four orders, the torpediniform torpedo rays, the pristiform sawfishes, the rajiform skates, and the myliobatiform stingrays. Skates are most diverse and abundant in deep water and at high latitudes, whereas stingrays are most diverse in tropical, inshore waters. Most skates have one or two dorsal fins and long, slender claspers that are depressed at their distal end, whereas stingrays have a serrated tail spine (the "sting"), lack dorsal fins, and have short, stout claspers that are cylindrical or only moderately depressed.

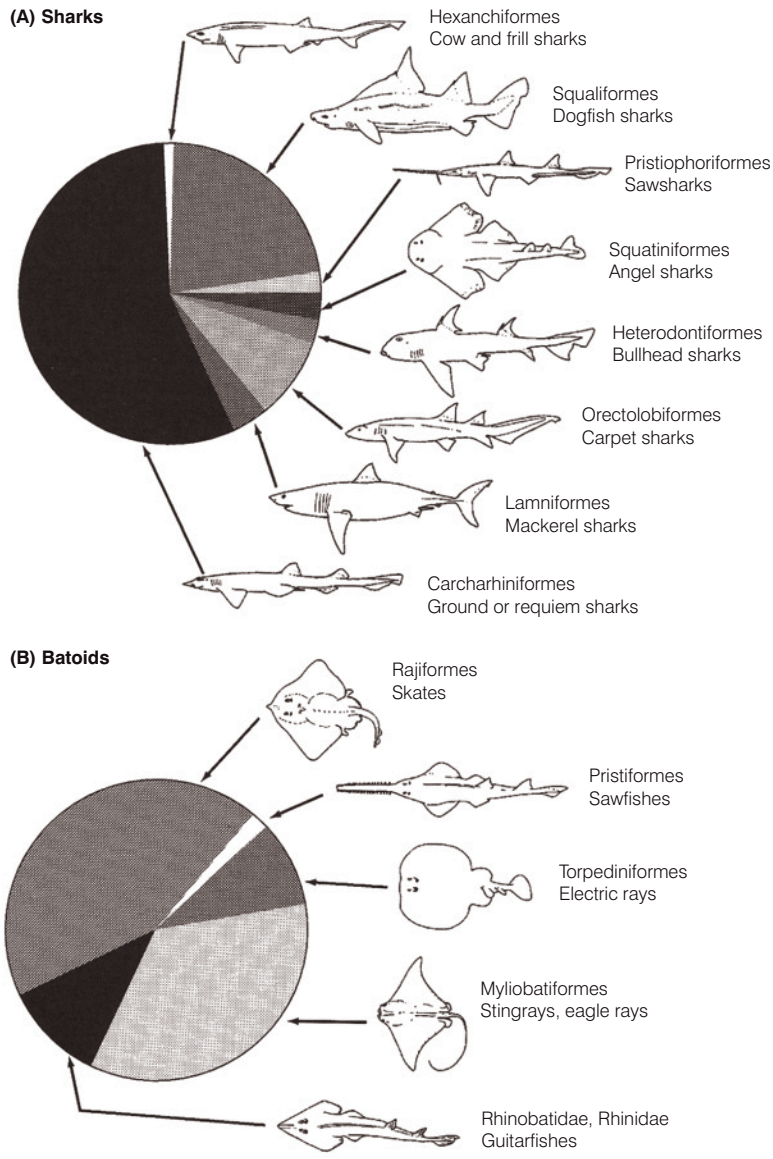

Figure 12.2

Taxonomic distribution and representative orders of the *c.* 950 species of modern sharks, skates, and rays. (A) Sharklike fishes in nine orders constitute 40% of modern euselachian species, with the carcharhiniform (ground or requiem) sharks outnumbering all other orders combined. The echinorhiniform bramble sharks, with two species, are not shown. (B) Raylike batoids make up 60% of the Euselachii, dominated by skates and stingrays; the four recognized orders are shown. Guitarfishes (Rhinobatidae, Rhinidae) are diverse members of the Rajiformes. Adapted from Compagno (1990b), used with permission.

Amidst this diversity, certain general patterns emerge that emphasize the unique traits and fascinating adaptations of elasmobranchs. These trends include: (i) large size; (ii) a marine habitat; (iii) mobility; (iv) slow metabolism and slow growth; (v) predatory feeding habits; (vi) reliance on non-visual senses; (vii) low fecundity and precocial (independent) young; and (viii) vulnerability to exploitation (see Compagno 1990b; Gruber 1991).

Body size

When compared with bony fishes, sharks as a group have always been relatively large. Modern sharks range from the 15 g, 17 cm Dwarf Lantern Shark, *Etmopterus perryi* (Etmopteridae), and several sharks in the 22–25 cm range (e.g., dalatiid pygmy sharks, *Squaliolus laticaudus* and *S. aliae*; proscyliid Pygmy Ribbontail Catshark, *Eridacnis radcliffei*) to the 4000 kg, 10 m Basking Shark, *Cetorhinus maximus*, and the 12,000+ kg, 12+ m long Whale Shark, *Rhincodon typus* (Rhincodontidae), the largest fish in the world. At least 90% of living sharks exceed 30 cm in body length, 50% reach an average length of about 1 m, and 20% exceed 2 m (Springer & Gold 1989). Maximum sizes of sharks, particularly the maximum size reached by the superpredatory White Shark (Lamnidae), is a subject plagued by misinformation and exaggeration (Box 12.1).

Large size is intimately linked with the feeding and reproductive ecology of sharks. As predators on other fishes, including other elasmobranchs, large size confers an advantage in terms of greater swimming speed during pursuit or long-distance cruising, and allows for larger mouth size and larger jaw muscle attachment. Such traits make sharks effective predators on smaller fishes and also

Box 12.1

The mismeasure of man eaters

Maximum sizes of shark species are a matter of much speculation and imagination. Researchers tend to be conservative and therefore accept only documented measurements with an accurate measuring tape and weighing scale, preferably accompanied by the preserved specimen, or at least by a photograph with a ruler for scale. However, very large animals are difficult to preserve and harder to store, and photographs can be doctored or just misleading because of problems with parallax. Hence verified maximum sizes and reported maxima ("bigger than the boat") vary considerably.

For example, the longest recorded Whale Shark is 12 m, but the species is known to grow much larger, perhaps as large as 18 m. Basking Sharks (Cetorhinidae) have been reliably measured at 9.76 m, but lengths of 12–15 m have been reported. Other accepted (vs. reputed) lengths for large predatory shark species include: Shortfin Mako (3.3 vs. 4.0 m), Great Hammerhead (5.5 vs. 6.1 m), Thresher Shark (5.7 vs. 7.6 m), Greenland Shark (6.4 vs. 7 m), and Tiger Shark (5.9 vs. 7.4 and 9.1 m) (Springer & Gold 1989; Herdendorf & Berra 1995).

Nowhere is the potential for sensationalism greater than in the case of the White Shark, *Carcharodon carcharias*. "Verified" lengths reported for this shark often include an Australian record of 36.5 ft (11.1 m). Some authors have taken the liberty of rounding off that measurement to 40 ft (12.3 m). Reexamination of the teeth and jaws from the reputed 36.5 ft specimen suggest that it was in fact only 16.5 ft (5 m) long and that the reported length resulted from a typographical error. The largest reliably measured White Shark was a 19.5 ft (5.944 m) long female caught off Ledge Point, Western Australia in 1984 (Randall 1973, 1987; Mollet et al. 1996). This length stands in contrast to a photograph published in *The Guiness book of animal facts and feats* (Wood 1982), of a purported 29.5 ft (9.1 m) Azores shark, but the photograph suggests a much smaller animal and no verification of the measurements has been possible.

Extrapolations from jaw dimensions of known sharks indicate that bite marks on dead whales could come from sharks larger than 6 m and several specimens in the 7 m range (all female) have been reported, but no such giants have been authenticated (Randall 1973, 1987; Ellis & McCosker 1991; Mollet et al. 1996). The heaviest White Shark reliably weighed had a mass of 3324 kg (Springer & Gold 1989). White Sharks are born at a length of around 100 cm and a mass of 13 kg (Ellis & McCosker 1991).

If the extant White Shark can attain a length of 6 m and weigh in excess of 3000 kg, then how large was the biggest member of the genus, the widespread "Megatooth" Shark, *Carcharodon megalodon*, that lived during the Mid-Miocene through Late Pliocene, 16 to 1.6 million years ago? Teeth from this giant are common at many fossil-bearing locales in Europe, Africa, Australia, India, Japan, and North and South America (Bruner 1997). Enamel heights (the vertical distance from the base of the enamel portion to its tip, Fig. 12.3) in excess of 100 mm are not unusual (the largest White Shark teeth are about 60 mm high); the largest *C. megalodon* tooth found had an enamel height of 168 mm (Compagno et al. 1993; see also Applegate & Espinosa 1996; Gottfried et al. 1996) (some researchers place the Megatooth Shark in the genus *Carcharocles*).

Paleontologists, and others, have assembled these teeth into reconstructed jaws of this shark and then extrapolated to total body length based on jaw dimensions. These reconstructions have been notoriously inaccurate. The most famous was produced by the American Museum of Natural History in 1909 (Fig. 12.3A). The jaws of this reconstruction were oversized because: (i) the preparators created a wider-than-accurate jaw by using all anterior (midline front) teeth of equal size across the jaws, whereas most sharks, including *C. carcharias*, have smaller lateral and posterior teeth at the sides; and (ii) the cartilaginous jaw of a shark is generally no broader than the enamel height of the biggest tooth. In the American Museum reconstruction, cartilage breadth was four times enamel height, creating a larger jaw. The two errors produced a jaw about 30% larger than it should have been, which created a larger shark.

Length estimates extrapolated from that jaw, influenced by tooth size : body length ratios of the mismeasured 36.5 ft Australian specimen, have ranged between 60 and 100 ft (18.5 to 31 m), which has been rounded to 120 ft (37 m) in some popular books. It was a Megatooth Shark that terrorized the New England town of Amity in Peter Benchley's (1974) novel *Jaws*. Given that snout length is 6% of total length in White Sharks, and assuming the ill-fated swimmer on the cover of the paperback version of the novel is 1.7 m tall, the Amity shark was a conservative 21 m long. Bruce, the mechanical shark used in the movie version of *Jaws* depicted a White Shark about 7.3 m long (Stevens 1987).

Recent reconstructions of *C. megalodon* (Fig. 12.3B) have used more quantitative methods in estimating size,

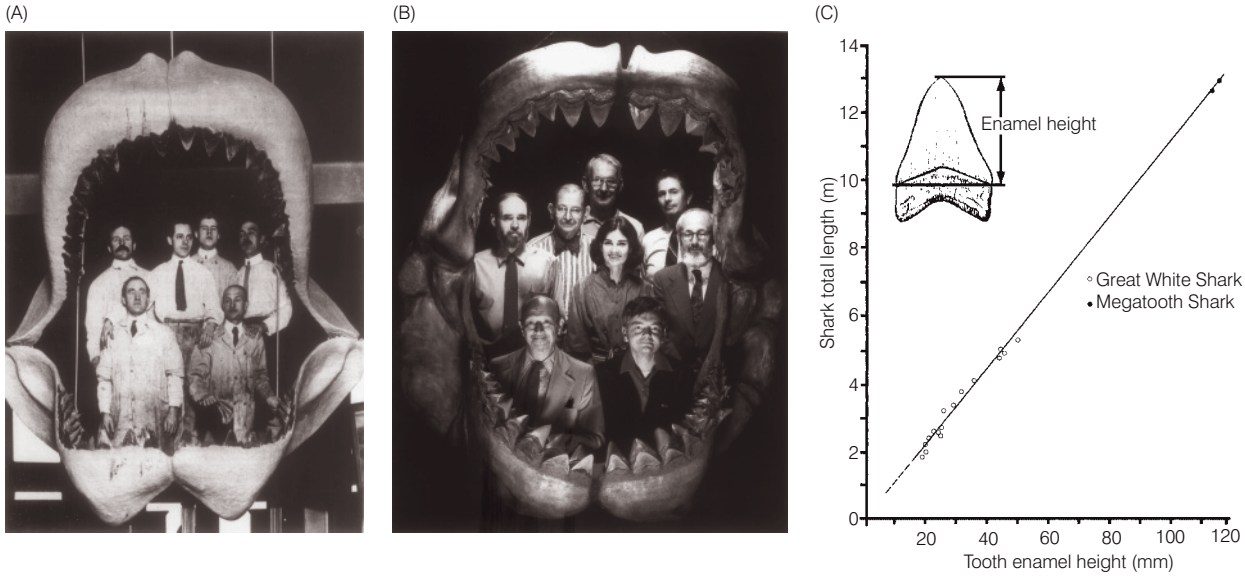

Figure 12.3

Reconstructing the jaws and estimating the size of the extinct Megatooth Shark, *Carcharodon megalodon*. (A) Jaw reconstruction as inaccurately prepared in 1909. The jaws are about one-third too large because equal-sized, anterior teeth were used throughout the jaws, and the cartilage is about four times broader than in living sharks. (B) Recent reconstruction by the Smithsonian Institution, suggesting a body length of about 13 m. (C) Calculating the lengths of White and Megatooth sharks. Total body length is directly related to maximum tooth size (enamel height) in White Sharks (*Carcharodon carcharias*); hence body length can be estimated for sharks from which only teeth are available. This gives a maximal size of 6 m for the White Shark. Assuming a similar relationship existed for the extinct Megatooth Shark, placement of two of the larger known teeth along the same regression line (closed circles) suggests a body length of about 13 m; the largest tooth found indicates lengths up to 16 m. The approximate equation for calculating total length from tooth height is:
Total length (m) = 0.096 (enamel height, mm) – (0.22).
Data from Randall (1973), Compagno et al. (1993), and Gottfried et al. (1996). (A) from American Association for the Advancement of Science, © 1971, used with permission; (B) photo by Chip Clark, National Museum of Natural History, Smithsonian Institution, used with permission.

such as the statistical relationships of tooth enamel height and jaw dimensions to body length and mass from known White Shark specimens (Fig. 12.3C). Extrapolating from *C. carcharias* to *C. megalodon*, a Megatooth Shark with a tooth enamel height of 168 mm would be about 16 m long and weigh approximately 48,000 kg (Compagno et al. 1993; Gottfried et al. 1996). If body proportions were similar to those of extant White Sharks, the jaws would be >1 m wide, the dorsal fin would be 1.4 m high, and the tail would be 1.75 m tall.

The Megatooth Shark, although probably the largest shark to ever live, occurred with other relatively gigantic Miocene/Pliocene predators, including the Speartooth Mako, *Isurus hastalis* (estimated at 6 m long), a hemigaleid, *Hemipristis serra*? (5 m), as well as the extant White Shark (Compagno 1990b).

decrease their own vulnerability to predators, either via rapid escape or active defense. It is suggested that sharks larger than 1 m long are relatively immune to shark predation, and it is not surprising that birth sizes of many sharks are close to the 1 m critical length (e.g., Sand Tiger, Odontaspididae; White and Longfin Mako, Lamnidae; Dusky, Carcharhinidae).

Sharks that give birth to smaller young often have relatively large litters or short intervals between reproduction (e.g., Atlantic Sharpnose, Carcharhinidae; Scalloped Hammerhead and Bonnethead, Sphyrnidae). Predation also affects nursery ground location and interacts with growth rate. Sharks that drop their pups in offshore or beachfront areas that are frequented by large sharks tend to have relatively rapid growth rates of 30–60 cm during the first year (e.g., Thresher, Alopiidae; Shortfin Mako; Blue, Tiger, Spinner, and Sharpnose, Carcharhinidae; Bonnethead). Sharks that release their young in relatively predator-free inshore nursery areas such as bays, sounds, estuaries, or shallow reef flats tend to grow only 15 cm in the first year

(e.g., Bull, Sandbar, and Lemon, Carcharhinidae; Scalloped Hammerhead) (Branstetter 1990, 1991).

Habitats

Most elasmobranchs are marine organisms of relatively shallow temperate and particularly tropical waters, although all oceans except the Antarctic have one or more species. Most inhabit continental and insular shelves and slopes: 50% of all species occur in <200 m of water and 85% occur in <2000 m. Only about 5% dwell in the open ocean, including a few myliobatiforms such as manta rays; another 5% occupy fresh water. Truly cold water, high-latitude sharks (not counting those that live in the perpetually cold, deep sea) are limited to the relatively large hexanchids (Sixgill Shark), Basking Shark and sleeper sharks (Cetorhindae, Somniosidae), smaller squaliform sharks, and some catsharks (Scyliorhinidae).

Although bony fishes inhabit ocean depths to 8000 m (see Chapter 18, The deep sea), sharks do not occur as deep. Deepsea sharks, those frequently captured in aphotic (lightless) waters below 1000 m, include several squaliform species (Portuguese, kitefin, lantern, sleeper, and rough sharks), carcharhiniform cat and false catsharks, and the Sixgill. Record depths include sightings of the Portuguese Shark, *Centroscymnus coelolepis*, at 3690 m (Clark & Kristof 1990); an unidentified spiny dogfish at 4050 m; and a disputed depth of 9938 m for the squalid *Euprotomicrus bispinatus* (see Herdendorf & Berra 1995). But these are exceptional occurrences because Chondrichthyes in general seldom occur in abyssal regions deeper than 3000 m, probably because of low food supplies and the high metabolic costs of maintaining a large, oil-rich liver used to maintain buoyancy (Priede et al. 2006). Hence sharks are restricted from 70% of the world's ocean volume and have no natural deepwater refuges from human exploitation.

Sharks have also failed to occupy other habitats characterized by environmental extremes of temperature, oxygen, turbulence, drought, and salinity, unlike bony fishes. Among the few exceptions are *Pentanchus* cat sharks that inhabit deep water basins that are characterized by relatively low oxygen levels and relatively high temperatures and salinities. These species have elongate gill regions and expanded gill filaments (Compagno 1984).

Although the ocean is home to most elasmobranchs, at least 170 species in 34 families are capable of entering estuarine and freshwater habitats, and 47 species are restricted to such regions (Martin 2005). Two families of rays – the Potamotrygonidae and Dasyatidae – contain truly freshwater fishes, seldom if ever entering marine conditions (Compagno 1990b). The potamotrygonid river stingrays include about 21 species restricted to fresh waters of Atlantic drainages of South America. Eight species of dasyatid whiptail stingrays in the genera *Dasyatis* and *Himantura* are restricted to rivers in Africa, Southeast Asia, New Guinea, and Australia, and another six dasyatid species are euryhaline, spending most of their lives in fresh water (Martin 2005). Included among the obligate freshwater forms is the Giant Freshwater Stingray or whipray, *Himantura chaophraya* of tropical Australia, New Guinea, Borneo, and Thailand (Fig. 12.4). *H. chaophraya* may be the world's largest stingray and perhaps the world's largest freshwater fish, reaching a length of 5 m, a width of 2.4 m, and a mass of 600 kg (Roberts & Monkolprasit 1990; Compagno & Cook 1995a).

Among selachians, three species of carcharhinid river sharks in the genus *Glyphis* are obligate freshwater inhabitants of rivers in India, Borneo, and tropical Australia. A few

Figure 12.4
The Giant Freshwater Whipray *Himantura chaophraya*. This endangered species occurs in rivers of Southeast Asia, New Guinea, and tropical Australia. Photo by Z. Hogan, used with permission.

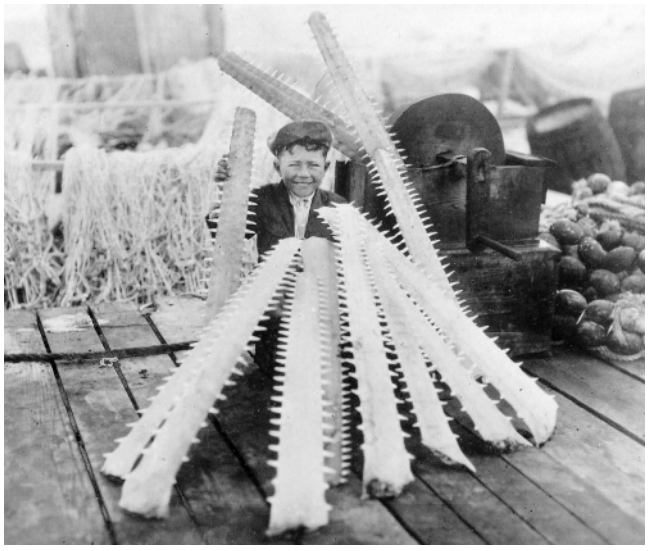

Figure 12.5

Sawfishes are among the most imperiled marine and estuarine fishes in the world. Although little directed fishing occurs for sawfishes, they are frequently entangled in nets of all types. Such bycatch remains the major threat to the US federally listed Smalltooth Sawfish *Pristis pectinata* and its congener, the Largetooth Sawfish *P. perotteti*. Both were once common from the Gulf of Mexico up the east coast from Florida to Cape Hatteras (Simpfendorfer 2000). Sawfishes in the USA now occur only in peninsular Florida, primarily in the Everglades region. Shown here are results from a fishing tournament, *c*. 1920, in Key West, Florida. Some of the fish were said to have weighed 765 kg. Photo courtesy of Matthew McDavitt, http://members.aol.com/_ht_a/nokogiri/index.html (photographer unknown).

carcharhinid sharks enter fresh water periodically, the most notable example being the Bull Shark, *Carcharhinus leucas*. Bull Sharks have been captured as far as 4200 km up the Amazon River, and also more than 1200 km up the Mississippi River at Alton, Illinois (Thorson 1972; Moss 1984). Bull Sharks regularly traverse the 175 km long Rio San Juan between the Caribbean Sea and Lake Nicaragua in Central America, and occur in other rivers and lakes of Mexico and Central and South America. Bull Sharks are the most likely perpetrators of attacks on humans in rivers worldwide (e. g., Coad & Papahn 1988). Finally, six species of pristid sawfishes (Batoidea) are strictly euryhaline. These include the Largetooth Sawfish, *Pristis perotteti*, which also moves regularly between lakes and the ocean in Central and South America and has established genetically distinct, reproducing populations in some lakes (Montoya & Thorson 1982; Thorson 1982) (Fig.12.5).

Sharks and sawfishes that move freely between marine and fresh water are able to adjust the osmotic concentration of their blood appropriately. Whereas in salt water the major problem is salt accumulation and water loss, in fresh water the problems reverse (see Chapter 7, Osmoregulation, ion and pH balance, and excretion). A Bull Shark in fresh water reduces the salt concentration of its blood by about 20% and urea concentration by about 50%. This cuts osmotic pressure of the blood in half, to about 650 mOsm. To accommodate additional water flowing in from the environment due to osmotic pressure, urine production increases 20-fold. Salt concentration of the urine is reduced by the same factor, thus conserving salts. The rectal gland, which functions in salt water to secrete excess NaCl back into the environment, shuts down. All of these changes are quickly reversed upon return to the ocean.

The truly freshwater potamotrygonid stingrays are restricted to low salinity conditions. Unlike all other chondrichthyans, they have lost the ability to concentrate urea (although the enzymes for urea production still occur in their livers) and they lack functioning rectal glands. These stingrays die in water with more than 40% the salt concentration of sea water (about 15 ppt salt). More typical marine elasmobranchs, including those that spawn in estuaries, can survive salinities as low as 50% of sea water if acclimated slowly. Unlike Bull Sharks, these typical elasmobranchs achieve an osmotic balance by reducing only the urea concentration of their blood, without reduction in salt concentration (Thorson et al. 1967, 1973; Moss 1984; Thorson 1991).

Because humans and their destructive activities are concentrated along rivers and estuaries, freshwater and estuarine elasmobranchs – as top predators with typical and vulnerable elasmobranch life histories – are even more threatened than is generally the case for chondrichthyans (Compagno & Cook 1995b; Martin 2005; see below, Shark conservation). The Giant Freshwater Stingray is listed as Vulnerable by the International Union for the Conservation of Nature (IUCN 2004; www.redlist.org) due to directed and bycatch fishing, habitat destruction, and range fragmentation from dams; Compagno and Cook (1995a) suggested that its status be elevated to Critically Endangered. Of the 47 obligate euryhaline and freshwater elasmobranch species, fully 18 have been assigned to high-risk categories (Critically Endangered, Endangered, or Vulnerable) by the IUCN (2004); another five are Data Deficient, indicating insufficient information to determine their status (Martin 2005).

Movement and home ranges

Water as a medium for locomotion exacts a high energetic price on any organism. The long evolutionary history of the elasmobranchs is characterized by the development of anatomical and physiological traits that appear to favor movement at the lowest possible energetic cost. Many of the features of the integument, fins, buoyancy devices, and swimming behavior of sharks, as well as short- and long-term movement patterns, reflect possible adaptations to these energetic constraints.

Most elasmobranchs have heterocercal tails (see Chapter 8, Swimming in sharks: the alternative approach), with asymmetry in both the internal support and external appear-

ance. The typical heterocercal tail is associated with an active life style above the bottom, as in most requiem sharks and hammerheads. Diversity in tail fin shape is however considerable (Bone 1988). Symmetrical tails preceded by lateral keels characterize high-speed, pelagic sharks such as the Mako, White, and Porbeagle (Lamnidae); large body size and symmetrical tails characterized the presumably pelagic, predatory edestoid holocephalans of the Carboniferous (see Chapter 11). Lateral keels are also found convergently on such pelagic predators as tunas (Scombridae) and billfishes (Istiophoridae).

Extreme heterocercality in contrast is usually found in relatively inactive, benthic sharks such as the wobbegong's and nurse sharks (Orectolobidae) and cat sharks that essentially lack a lower tail lobe. A specialized, extreme heterocercal tail occurs in active swimmers such as the thresher sharks, in which the dorsal tail lobe, which may constitute 50% of the body length, is purportedly used for herding and stunning prey. Many rays lack a tail fin (e.g., stingrays, eagle rays, manta rays) and swim by flapping or undulating their scaleless pectoral fins. Angel sharks show reversed symmetry, with the lower tail lobe enlarged.

The placoid scales of sharks have a morphology that apparently serves a streamlining function (Fig. 12.6). Unlike the relatively flat scales of many osteichthyans, each placoid denticle of a shark has a pedestal and an expanded top, which often has ridges running parallel to the body of the shark. It has been postulated that this particular shape, which is mimicked in the winged keels of high performance sailboats, helps reduce swimming-induced drag by reducing turbulence along the shark's body. Swim suits designed for competitive swimmers have purportedly incorporated denticle patterns in their construction to promote drag reduction, although comparative tests indicate no significant improvement in swimming times (Toussaint et al. 2002; www.coachesinfo.com/article/146).

Additionally, the shape and arrangement of adjoining scales in active sharks may also aid in prey capture. Hydrophones detect much less noise from swimming sharks than from swimming bony fishes, suggesting that turbulence reduction also enhances stealth in sharks. Not surprisingly, the scales of benthic and slow-swimming sharks, as well as many rays, lack apparent streamlining features and are instead enlarged for protection or are absent (e.g., Bramble Shark, Echinorhinidae; Thorny Skate, Rajidae) (Moss 1984). The sting or barb on the dorsal surface of the tail of a stingray is a modified, elongate placoid scale with serrate edges and a venom gland at its base.

Maintenance of a constant depth is potentially expensive if a fish must constantly swim to overcome gravity. Bony fishes control their buoyancy by filling or emptying a gas bladder (see Chapter 5, Buoyancy regulation). Sharks have arrived at a completely different solution to the challenge of buoyancy control: they both reduce their body weight and fill their body with low-density substances. Weight

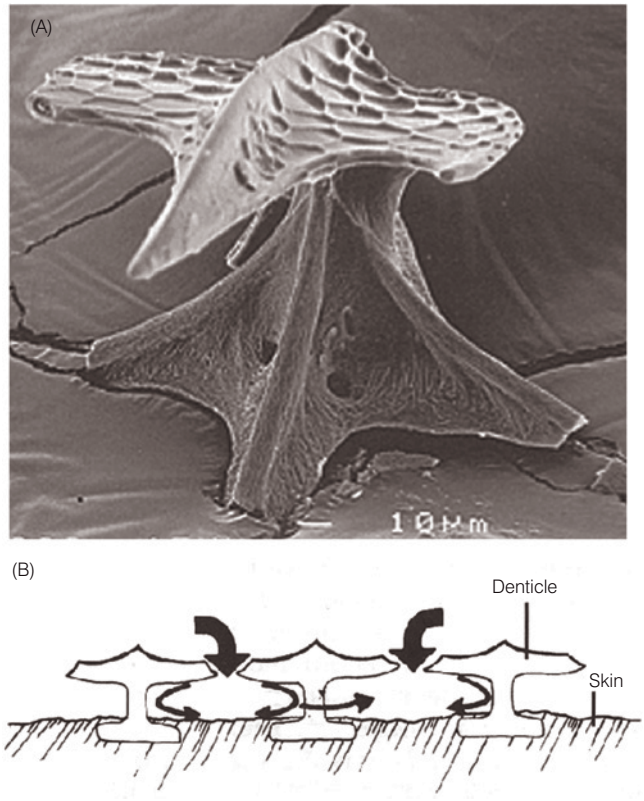

Figure 12.6

The role of scales in drag reduction in sharks. (A) Scanning electron micrograph of a single denticle from a scyliorhinid cat shark, showing the pedestal and winged keel arrangement thought to absorb turbulence, which reduces drag. (B) Cross-sectional representation of placoid scales, showing reduction of turbulence along the body. Strength of water flow corresponds to thickness of the black arrows. (A) from Konstantinou et al. (2000); (B) from Moss (1984), used with permission.

reduction comes largely from a skeleton made of cartilage, which has 55% the specific gravity of bone (1.1 vs. 2.0). Buoyancy can also be enhanced by the oils contained in the large liver, which may constitute up to 30% of the weight of the fish. Deepsea squaloid sharks and some pelagic species such as Whale, Basking, and White Sharks have large livers that are as much as 90% oil. These sharks are almost neutrally buoyant (e.g., a Basking Shark that weighs 1000 kg in air weighs only 3.3 kg in water, or about 0.3% of its air weight). Typical bony fishes with their gas bladders deflated have in-water weights about 5% of air weights, i.e., a 100 kg fish weighs 5 kg in water. The oil in a shark's liver is primarily **squalene**, which has a specific gravity of 0.86 (the specific gravity of sea water is 1.026) (Baldridge 1970, 1972; Moss 1984; Bone 1988).

An oil-based buoyancy system may have advantages over a gas-filled system. To maintain neutral buoyancy, bony fishes use energy to fill or empty the gas bladder or they will sink rapidly or float uncontrollably. The physics of gas secretion and absorption limit the rate at which bony fishes

can change depth. Oil, unlike gas, is incompressible and provides constant buoyancy regardless of depth and pressure. Sharks can therefore move up and down repeatedly over tens or hundreds of meters on a daily basis without having to make adjustments in their buoyancy control mechanism. In recent years, telemetry studies have shown vertical movements to depths of more than 400 m in hammerheads, 590 m in Bigeye Thresher Sharks (*Alopias superciliosus*), 750 m in Basking Sharks, and to at least 980 m in Whale Sharks and White Sharks (e.g., Sims et al. 2003; Weng & Block 2003; Bonfil et al. 2005; Wilson et al. 2006b; see also Carey and Scharold (1990) on Blue Sharks and Carey and Clark (1995) on Sixgill Sharks).

Such rapid and repeated vertical migration, with its attendant exposure to tremendous pressure and temperature changes, is uncharacteristic of most bony fishes. An additional energetic advantage of an oil-filled liver is that it serves as an energy reserve; many sharks metabolize their liver oils when starved. An apparent downside of this adaptation is that producing lipids for liver storage is energetically costly.

Activity spaces, or home ranges, of most sharks are poorly known. Recent advances in electronic telemetry have permitted the fitting of ultrasonic transmitters to sharks and tracking them through several days and even weeks of activity (Nelson 1990). Juvenile Lemon Sharks less than 1 m long in Bimini initially patrol shallow beach areas of about 0.7 km^2. This area increases with age: a 1.8 m long shark may have a range of 18 km^2, and a 2.3 m long shark's range encompasses more than 90 km^2. Habitats change with age also, as the shark moves from the shallow nursery area to open sand flats and finally to the reef and beyond (Sundstrom et al. 2001). Daily homing movements, involving daytime aggregation at seamounts and nighttime foraging in open water several kilometers away, have been demonstrated in Scalloped Hammerheads, *Sphyrna lewini* (Klimley & Nelson 1981).

On a larger scale, many sharks make extensive movements and migrations on the order of hundreds and even thousands of kilometers. Based on tag-and-recapture data, sharks can be classified as local, coastal, or oceanic. Local sharks, including Bull, Nurse, and Bonnethead sharks, spend the majority of their adult lives in a relatively confined, nearshore area of a few hundred square kilometers. Coastal species, such as Sandbar, Blacktip, and Dusky sharks, stay near continental shelves but move 1600 km or more. Bigeye Threshers move from waters off New York to the eastern Gulf of Mexico, a distance of 2767 km. Sandbar Sharks move between the northern Atlantic region of the USA and the Yucatan Peninsula of Mexico, a distance of about 5600 km. Even comparatively small, coastal sharks can cover large distances during their lifetimes. A *c*. 1.5 m long School Shark, *Galeorhinus galeus*, tagged off New Zealand's South Island was caught 4940 km away off South Australia, 3.5 years later (Hurst et al. 1999). A Spiny Dogfish, *Squalus acanthias*, tagged off Washington state moved 8704 km during the 10-year period between release and recapture (see Kohler & Turner 2001 for an extensive review).

Oceanic species may cross entire ocean basins, sometimes repeatedly. Maximum distances traveled by oceanic species in the North Atlantic include 7800 km (Blue Shark), 6700 km (Tiger Shark), 4500 km (Mako), and 2800 km (Oceanic Whitetip) (these are underestimates because they record only start and end points). Telemetered movements using satellite tracking are even more impressive. A Whale Shark tagged in the Sea of Cortez, Mexico traveled 13,000 km in 37 months to the western North Pacific Ocean (Eckert & Stewart 2001). One Whale Shark tagged in the Sulu Sea of the Philippines traveled to the South China Sea off Vietnam 4567 km distant in 2.5 months, while another tagged off the northwestern coast of Malaysia moved 8025 km over a 4-month period (Eckert et al. 2002).

Most spectacularly, some sharks recross major oceans. Blue Sharks make return trips between North America and Europe, a distance that exceeds 16,000 km (Casey & Kohler 1991). White Sharks are now known to migrate between central California and Hawaii, a minimum distance of 3800 km (Boustany et al. 2002). A 4 m female White Shark nicknamed Nicole (after Australian actress Nicole Kidman, an advocate of shark conservation) was followed via satellite telemetry across the Indian Ocean and back between South Africa and Australia. The round trip took 9 months and covered a minimal distance of 22,000 km (Bonfil et al. 2005) (Fig. 12.7). These and other large-scale movements across political boundaries have substantial conservation implications because management regulations and enforcement vary greatly among nations.

Metabolism and growth rate: life in the slow lane

Many aspects of the biology of sharks point to a strong emphasis on **efficient energy use** when compared with bony fishes. In addition to the anatomical features such as fin and scale morphology mentioned above, physiological attributes of sharks indicate a premium placed on energy conservation. Resting metabolic rates of a 2 kg Spiny Dogfish average 32 mg O_2/kg body weight/h, about one-third of the average resting rate for comparably sized teleosts. In dogfish, the active metabolic rate is only triple that of the resting rate, whereas teleost active rates often go up 10-fold (Brett & Blackburn 1978). Extrapolated prey intake rates indicate that a 2 kg dogfish would need only 8 g fish prey per day for maintenance, whereas a similar-sized salmon would require four times that amount.

Comparable data for larger sharks are unavailable, for obvious logistic reasons. Estimated oxygen consumption suggests that sharks consume about half the oxygen of

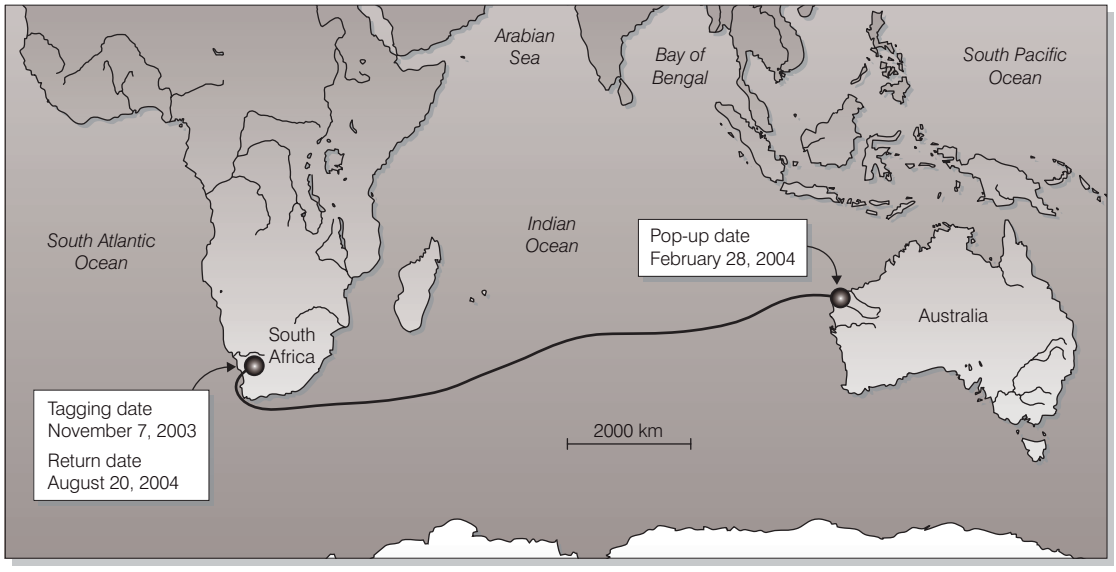

Figure 12.7

The track of Nicole, a 4 m White Shark that had been seen over a 6-year period in South Africa. Nicole was then followed via satellite telemetry from South Africa to Australia between November 2003 and February 2004, and was then seen again off South Africa in August 2004. Her minimal roundtrip distance was 22,000 km. After Bonfil et al. (2005).

equivalent-sized bony fishes (Moss 1984). For example, calculations of energy consumption have been made for a 4.5 m White Shark that was harpooned with a temperature-recording ultrasonic transmitter (Carey et al. 1982). Based on the rate at which the temperature of the shark's muscle mass changed as it passed through a thermocline (region of rapid temperature change), its oxygen consumption rate was calculated to be about 60 mg O_2 or 0.2 kcal/kg body weight/h (a 60 kg human consumes about 1.6 kcal/kg/h).

Low metabolic requirements may translate into reduced energetic needs compared to bony fishes. White Sharks feed commonly on dead whales. Based on the caloric value of 30 kg of whale blubber found in a 940 kg White Shark's stomach and on the above calculations of metabolic rate, it was estimated that White Sharks can maintain themselves by feeding on whales only once every 6 weeks (Carey et al. 1982).

Food consumption rates vary greatly among shark species but are apparently most closely related to degree of activity (Duncan 2006). Relatively sedentary sharks, such as the Nurse Shark, consume 0.2–0.3% of their body weight per day and digest an average meal over at least 6 days. Moderately active sharks, such as Sandbar and Blue sharks, consume 0.2–0.6% of body weight per day, digesting a meal in only 3–4 days. Very active sharks such as the Mako, which are "warm-bodied" (see Chapter 7, Temperature relationships), eat 3% of their body weight per day, digesting their meals in 1.5–2.0 days. Translated into annual consumption rates, the Mako eats about 2 kg/day, or about 10–15 times its body weight per year. Although such figures appear large, they are about half the annual consumption of an individual teleost, emphasizing the relative energy efficiency of feeding in sharks.

To the list of possible energy-saving mechanisms of sharks can be added an intriguing but as yet puzzling characteristic, namely heat conservation. Lamnid sharks and to a lesser extent thresher sharks are able to conserve some of the heat generated during muscle contraction and thereby maintain their muscle and stomach temperatures at about 7–10°C above ambient water conditions (Carey et al. 1982; McCosker 1987). Heat generated during muscle contraction in most sharks is dissipated because cold, oxygenated blood coming from the gills moves into the deeper parts of the body. In lamnid sharks, a **countercurrent exchange** arrangement helps warm arterial blood flowing from the gills (see Chapter 7). This is not true thermal regulation as happens in birds and mammals or even tunas; body temperature is not constant but varies with external temperature. The potential adaptive significance of this elaborate structure and process is a matter of conjecture. Higher body temperatures may permit maintenance of a higher metabolic level and generation of more muscle power, thus facilitating the capture of fast swimming prey (including endothermic marine mammals), and may increase the rate at which food is digested (Carey et al. 1982; Bone 1988). All of these factors might extend the ability of these large predators to invade cool waters at high latitudes (Block & Finnerty 1994).

Low metabolic demands may be linked to relatively **slow growth** and **long life spans**. After an initial rapid growth

phase of 15–60 cm increase per year (see above), growth in most sharks slows considerably. Growth rates of juveniles and adults of 12 species of medium- to large-sized sharks averaged only 5 cm/year (Thorson & Lacy 1982; Branstetter & McEachran 1986). Longevity estimates vary considerably among and within species, but chondrichthyans on average live longer than bony fishes (Cailliet & Goldberg 2004). Among batoids, sawfishes live 30–44 years, stingrays 3–28 years, and skates 9–24 years (except in Europe's largest skate, the Critically Endangered Common Skate, *Dipturus batis*, that can live to 50 years). Sharks are similarly long-lived, again with much variation. Angel sharks live to 35 years, carpet sharks 19–35 years, dog sharks 12–70 years (including the longest lived species, the deep-water *Centrophorus squamosus*), mackerel sharks 10–25 years, and ground sharks 4–32 years (most chimaeras live 5–10 years, with a maximum longevity of 29 years in *Chimaera monstrosa*). Age estimation in sharks is frustrated by a lack of retained, calcified structures; growth rings in vertebrae are the most commonly used indicator of age when more direct measurements are unavailable (Cailliet 1990; Cailliet & Goldman 2004).

Feeding habits

Sharks are apex predators throughout the world, stationed at the top of the food webs in which they occur. All elasmobranchs are carnivorous, taking live prey or scavenging on recently dead animals. No evidence of herbivory or detritivory exists, and the only departures from feeding on relatively large prey are the huge, filter-feeding, zooplanktivorous Basking, Megamouth, and Whale sharks and manta rays. For most shark species, bony fishes constitute 70–80% of the diet. Feeders on other prey types include carcharhinid Tiger, Bull, and Galápagos sharks (other sharks); hammerheads (stingrays); White, Tiger, Sleeper, and Cookie Cutter sharks (marine mammals); Tiger Sharks (seabirds); and Leopard, Nurse, and Green Dogfish sharks and most skates and rays (invertebrates). Somniosid sleeper sharks in Antarctica feed on the ocean's largest invertebrates, the giant and colossal squids (Cherel & Duhamel 2004).

The characteristic ventral mouth of most sharks (exceptions include the Megamouth, Frill, Whale, and angel sharks and the manta rays) is apparently linked to dependence on bite strength rather than suction during feeding. Nurse sharks, as well as some heterodontiform sharks and many rajiforms, utilize suction extensively while feeding, but negative pressures are produced by expansion of the enlarged orobranchial cavity rather than enlargement of the mouth via jaw protrusion. Underslung jaws in sharks provide larger regions for muscle attachment than in fishes whose jaw bones extend all the way to the tips of their snouts. The shark configuration allows for both protrusion of the palatoquadrate (upper jaw) and the generation of the powerful biting forces required to cut through the skin, bone, and muscle of their prey (Fig. 12.8). Hence sharks are not limited to prey that can be swallowed whole, whereas the vast majority of osteichthyans are "**gape-limited**" and risk suffocation if they attack prey larger than they can swallow whole.

Separation of the palatoquadrate from the cranium serves as more than a diagnostic character for identifying elasmobranchs. This separation also allows upper jaw teeth to be retracted during nonfeeding periods, which aids in streamlining of the head profile. **Protrusion** during the bite

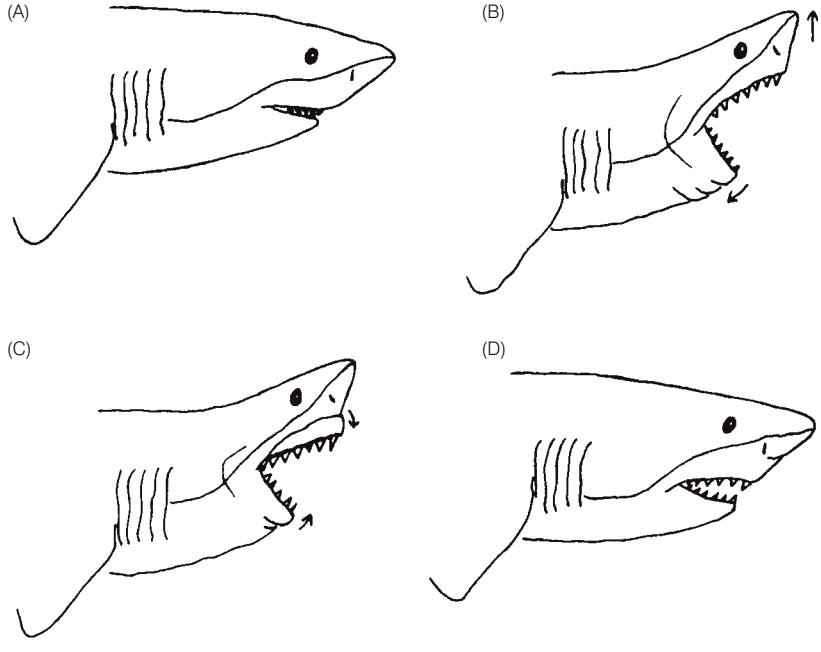

Figure 12.8

Head and jaw movements associated with feeding in the White Shark, *Carcharodon carcharias*. (A) Normal resting position; (B) snout is lifted and lower jaw depressed, achieving maximal gape; (C) lower jaw is lifted forward and upward and the palatoquadrate (teeth-bearing upper jaw) is rotated forward and downward, thereby closing the jaws (= the bite); (D) snout is dropped back down and palatoquadrate is retracted to resting position. The bite (component C) occurs quickly, requiring on average 0.8 s. From Tricas and McCosker (1984), used with permission.

increases bite efficiency, jaw closure speed, and prey manipulation (Wilga et al. 2001). Hence prey can be efficiently cut by the closing action of the jaws and serrate teeth, rather than merely grasped.

In many carcharhiniform and lamniform sharks, lower jaw teeth are spikelike whereas upper jaw teeth are flat-bladed with serrated edges. In a typical jaw closing sequence (Fig. 12.8), the lower jaw is lifted first, impaling the prey, and then the upper jaw is brought down, once or repeatedly. Once prey are grasped, many sharks also shake their head and upper body, or even rotate the entire body about its long axis. During this movement, the upper jaw teeth slice through the prey, eventually removing a chunk of flesh (Moss 1977, 1984; Tricas & McCosker 1984). Jaw protrusion is extreme in some rajiforms due to the loss of ligamental connections between the palatoquadrate and cranium. These fishes dexterously pick up food objects from the bottom with their jaws through a combination of suction and grasping (Moss 1977, 1984).

One departure from this norm occurs in some squaloid sharks, in which the lower teeth are more bladelike than the uppers and are arranged in a flat band across the lower jaw, perpendicular to the axis of the body. To this group belongs the highly specialized, 40 cm long, bioluminescent Cookie Cutter Shark, *Isistius brasiliensis* (Dalatiidae), the only ectoparasitic elasmobranch (Fig. 12.9). Craterlike wounds about 4 cm across are frequently found on tunas, dolphins, whales, and even Megamouth Sharks, all animals that spend part of their time at mesopelagic depths (200–1000 m). These wounds match precisely the mouth size of the Cookie Cutter Shark and it has been deduced that the small sharks lurk among small mesopelagic organisms and prey on the larger predators that move into this region to feed (Jones 1971; Shirai & Nakaya 1992). The pattern and nature of the green-emitting photophores (light organs) on *Isistius* suggest that it is essentially invisible because its light output closely matches the spectrum of background light at the depths where it swims (Widder 1998). The symmetrical craterlike wounds may be formed when the shark attaches to the side of its victim and then spins about its long axis, removing a flat cone of tissue (E. Clark, pers. comm.). Similar but much larger wounds on the sides of seals and beluga whales may be the result of attacks by large Greenland Sharks (Somniosidae), which have a dentition pattern similar to that of *Isistius* (A. Fisk, pers. comm.).

Dentition morphology, an important taxonomic characteristic for identifying species, correlates strongly with food type in most sharks (Fig. 12.10). Predators on fishes and squids, such as mako, Sand Tiger, and Angel sharks, have long, thin, piercing teeth for grasping whole prey, which they often swallow whole. Most requiem sharks, which are also piscivores, have such piercing teeth in the lower jaw and bladed teeth with finely serrate edges for cutting prey in the upper jaw (see above). Sharks and rays that feed on hard-shelled prey such as mollusks and large crustaceans have specialized, broad dentition for crushing (Fig. 12.11).

(A)

(B)

(C)

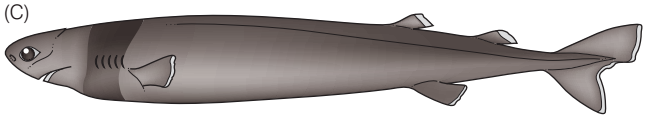

Figure 12.9

Cookie cutter sharks. (A) *Isistius brasiliensis*, the Cookie Cutter Shark, is a small (about 40 cm) tropical species that lives at mid-ocean depths and parasitizes tunas, other fishes, Megamouth Sharks, and marine mammals, gouging circular plugs of flesh out of their sides with its specialized dentition. (B) The congeneric Largetooth Cookie Cutter Shark, *I. plutodus*, has the largest teeth for its body size of any known shark. Its teeth are twice as large relative to body size as a Great White Shark's teeth. (C) Drawing of the Cookie Cutter Shark, *I. brasiliensis*. (A) photo by C. S. Johnson, from Springer and Gold (1989), used with permission of the Smithsonian Institution Press; (B) from Compagno (1981), used with kind permission from Kluwer Academic Publishers; (C) after P. Vecsei.

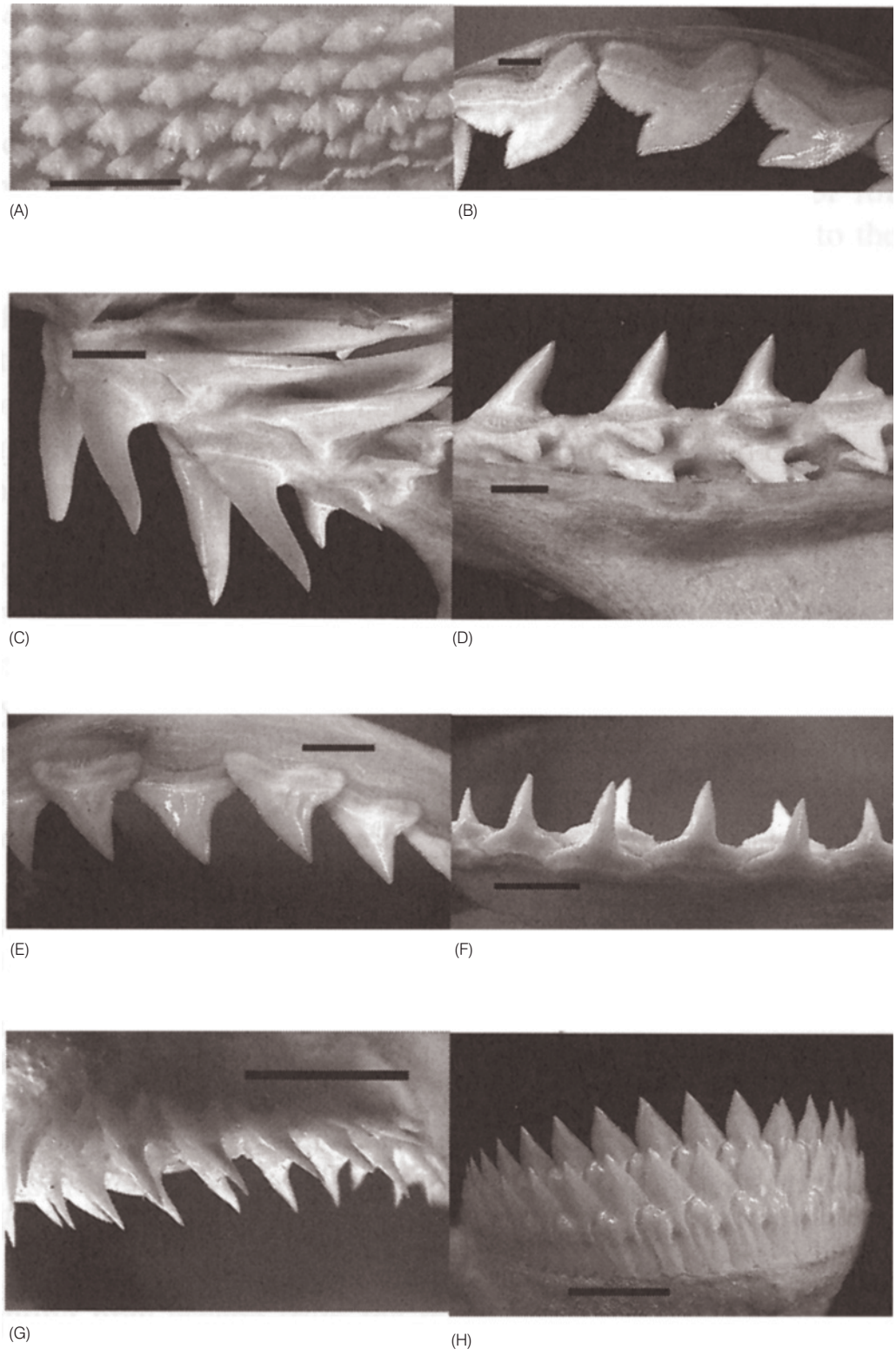

Figure 12.10

Representative tooth types of modern sharks: (A) Nurse Shark; (B) Tiger Shark; (C) Shortfin Mako, upper jaw; (D) Shortfin Mako, lower jaw; (E) Sandbar Shark, upper jaw; (F) Sandbar Shark, lower jaw; (G) Kitefin Shark, upper jaw; and (H) Kitefin Shark, lower jaw. All except the Nurse Shark feed largely on fish and squid; Nurse Sharks eat a variety of reef invertebrates such as lobsters. Black bars are 1 cm. From Motta (2004), used with permission.

(A)

(B)

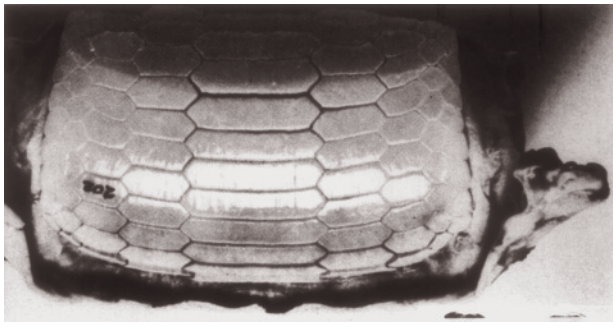

Figure 12.11

Pavement or molariform, crushing teeth characterize sharks and rays that feed on hard-bodied prey. (A) Lower jaw of the Horn Shark, *Heterodontus francisci* (Heterodontidae); the anterior teeth grasp and the posterior teeth crush prey. (B) Lower jaw dentition of a Cownose Ray, *Rhinoptera bonasus*, a predator on clams. (A) from Motta (2004), used with permission; (B) from Case (1973), used with permission.

(Bamboo Sharks can feed on hard-bodied prey with sharp teeth by bending the teeth backwards such that the anterior surfaces crush rather than pierce the prey, see Chapter 8, Dentition.)

Whereas most sharks engage only the anterior, peripheral row or rows of teeth while feeding, in mollusk feeders most of the posterior rows participate in the crushing action. Filter-feeding sharks typically have greatly reduced teeth that may function minimally during feeding; they instead use their gill rakers to trap small prey. In bony fishes, teeth are attached directly to the bone of the jaws, whereas in sharks the teeth are embedded in the connective tissue. Sharks have teeth only on their jaw margins, not attached to other bones and structures in the mouth, as in bony fishes. Shark teeth are basically enlarged scales, derived embryologically from the same tissues as the dermal denticles.

Dentition **replacement** is characteristic of all sharks, although detailed information on patterns of replacement is limited to a few species. Some sharks, such as White Sharks and hammerheads, replace teeth individually as they are worn out or lost. In contrast, Spiny Dogfish, Greenland, and Cookie Cutter sharks apparently replace entire rows. Replacement occurs regardless of use; nonfunctional teeth in interior rows continue to grow and move forward, eventually displacing or replacing functional teeth. Teeth also grow as the shark grows and hence teeth in the most internal, nonfunctional rows are larger than the functional teeth about to be replaced. Turnover rates have been calculated for a few species in captivity. Lemon Sharks replace a functional tooth about every 8–10 days, Sand Tigers every 2 days, Leopard Sharks every 9–12 days, Nurse Sharks every 9–28 days, and Horn Sharks every 28 days (Motta 2004). Given these numbers, it has been estimated that a shark may produce on the order of 30,000 teeth during its lifetime (Moss 1967; Springer & Gold 1989; Overstrom 1991).

Some sharks use structures other than jaw teeth to capture prey. Thresher sharks possess a long, scythelike upper caudal lobe. Threshers herd fish into tight schools by circling and splashing with the tail, then stunning prey with quick whips of the tail. Evidence that thresher sharks use their tails in prey capture comes from observations of many threshers caught by the tail on baited hooks (Compagno 1984).

Two unrelated families of elasmobranchs have evolved armed rostral regions used in prey acquisition. Pristid **sawfishes** (Rajiformes) and pristiophorid **sawsharks** (Pristiophoriformes) both possess bladelike snouts armed with lateral teeth (modified denticles) which they slash laterally to stun and disable prey. The lateral projections of the rostral cartilage of hammerhead sharks have long intrigued anatomists. Recent observations by divers indicate that hammerheads, which tend to specialize on stingrays, may use the hammer to pin their stingray prey to the bottom while taking bites from the margins of the stingray's disk (Strong et al. 1990; see Box 19.1).

A spectacular non-oral prey capture device is evident in the strong electric discharges of torpedo rays (Torpedinidae). These batoids possess modified hyoid and branchial musculature capable of emitting electric discharges of up to 50 volts and 50 amps, producing an output approaching 1 kW. Although electric discharges can occur when the

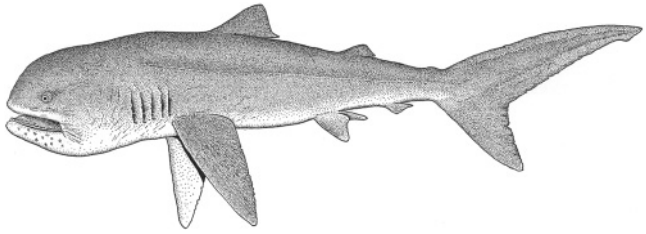

Figure 12.12
The Megamouth Shark, *Megachasma pelagios*. This 4–5 m long zooplanktivore was first captured in 1976, northeast of Hawaii (Taylor et al. 1983). It became entangled at a depth of 160 m in a parachutelike sea anchor of a naval research vessel over much deeper water. As of July 2008, only 40 individuals were known, mostly from tropical and subtropical regions (www.flmnh.ufl.edu/fish/Sharks/Megamouth/mega.htm). Drawing by P. Vecsei.

torpedo is disturbed and hence may serve as a predator deterrent, the more interesting function appears to be in prey capture. Torpedos will lie on the bottom and ambush prey during the daytime, but at night they swim or drift slowly in the water column. Upon encountering a potential prey fish, they envelope it with their pectoral fins and emit pulsed electric outputs that are modified in terms of rate and duration in response to prey reaction. The stunned, immobilized prey fish is then pushed towards the torpedo's mouth via water currents produced by undulations of the pectoral disk (Bray & Hixon 1978; Fox et al. 1985; Lowe et al. 1994). Torpedos differ from most other batoids in that they possess a well-developed caudal fin that is used during locomotion. Most batoids use their pectoral fins for locomotion, but this anatomical region has been usurped for electric organ function in torpediniforms.

Filter feeding occurs in four different groups of sharks and rays and in each has taken a slightly different evolutionary route. The Megamouth Shark, *Megachasma pelagios* (Megachasmidae), is the most spectacular shark species discovered in the 20th century (Fig. 12.12). Megamouth Sharks feed on euphausiid krill, jellyfish, and small schooling fishes. Megamouth cartilage is poorly calcified and body musculature is relatively soft, suggesting a sluggish filter feeder with a terminal mouth. Prey are ingested via suction and then captured on dense gill raker papillae (Compagno 1990c; Yano et al. 1997).

Manta rays, which can be over 6 m wide, filter feed via **ram feeding**, which involves swimming with the mouth open. Small crustaceans and fishes are additionally guided into the pharynx with the **cephalic horns** and the prey are then caught on pharyngeal filter ridges. The cephalic horns are anterior subdivisions of the pectoral fins, making manta rays the only extant vertebrates with three functioning pairs of limbs. Whale Sharks use ram feeding while swimming and also a **suction/gulp-and-drain** mechanism when stationary to feed on plankton or small fish, which are filtered through cartilaginous rods (Compagno 1984, 1990c). Basking Sharks swim at a constant speed of about 1 m/s with their mouths open, using passive ram filtration that employs gill raker denticles and mucous to capture very small zooplankters. Basking Sharks were thought to shed raker denticles, cease feeding, and enter a torpid state when zooplankton abundances declined in winter. However, recent behavioral observations, plankton density measurements, tracking with archival tags, and energetics calculations indicate that most retain their denticles, can feed well into the winter, and migrate to regions of high plankton productivity during colder months and continue feeding (Sims 1999; Sims et al. 2003).

Although sharks swim actively throughout the diel cycle and will capitalize on opportunities to feed at any time, available data indicate that the primary foraging times of most species are during twilight and nighttime. Such crepuscular/nocturnal foraging has been confirmed by catch statistics and more recently by ultrasonic telemetry and direct observation. Catches of sharks on baited hooks are greater by night than by day. Activity cycle data from telemetered Lemon Sharks indicate a doubling of swimming speed during twilight as compared to daytime or nighttime speeds (Sundstrom et al. 2001). Increased nocturnal swimming has also been found in Gray Reef, Blue, Scalloped Hammerhead, Horn, angel, and Swell sharks, as well as torpedo rays (Myrberg & Nelson 1991). In contrast, the White Shark is primarily a diurnal feeder, at least where its major prey is diurnally active marine mammals (Klimley et al. 1992; Klimley 1993).

Sensory physiology

As most sharks are primarily nocturnal foragers, it is not surprising that non-visual senses are particularly well developed. **Olfactory sensitivity** has long been recognized as extreme in sharks. Fish extracts can be detected by Lemon Sharks at levels as low as 1 part per 25 million parts sea water, and in Blacktip and Gray Reef sharks at 1 part per 10 billion, equivalent to about one drop dispersed in an Olympic-sized swimming pool (50 m × 25 m × 2 m deep). This sensitivity, which is greatest to proteins, amino acids, and amines, is achieved at several levels of operation. Water flows into the shark's nasal sacs located under the front of the snout, perfusing the underlying, large olfactory organs. Receptor cells in the organs receive stimuli which are then transmitted via the olfactory nerve to the olfactory bulb and lobes of the forebrain for integration. Olfactory lobes/bulbs in the shark brain are greatly enlarged.

Using this sensitivity, sharks are exceptionally adept at following odor trails in the water, even without currents to guide them upstream to an odor source (Montgomery 1988). Odor localization may be accomplished by comparing the intensity of stimulation in either chamber. This scenario suggests another possible function of the expanded rostral cartilage of hammerhead sharks. Lateral displace-

ment of the nostrils on the margins of the hammer might provide improved stereo-olfaction, making odor localization easier. Olfaction also plays a role in breeding, as evidence exists that sexual behavior is mediated by chemical sexual attractants (pheromones) produced by females (Hueter & Gilbert 1991).

Contrary to conventional wisdom, sharks have good vision. As a group, sharks tend to be slightly myopic (far-sighted). The shark retina is dominated by rods, as would be expected of fishes that are chiefly active at night and twilight. Nocturnal sensitivity is enhanced by an additional layer of reflective guanine platelets behind the retina, called the **tapetum lucidum**. The tapetum reflects light back through the eye (hence the "eye shine" of sharks and other nocturnal animals), which allows light entering the eye to strike the retinal sensory cells twice, increasing the likelihood of detection. Platelets are angled such that reflected light passes through the same receptors as incoming light, thus preserving acuity.

Sharks also typically have low densities of cone cells in their retinae, which generally increase daytime acuity and are associated with **hue discrimination** (color vision). Color vision has been demonstrated in Lemon Sharks. Sharks differ from most other fishes, and are more similar to mammals, in that they possess a **pupillary response** to changing light levels, which means they can regulate the amount of light entering their eyes. In many batoids, an additional eyelid-like structure called the **operculum pupillare** expands under bright light conditions to shade the eye and perhaps increase responsiveness to movement.

Acoustic sensitivity and **sound localization** capabilities are also greatly developed in sharks. Sharks hear sounds below 600 Hz (the fundamental of E below high C on a piano), including infrasonic sound below 10 Hz. Hearing is centered in three chambers within the inner ear that contain the **maculae** (sing. = macula). The maculae contain specialized nerve cells that are linked to small granules of calcium carbonate that vibrate in response to sound stimuli. The chambers are connected to the environment via two small pores, the endolymphatic ducts, on the top of the shark's head. A fourth macula, the **macula neglecta**, is located below an opening in the skull. The three major maculae are apparently involved in detecting low-frequency pulsed sounds, whereas the macula neglecta may provide information on the direction of the sound (Hueter & Gilbert 1991; Myrberg & Nelson 1991).

In addition to sensing vibratory cues in the surrounding medium (sound), sharks are also sensitive to minor variations in water displacement. This "**distant touch**" **sensitivity** is accomplished via mechanoreceptors distributed both along canals such as the lateral line and as independent "pit organs" scattered about the body. Distant touch sensitivity also has a directional component, suggesting that as a shark moves through the water, it can detect the presence, location, direction of movement, and relative speed of moving objects that displace water, or of stationary objects that reflect water moving off the body of the shark.

Sharks have an additional channel for sensory input that is anatomically and developmentally related to distant touch and hearing, namely **electroreception** (Collin & Whitehead 2004) (see Chapter 6). Input for electroreception begins at numerous small pores spaced precisely on the shark's head, snout, and mouth. The pores lead to conductive, jelly-filled canals that terminate in ampullary receptor cells termed **ampullae of Lorenzini** (not Alloplurus of Lixiniri, as was once suggested on an ichthyology exam). The receptor cells, which are anatomically similar to hair cells of the lateral line, fire in response to weak electric fields, sending afferent fibers via the lateral line nerve to regions in both the mesencephalon and telencephalon of the brain. The function of the ampullae, which are an obvious external feature on most sharks, remained a substantial mystery prior to the discovery of electroreceptive capabilities in sharks.

Sensitivity to weak electric fields is an ancestral trait in bony fish lineages that was lost and then re-evolved in neopterygians (see Chapter 6, Electroreception). Elasmobranchs as a group have retained and fine-tuned their electrical sensitivity to a level apparently unequaled by any other animal group. Many biological activities have as an integral component the generation of weak electricity. Most notable are muscular contraction, such as heart function and breathing, nerve conduction, and the voltage created by ionic differences between protoplasm and water. A resting flatfish (Pleuronectiformes) creates a low-frequency direct current bioelectric field with a strength of more than 0.01 μV/cm (1/100th of a microvolt) measured 25 cm away.

Experiments have shown that predatory sharks use weak electrical cues, and ignore strong olfactory cues, to home in on prey. The electrical sensitivity of large sharks is truly amazing. Human sensitivity is on the order of 0.1 volt. Sharks have demonstrated **detection thresholds** of 1×10^{-9} V/cm, or 1 billionth of a volt, approximately 10 times more sensitive than the 0.01 μV output from prey. Such sensitivity would be sufficient to detect the electric output of a standard D-cell flashlight battery several kilometers away (assuming no background geomagnetic interference), or the bioelectric output of a human 1–2 m away.

Sharks are sufficiently electrosensitive that, theoretically, they can detect the earth's magnetic field and currents induced by their swimming through that field. Sharks could therefore determine their compass headings during transoceanic migrations. This idea has yet to be confirmed, although stingrays in the lab can learn to orient in uniform direct current fields weaker than the earth's field. In learning trials, stingrays also reverse the location where they search for food when the electric field around them is artificially reversed, suggesting that geomagnetic cues can be used in normal daily activities (Kalmijn 1978). **Magnetite**

in the inner ear has been implicated as a component of geomagnetic orientation (Vilches-Troya et al. 1984).

It has been noted that the ampullary electroreceptors are geometrically centered around the mouth of many elasmobranchs. This positioning could allow a shark or ray to home precisely on a potential food source solely by electroreception, effectively aligning the food in the "sights" of its receptor field and then engulfing the prey. In this way, sharks can detect prey buried in the sand or sit motionless in the dark and snap up prey that swim nearby (Kalmijn 1982; Tricas 1982).

Extreme sensitivity to environmental stimuli is of no use to an animal unless the information can be collected, processed, and acted upon. Such **integration** is the role of the central nervous system, particularly the brain. Not surprisingly, the ratio of brain to body weight in sharks is greater than for most bony fishes, except perhaps the electrogenic elephantfishes (Mormyridae; see Chapter 14). The ratio of brain to body weight in sharks is actually more comparable to that of "higher animals" such as some birds and marsupials (Fig. 12.13A). Within feeding types and habitat zones, many sharks have larger brains than ecologically comparable bony fishes such as pelagic, predatory billfishes and tunas, which in fact have relatively large brains relative to other teleosts (Lisney & Collin 2006) (Fig. 12.13B). Requiem and Mackerel sharks have large forebrains and complex cerebellums; eagle rays and other stingrays have the most complex brains (Northcutt 1977).

Reproduction and development

A few generalizations can be made about shark reproduction (Carrier et al. 2004; Musick & Ellis 2005). Ages at

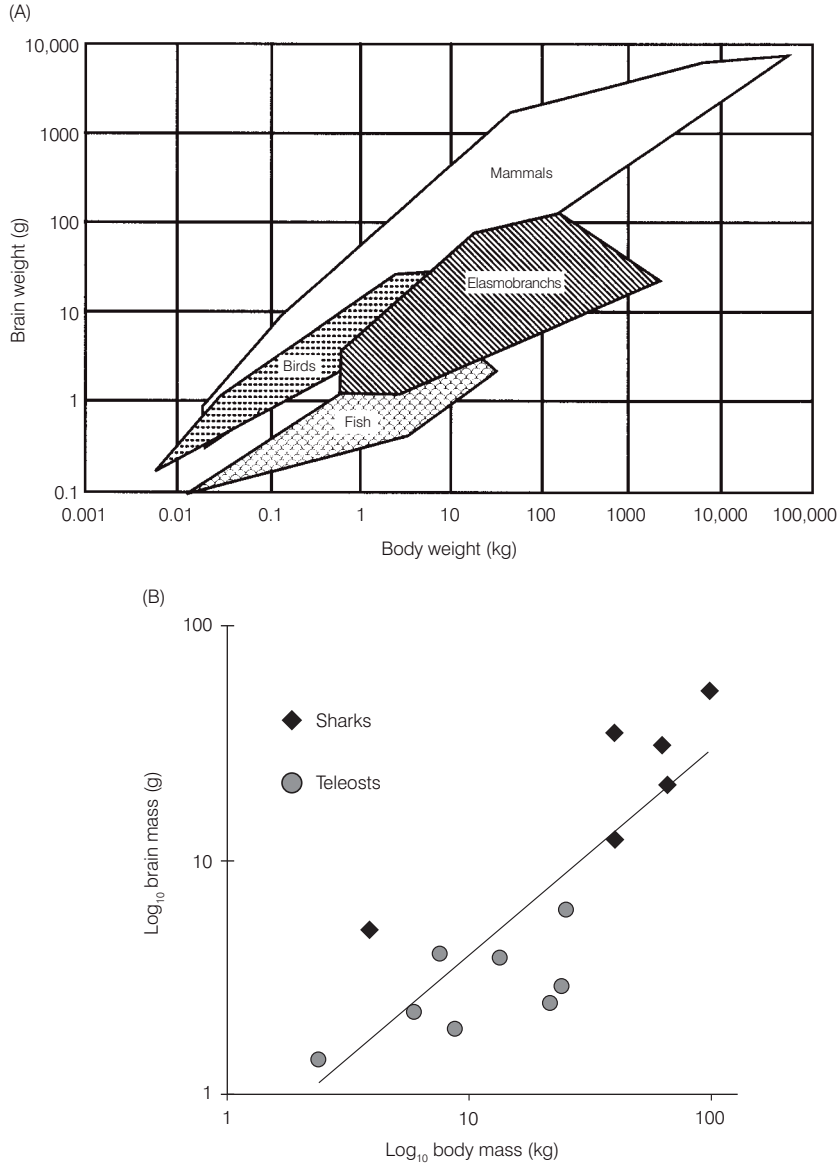

Figure 12.13

Brain size in sharks. (A) Sharks have relatively large brains for their body size, overlapping in this respect with birds and mammals as much as with bony fishes. (B) Among pelagic, predatory fishes, many sharks have relatively large brains for their body mass. (A) from Springer and Gold (1989), based on Northcutt (1977) and Moss (1984), used with permission; (B) after Lisney and Collin (2006).

maturation vary widely among shark species but are typically older than for most teleosts. Most sharks mature in 6–l8 years, although much greater ages are not uncommon. For example, Lemon Sharks (*Negaprion brevirostris*) in south Florida mature at an average of 24 years, and Spiny Dogfish (*Squalus acanthias*) in British Columbia mature at an average age of 35 years (Saunders & McFarlane 1993). Longer lived species tend to mature at greater ages: sawfishes at 10 years old, Angel Sharks and Common Skates at 11 years old, Nurse and Whale Sharks at 16–25 years, and some dog sharks at 30 and 45 years (Cailliet & Goldman 2004).

Sharks produce relatively few, large young with a long gestation period. Newborns are small replicas of the adults; no larval stage exists. No parental care is given after egg laying or birth, with the possible exception of a bullhead shark (Heterodontidae) in which the female picks up her recently laid eggs in her mouth and wedges them in crevices in rocks or plants.

Fertilization in all sharks is internal, and has been throughout the known evolutionary history of the class. Male sharks possess intromittent organs in the form of modified pelvic fins termed myxopterygia or **claspers** (the term "claspers" apparently arose from Aristotle's misconception that the structures were used to hold the female, rather than to inseminate her). Females of some species can store sperm in the shell gland for years. Maternal–embryo relationships in advanced sharks rival that in mammals, contrasting sharply with the simpler reproductive features of most bony fishes (see Chapter 21, Parental care).

Although fertilization is internal, postfertilization development and embryonic nutrition vary among taxonomic groups (Wourms et al. 1988; Compagno 1990b; Pratt & Castro 1991; Wourms & Demski 1993a; Musick & Ellis 2005). The major contrasts involve whether young develop internally or externally and whether and how the mother provides nutrition for the growing embryo (Table 12.1). The ancestral condition in chondrichthyans, and the most common condition among extant species, is **viviparity**, or live-bearing (Musick & Ellis 2005). In about half of live-bearing species, the developing embryo is retained in the uterus and nourished with yolk provided by a yolk sac that is attached directly to the digestive system of the embryo (termed variously **yolk sac**, **lecithotrophic**, or **aplacental viviparity**, and also **ovoviviparity**).

Some viviparous sharks have evolved an additional form of nourishment. After about 3 months, yolk reserves are exhausted and the young then feed directly on eggs ovulated by the female (**oophagy**). Oophagous sharks include Threshers, Whites, Makos, and Sand Tigers. Sand Tigers have carried this one step further. The first embryo to consume its yolk then turns on its siblings and eats them (**embryophagy**) before assuming an oophagous existence (Gilmore et al. 1983; Gilmore 1991). At birth, Sand Tiger litters are composed of two large (1 m long) young, one in each uterus.

The most complex developmental pattern, **placental viviparity**, characterizes advanced members of the most diverse modern family of sharks, the Carcharhinidae, as well as the closely related hammerheads (Sphyrnidae). Yolk is consumed and then the spent yolk sac attaches to the uterine wall to form a **yolk-sac placenta**. In a construction strongly analogous to the mammalian condition (although involving different embryonic tissues), the stalk of the yolk sac, which is attached to the embryo between the pectoral fins, forms an umbilical cord that transports nutrients and oxygen to the embryo and carries metabolic wastes to the mother. In some sharks, such as the Sharpnose and hammerheads, the umbilical cord diversifies further and develops **appendicula** or outgrowths that serve as additional sites for exchange of materials, including uptake of nutrients in histotroph or "uterine milk" secreted by special cells in the wall of the uterus (Fig. 12.14). Uterine milk may be absorbed through the skin and mouth and also via modified gill filaments that exit from the spiracle and gill slits of the developing embryo. In the myliobatoid stingrays and manta rays, nourishment is solely via ingestion of uterine milk without a placental connection (**uterine viviparity**).

Clutch sizes in viviparous sharks range from two (Sand Tigers, threshers, Longfin Mako) to as many as 70–135 (Tiger and Blue Sharks), with an average of around 8–10 (Branstetter 1990). Whale Sharks, once thought to be oviparous, have been found with as many as 300 embryos inside, making that species the most fecund shark known. A gravid female may contain smaller embryos still in their egg cases, whereas larger individuals are free-living.

Table 12.1

A summary of embryonic development and nutrition in chondrichthyans. From Nelson (2006), after Musick and Ellis (2005).

I All nutrition from yolk sac
- A. Yolk sac viviparity (= lecithotrophic viviparity, ovoviparity): all living orders except heterodontiforms, lamniforms, and rajiforms
- B. Yolk sac oviparity (= lecithotrophic oviparity): all living holocephalans, all heterodontiforms, and all Rajidae

II Some nutrition from mother (= matrotrophy)
- A. Nutrition from uterine secretions (= histotrophy): many squaliforms and carchariniforms, and all myliobatiforms
- B. Nutrition from eating unfertilized eggs (= oophagy): all lamniforms and some carchariniforms (includes embryophagy of *Carcharias taurus*) and pseudotriakids

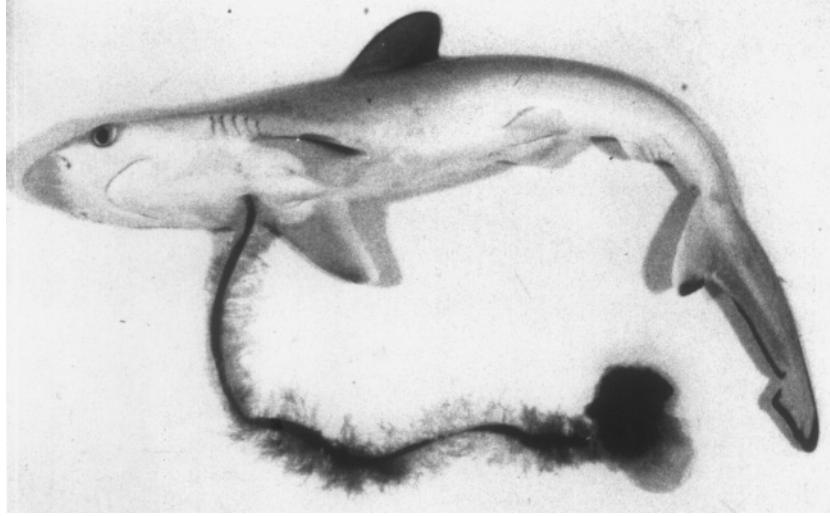

Figure 12.14
Placental viviparity in advanced sharks. A newborn Atlantic Sharpnose Shark (Carcharhinidae) showing the umbilical cord with outgrowths ("appendicula") for nutrient uptake. The cord terminates in a placenta that attaches to the uterine wall of the mother. Photo by W. Hamlett, from Hamlett (1991), used with permission.

Whale Shark pups are born at around 60 cm long (Joung et al. 1996).

Gestation periods in sharks average 9–12 months, but may be as short as 3 or 4 months (Bonnethead) or as long as 2 years (Spiny Dogfish) to perhaps 3.5 years (Basking Shark, Frilled Shark *Chlamydoselachus anguineus*). Production of young apparently exacts a large energy cost on females, which appear emaciated at the end of the gestation period. Females of many species reproduce only in alternate years, suggesting it takes at least a year for the female to recover from her last clutch. Such long **reproductive intervals** slow the potential rate at which shark populations can grow and thus recover from exploitation (see below, Shark conservation).

Certain accommodations must be made in live-bearing sharks to facilitate the passage of relatively large young through the birth canal. The expanded lateral lobes of the cranium of hammerhead sharks are soft and pliable at birth and then stiffen shortly after. Spines on embryonic Spiny Dogfish are covered with pads of tissue until after the young are born. The saw of fetal sawfish is at first soft and contained in a rubbery envelope to protect both the rostrum and the mother during gestation and birth.

The alternative condition is egg-laying (**oviparity**), with the embryo deriving all nutrition from its large yolk reserves. About 40% of living elasmobranchs are oviparous, including bullhead sharks (Heterodontiformes), many nurse sharks (Orectolobiformes), as well as all skates (Rajiformes). Clutch sizes among oviparous sharks and batoids both average about 60 eggs per year (Musick & Ellis 2005). Unlike bony fish eggs, shark and skate egg cases, termed **mermaid purses**, are large (2–4 cm) and are protected by a tough, keratinoid (horny) shell secreted by a maternal nidamental or shell gland. The egg case, which contains a single embryo, is attached to seaweeds or other structures and the embryo develops for a relatively long period (several weeks to 15 months) and emerges at a relatively large size.

The protective nature of mermaid purses is attested to by instances of their being transported in air for several days and still hatching out healthy young (Lagler et al. 1977). However, mermaid's purses are not free from predation. They have been found in the stomachs of other sharks, flatfishes, and elephant seals, and are actively preyed upon by boring gastropod mollusks such as whelks (Cox & Koob 1993). A small number of sharks in these orders retain the encased eggs in the oviduct before laying them (termed **retained oviparity**). Clutch size in oviparous sharks is difficult to assess because females may lay two eggs at a time repeatedly over several months (Lineaweaver & Backus 1970).

Regardless of maternal–embryo relationships, courtship and copulation commonly involves the male holding the female in his teeth while the claspers are inserted (Pratt & Carrier 2001). This pattern has been observed in a half dozen sharks and an equal number of batoids and is inferred from bite marks in many others. Bite scars are common on the pectoral fins and flanks of adult females but appear to do little actual damage because the skin of females is typically much thicker than that of males. In Blue Sharks, the female's skin is three times as thick as the male's and, more importantly, thicker than the male's teeth are long (Fig. 12.15). In some ray species, males develop more pointed dentition upon maturation and during the mating season. Males may also use their electrosensory system to detect responsive females, as has been shown in the Round Stingray *Urolophus halleri* (Tricas et al. 1995).

Shark conservation

Shark populations globally have decreased 50–80% since the 1970s. Steepest declines occurred in the late 1980s, when international fishing accelerated, in no small part because of increased demand for fins (Rose 1996) (Box 12.2). In the Gulf of Mexico and northwest Atlantic, both already heavily overfished, additional declines occurred between 1985 and 2000 (Baum et al. 2003; Baum & Myers 2004): Silky Sharks

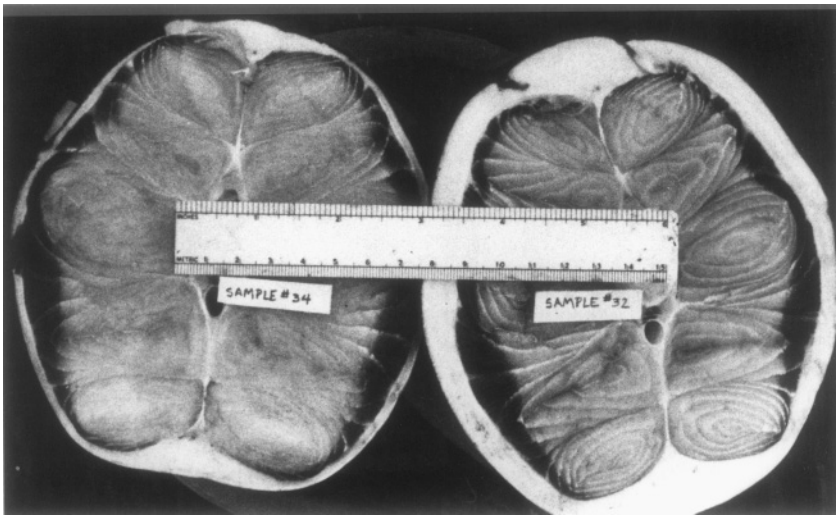

Figure 12.15
Sexual dimorphism in the skin thickness of sharks. On the left is a cross-section through a male Blue Shark, on the right a female. Female sharks often have thicker skin than males, probably because during mating males typically bite and hold females. Photo by H. W. Pratt, from Pratt and Carrier (2001), used with permission.

declined 90%, hammerheads were reduced another 89%, thresher sharks 80%, White Sharks 79% (>6000 captured!), Oceanic Whitetips 70–99%, Tiger Sharks 65%, the coastal species complex 61% (range 49–83%), and Blue Sharks 60%. Only mako sharks suffered losses of less than 50%. Although disagreement exists on the exact magnitude of the declines (e.g., Baum et al. 2005; Burgess et al. 2005), it is generally accepted that these numbers are likely representative of trends in other oceans, indicating that, ". . . overfishing is threatening large coastal and oceanic sharks . . . [and] several sharks may also now be at risk of large-scale extirpation" (Baum et al. 2003, p. 390).

Many of the life history features of sharks explain this **vulnerability to exploitation**. As apex predators, sharks seldom occur in the large numbers that characterize more resilient fish species (e.g., herrings and mackerels feed much closer to the base of the marine food chain). Importantly, sharks replace themselves slowly. Slow growth and maturation rates, long gestation periods, long intervals between reproductive bouts, and relatively small clutch sizes suggest that shark species have evolved in circumstances where juvenile mortality is typically low compared to the much more prolific bony fishes on which sharks feed. Under natural circumstances, sharks have few predators aside from other sharks, and most of these can be avoided by attaining large size. The unfortunate outcome of this particular life history strategy is that shark populations are not capable of overcoming the high mortality rates imposed by commercial exploitation.

Sharks are exploited for meat, skin, teeth (White Shark jaws can sell for as much as US$10,000; Heneman & Glazer 1996), organs for medicine (fallaciously), and fins for soup (reprehensibly) (see Box 12.2). The history of commercial shark fishing is a history of collapsed fisheries. Examples include fisheries for Thresher Sharks in California, School Sharks in Australia, Spiny Dogfish in the North Atlantic, Porbeagles off Newfoundland, Basking Sharks off Ireland, Bull Sharks and sawfish in Lake Nicaragua, and Soupfin Sharks off the US Pacific coast.

Two examples typify the boom and bust pattern that characterizes commercial exploitation of shark populations. The Porbeagle (*Lamna nasus*) fishery of the western North Atlantic has been well documented. The fishery was wiped out in only 7 years. In 1961, uncontrolled exploitation began and about 3,500,000 pounds (1,575,000 kg) were caught. Catch peaked only 3 years later at 16 million pounds, then crashed. By 1968, only a few hundred sharks could be found. Twenty years later, populations had not returned to pre-exploitation levels (Campana et al. 2002).

Before 1937, about 600,000 pounds or 6000 individual Soupfin Sharks, *Galeorhinus zyopterus*, were landed annually in California. With the development of a market for shark liver oil, this fishery expanded rapidly to 9,000,000 pounds (90,000 fish) in 1939, fell to 5,000,000 pounds in 1941, and by 1944 was back to 600,000 pounds, despite continued intensive effort. Importantly, catch rates fell from 60 sharks per set in 1939 to one shark per set in 1944, indicating a significant decline in the population. Thirty years later, populations had still not returned to pre-1939 levels (Moss 1984; Anderson 1990; Manire & Gruber 1991).

Most shark populations cannot withstand a fishing mortality even as low as 5% removal of the existing population each year (Pratt & Castro 1991). The estimated US maximum sustainable yield (MSY) of sharks has been estimated at 16,250 metric tons, but total mortality exceeds the MSY by nearly 6000 metric tons annually. Between 1986 and 1990, commercial shark landings doubled every year in the USA. All indicators suggest that North American shark populations are in decline and that management plans, including a moratorium on the capture of some species, are desperately needed.

Box 12.2

Of fins and vertebrae: wasting sharks

The recent and dramatic increase in buying power among Asian nations, especially in China, has created and fed a high demand for shark fins (Rose 1996, 1998; Fong & Anderson 2002). Fins are dried and then the ceratotrichia are processed for soup production. Shark meat may bring only US$1.10–1.30/kg to the fisher, and steaks and fillets can run to $7.70–22.00/kg depending on the species. But shark fins have become one of the world's most valuable fishery products, worth $55/kg wet, and when processed and sold in Asia, as much as $1650/kg. A bowl of shark fin soup may sell for as much as $150 (Rose 1996; Vannuccini 1999). Hong Kong imported 7800 metric tons of shark fins in 1996, estimated to be worth $250 million. In that year, the US shark fishery for sharks other than dogfish similarly weighed 7000 metric tons but was worth only $10 million (Branstetter 1999; Kuang 1999).

The different values of meat versus fins explains the practice of **finning**. The fins are cut off a live shark – now referred to as a "log" – the log is tossed overboard, where it sinks to the bottom to starve while being slowly eaten by crabs and small fishes. Processing and storing shark meat is time- and space-consuming. Fins in contrast can be removed quickly and take up minimal room. The fins are sold and resold, processed, and eventually used for shark fin soup, which in Hong Kong is expected on the menu for special occasions such as weddings (Kuang 1999). Ironically, shark fin soup often contains very little actual shark product. The fin material is often used primarily as a thickener, with most of the soup flavor coming from chicken or other meat stock. Or the fin parts may be filtered out of the soup and the solid fin parts discarded.

Besides fins and meat, commercial shark products have included cartilage as a cancer cure. Because sharks are reportedly immune to cancer, it was thought that shark cartilage could prevent cancers in humans. Sharks actually do get cancer, including carcinomas of cartilage (Borucinska et al. 2004; Ostrander et al. 2004; G. K. Ostrander, pers. comm.). That inconvenient truth – and US Food and Drug Administration and Federal Trade Commission injunctions against companies making anticancer claims for shark cartilage – have not deterred unscrupulous individuals from capitalizing on the need for a cancer cure (Barrett 2000). Shark cartilage powder has sold for as much as $145/g (Vannuccini 1999), and a single plant in Costa Rica alone processed 235,000 sharks/month to make cartilage pills (Camhi 1996).

The link between shark cartilage and cancers is that cancers grow because of increased blood supply, and processed cartilage can inhibit blood vessel proliferation (e.g., Berbari et al. 1999; Cho & Kim 2002). However, clinical trials have shown no significant pharmacological effect of cartilage pills on cancerous cells themselves, leading to "unsatisfactory patient outcome[s]" (Gonzalez et al. 2001). Regardless, sharks are still processed for their cartilage, and "Super-Potency" 750 and 800 mg capsules were still being sold via the internet in 2009 (e.g., www.iherb.com, www.doctorstrust.com).

Sharks do produce anticancer drugs that are effective in treating lung and ovarian cancers. The active substance is the aminosterol **squalamine**. It is not cartilage-derived but comes from shark liver, stomach, and gall bladder. Squalamine is patented, is produced by reputable drug manufacturers, and most importantly, is synthesized. There is no need to kill sharks to obtain squalamine (Bhargava et al. 2001; Zhang et al. 2003a; see www.nu-gen.com). Sharks are a real and potential source of useful drugs, thus further justifying their conservation.

The repeated scenario of large initial catches, rapid decline, and slow if any recovery highlight the need for careful management of all exploited shark stocks. Interestingly, sharks exhibit a remarkably close relationship between **stock size and recruitment**. Fisheries managers can predict future recruitment into populations based on existing reproductive stocks. This degree of predictability characterizes few other commercial species. The unfortunate fact is that shark fishing remains one of the least regulated commercial fishing activities. Management plans have been proposed but not implemented in many countries. The USA did not put a management plan into effect until 1993, and those regulations proved insufficient and had to be tightened further in 1997 (Poffenberger 1999). But even with implementation, shark conservation is complicated by shark biology. Local management is not sufficient to protect shark populations because so many species undergo long distance movements through international waters. International efforts at conservation, which are historically difficult to negotiate, are crucial.

Against this backdrop of decline and mis- (or non-existent) management are efforts to conserve sharks, as well as economic ironies. The Shark Specialist Group of the IUCN assessed population status of about one-third of the world's sharks, skates, and rays. The IUCN assigned high-risk status to 86 species: 14 were Critically Endangered, 26 were Endangered (including Barndoor and Common skates), and 46 were Vulnerable (including Great White and Whale sharks) (see www.redlist.org). Such attention often leads to protective legislation at national and international levels. For example, in 2004, the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) listed Whale, Basking, and White sharks in Appendix II, regulating and restricting capture and trade in these species (see www.cites.org/eng/app/appendices.shtml).

Ironically, in many countries, including in the developing world where fishing provides an important livelihood for a large population segment, live sharks are worth considerably more than dead sharks. People are willing to spend money just to watch sharks, making **ecotourism-related shark viewing** a profitable diving activity. Whale Shark watching is popular in the Maldives, Western Australia, Philippines, and Mexico, and in many locales divers spend large sums to watch reef sharks, manta rays, and stingrays. A shark can be captured once but can be viewed many times. Individual sharks in the Bahamas may be worth US$750,000 alive but only $40–50 dead (S. Gruber, pers. comm., in Daves & Nammack 1998). An economic analysis for the Republic of Maldives indicated an impressive 100- to 1000-fold difference in value (Anderson & Waheed 2001). Shark watching is an imminently sustainable commercial activity; shark fishing is not.

For more information on shark conservation, see Gribble et al. (1998), Walker (1998), Musick (1999), Martin (2005), Helfman (2007), and websites listed at the end of this chapter. Also write your congressperson.

Subclass Holocephali

Class Chondrichthyes
- Subclass Holocephali[a]
  - Superorder Holocephalimorpha (six extinct orders and modern chimaeras)
    - Order Chimaeriformes (modern chimaeras) (33 species, marine): Callorhinchidae (plownose chimaeras), Rhinochimaeridae (longnose chimaeras), Chimaeridae (shortnose chimaeras or ratfishes)

[a] We follow Nelson (2006) here, but Grogan and Lund (2004) recognize the subclass as the Euchondrocephali, subdivided into the superorder Paraselachii (six extinct orders) and the subclass Holocephali, the latter containing six extinct orders and all modern forms.

Chimaeras

Although knowledge of holocephalan taxonomy has increased markedly in recent years, surprisingly little remains known about their general biology and natural history (for reviews see Didier 2005; http://clade.acnatsci.org/dagit). Most of the characters that define the elasmobranchs also describe the Holocephali, indicating a common albeit unknown ancestor. Chimaeras, also known as **ratfishes** or **rabbitfishes**, share with sharks a cartilaginous skeleton and male intromittent organs, a sutureless skull, ceratotrichial fins, and spiral valve intestine. Holocephalans similarly lack lungs and gas bladders, also using an oil-filled liver for buoyancy. Development is again direct, without a larval stage (Bigelow & Schroeder 1953a; Compagno 1990b).

In contrast to sharks in which the upper jaw has a ligamentous connection to the cranium (the **amphistylic** condition), chimaeras have upper jaws that are immovably attached to the braincase (the **holostylic** condition). The name Holocephali ("whole head") refers to this fusion of palatoquadrate and neurocranium in modern chimaeras. Teeth differ from those of sharks, being continually growing, crushing or cutting plates instead of replaceable dentition. Chimaeras have three pairs of hypermineralized toothplates, two vomerine and palatine toothplate pairs in the upper jaw and a large pair of mandibular toothplates on the bottom (hence the name rabbitfish). The anterior plates are bladelike, whereas the posterior plates are flattened for crushing hard-bodied foods.

As in bony fishes, a single gill flap covers four internal gill openings, rather than the five or more external gill slits of sharks. Chimaeras lack distinct vertebral centra and a spiracular gill opening (embryonic chimaeras have a spiracle). Instead of a cloaca, they possess separate anal and urogenital openings. Males have sharklike pelvic claspers that are extensions of the pelvic fins, through which sperm is transferred. Anterior to the pelvic girdle are prepelvic **tenaculae** contained in prepelvic pouches. Tenaculae consist of a single row of stout spines and are used to anchor the female during copulation. Males of some species also have an additional frontal tenaculum on the head that is used to grasp the posterior edge of the female's pectoral fin during copulation (Fig. 12.16). Chimaeras are oviparous, laying a few, 10 cm long eggs with horny shells similar to those of sharks (e.g., Moura et al. 2004); development may take 5–10 months prior to hatching.

Holocephalans lack scales except for small dermal denticles along the midline of the back and on the claspers of the males. The first dorsal fin, with its poison-laden spine, is erectable, not fixed. The body generally tapers posteriorly to a pointed tail, hence the alternative common name ratfish. Chimaeras locomote via a combination of body undulations and pectoral fin flapping.

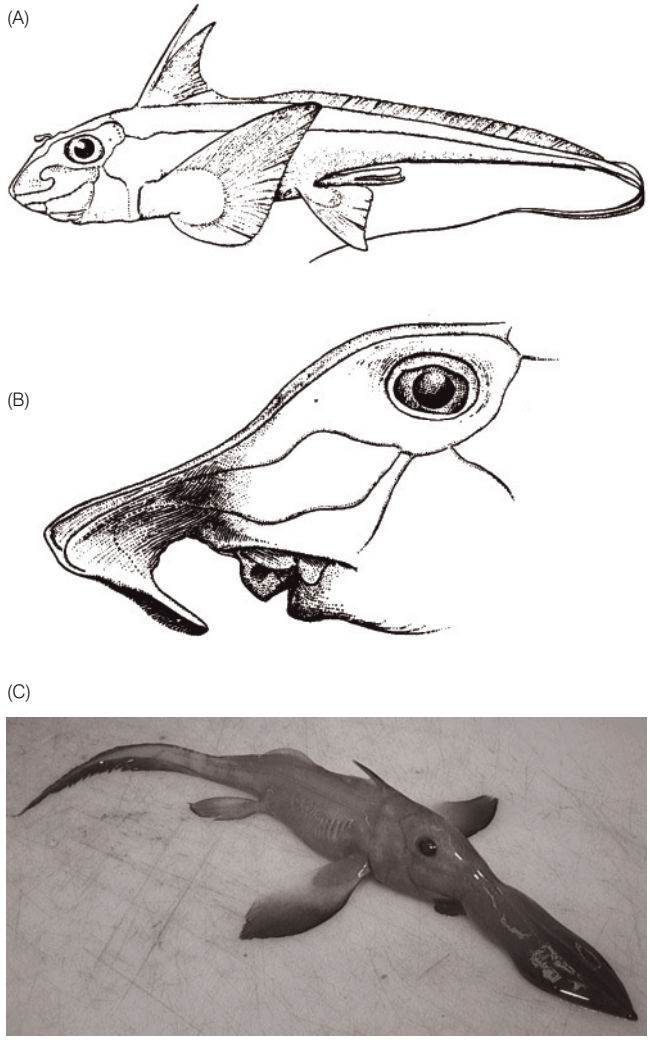

Figure 12.16

Modern holocephalans. (A) *Chimaera cubana*, a 50 cm long Caribbean chimaerid; note the pelvic claspers and also the frontal clasper or tenaculum on the forehead of the male. (B) Head of a callorhinchid chimaera, *Callorhinchus milii* (the Elephant Fish), showing the unique hoe-shaped proboscis. (C) A juvenile *Rhinochimaera pacifica*, the Pacific Spookfish, which grows to 1.5 m and could do anything with that fleshy snout. (A, B) from Bigelow and Schroeder (1953a), used with permission; (C) photographer unknown.

Six genera and 33 species of chimaeras are recognized, with perhaps another dozen species remaining to be named. Adult size ranges from 60 to 200 cm, with females often larger than males. Chimaeras are cool water, marine fishes. Although geographically widespread, low-latitude species occur in deeper water. As a group they are mostly found below 80 m to as much as 2600 m and are usually captured close to the bottom. In contrast to many bony fishes, younger chimaeras often occupy deeper water than adults, the latter partaking in seasonal, inshore migrations (Didier 2005). Chimaeroids feed mostly on hard-bodied benthic invertebrates, which they crush with their toothplates.

Extant holocephalan species represent a small fraction of a previously successful and diverse group (Lund 1990; Grogan & Lund 2004; see Chapter 11). Although only three families in a single order are alive today, 12 fossil orders, represented by perhaps 22 families, lived during Paleozoic and Mesozoic times. Several groups had more sharklike dentition, or dentition unlike any living or other extinct chondrichthyans. The modern families have fossil records dating back to the Jurassic and Cretaceous (Carroll 1988; Nelson 2006).

Summary

SUMMARY

1. The Chondrichthyes contain two living subclasses, the elasmobranchs (sharks and rays) and the holocephalans (chimaeras). Elasmobranchs are represented by one living infraclass, the Euselachii, which contains nine orders and 400 species of sharklike fishes in two superorders, and four orders and 530 species of skates and rays. Carchariniform requiem sharks and squaliform dogfish sharks are the most diverse shark orders, and rajiform skates and myliobatiform stingrays are the most diverse batoid orders.
2. Elasmobranch vertebrae consist of calcified cartilage. Teeth are replaced throughout life and are not fused to the jaws. The upper jaw is not fused to the braincase and the mouth is usually subterminal. Fin rays consist of horny ceratotrichia. Most elasmobranchs have five external gill slits. Fertilization is internal. In general, elasmobranchs are marine, mobile predators that grow slowly and have slow metabolism, rely on non-visual senses, produce small numbers of young, and are extremely vulnerable to commercial exploitation.
3. Sharks are relatively large, many exceeding 1 m in length. The largest sharks are the Whale Shark (>12 m), Basking Shark (9 m), and hammerhead, thresher, sleeper, and Tiger sharks (5–6 m). The largest verified White Shark was 6 m long and weighed 3300 kg. The extinct Megatooth Shark was 16 m long and weighed approximately 48,000 kg. Some deepwater Lantern Sharks are <20 cm long.
4. Most sharks live in shallow, marine habitats, and very few occupy depths beyond 3000 m. Two families of rays inhabit fresh water, and sawfishes and Bull Sharks frequently move into rivers, the latter occurring as far as 4000 km from the ocean. Elasmobranchs that inhabit fresh water osmoregulate to counteract influx of water and loss of salts.
5. Sharks are active predators with relatively large home ranges. Many coastal and oceanic species undertake migrations of 1000–16,000 km. Locomotion is very efficient. Placoid scales are shaped to minimize drag, and dorsal fins work in conjunction with the heterocercal tail and pectoral fins to maximize propulsion. The large, lipid-filled liver provides buoyancy. Sharks have slower metabolism and require less food for a given body weight than do bony fishes. White Sharks may only need to feed once every 6 weeks. Slow metabolism leads to slow growth and old age in many species.
6. Except for the largest sharks and manta rays, which are plankton feeders, most sharks use their protrusible jaws and sharp, often serrated teeth to dismember prey. Teeth are replaced every few days; a shark may produce 30,000 teeth during its life. Feeding specializations include suction feeding and molariform teeth for crushing mollusks (many rays), elongate tails or snouts for striking and incapacitating prey (thresher sharks, sawfishes, sawsharks), and muscles modified for electricity production to stun prey (torpedo rays).
7. Sharks have good vision, particularly at night. They are exceptionally sensitive to chemical stimuli, can localize sound, and can detect weak electrical or geomagnetic cues, which they use to localize prey and perhaps to navigate in the open ocean. Sharks have relatively large brains compared to bony fishes.
8. Sharks mature at a relatively old age, between 6 and 18 years, some much older. Fertilization is internal; some species lay eggs, whereas others gestate young internally. Gestation is long, and the young are small replicas of adults. No parental care is given after birth, but female investment during gestation is very high, particularly in those species with complex placental structures. Relatively few young are produced at a time.
9. Because of slow growth, slow maturation, and low fecundity, sharks are very susceptible to overfishing. Shark fisheries typically boom then quickly bust and do not recover, as exemplified by the Porbeagle fishery of the western North Atlantic and the Soupfin Shark fishery in California. North American shark populations are in decline and a general moratorium on the capture of many species is needed.
10. Holocephalans (chimaeras, ratfishes, rabbitfishes) include six genera and 33 species of cartilaginous fishes. They differ from sharks by having the upper jaw fused to the braincase, a single gill cover, separate anal and urogenital openings, and an erectable dorsal spine. They are entirely marine, inhabiting shallow to moderate depths. As in the sharks, holocephalans were much more diverse during the Paleozoic and Mesozoic than they are today.

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Chapter 13

Living representatives of primitive fishes

Chapter contents

CHAPTER CONTENTS

A small number of anatomically primitive and unusual fish species occur on all the earth's major continents, often in tropical or subtropical, swampy habitats. These fishes represent the last remaining representatives of groups that dominated aquatic environments during the Paleozoic and Mesozoic periods. The ancestry of several species can be easily traced to otherwise extinct groups, whereas other species are obviously highly derived, specialized fishes whose close affinities can only be surmised from anatomical similarities. These "living fossils" include some of the most spectacular and controversial ichthyological discoveries of the past two centuries and typify the dictum that every species is a mixture of ancestral and derived characteristics.

Jawless fishes: lancelets, hagfishes, and lampreys

Phylum Chordata
- Subphylum Cephalochordata
  - Order Amphioxiformes (lancelets) (30 species, marine, tropical and temperate): Branchiostomatidae, Epigonichthyidae
- Subphylum Craniata
  - Superclass Myxinomorphi
    - Class Myxini (living hagfishes) (about 70 species, temperate marine)
      - Order Myxiniformes: Myxinidae (hagfishes)
  - Infraphylum Vertebrata
    - Superclass Petromyzontomorphi
      - Class Petromyzontida
        - Order Petromyzontiformes (living lampreys) (38 species, temperate fresh water and anadromous): Petromyzontidae (northern lampreys), Geotriidae (southern lampreys), Mordaciidae (southern topeyed lampreys)

Amphioxiforms

It can be argued that lancelets are not fishes because they lack many diagnostic characters. However, cephalochordates – which are sometimes referred to as invertebrate

chordates along with urochordates and hemichordates – seldom receive treatment in invertebrate textbooks. Their evolutionary and anatomical affinities are much closer to the vertebrates (see Northcutt & Gans 1983; Gans et al. 1996), and lancelets are studied primarily by ichthyologists, providing justification for their inclusion in an ichthyology textbook.

Lancelets are small (up to 8 cm), slender organisms that as adults occupy sandy, usually shallow bottoms in all major oceans (Fig. 13.1). They commonly bury themselves in the sediments with just the anterior portion of the body protruding from the bottom. Lancelets filter diatoms and other small food items from the water via cilia that transport water through the mucus-laden mouth and pharynx and out through the **atriopore**. Food-trapping mucus is produced by the **endostyle**, a pharyngeal organ that also functions in iodine uptake and may therefore be homologous to the thyroid of higher vertebrates (Nelson 2006) (Box 13.1).

Spawning in most species occurs in early summer. Spawning adults swim up into the water column, the females following the males. Larvae metamorphose after 2–5 months. Larvae are free swimming, ciliated, planktonic animals that have the mouth and anus on the left side of the body. The mouth eventually moves to the middle, but the anus remains on the left side. Larvae can be very abundant at times, reaching densities of 1000/m^3 in regions of upwelling. The larvae settle on sandy or sandy-shell bottoms, mature in 2 or 3 years, and live as adults for 1–4 years depending on the species. Both larvae and some immature adults undergo diel vertical migrations, moving to surface waters at night (Bigelow & Perez Farfante 1948; Boschung & Shaw 1988).

Lancelets are intriguing in their lack of many typical chordate structures. They differ from conventional fishes by lacking most parts of a head (e.g., there is no cranium, brain, complex eyes, external nostrils, or ears); hence they

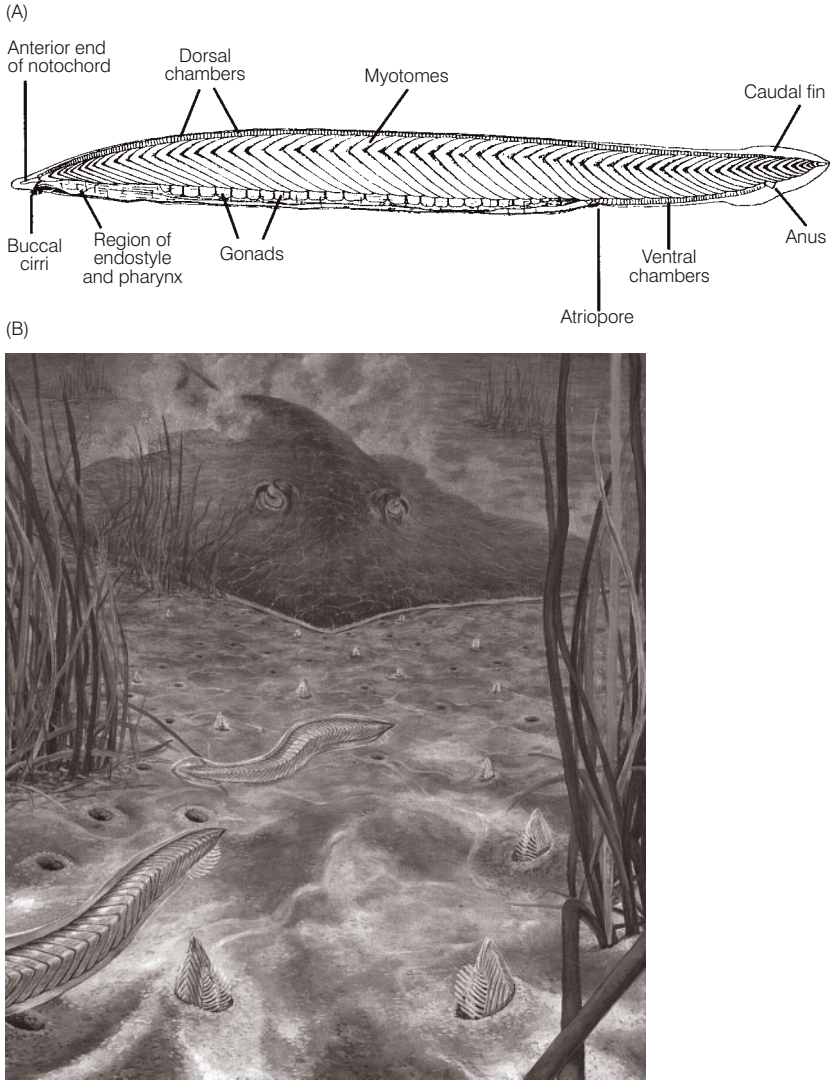

Figure 13.1
An adult lancelet, *Branchiostoma longirostrum*; actual length, 43 mm. (B) A stingray searches through a sand and seagrass bed off the west coast of Florida, spreading terror among Florida lancelets, *Branchiostoma floridae*. (A) adapted from Boschung (1983), used with permission; (B) drawing by D. W. Miller in Stokes and Holland (1998), used with permission (see www.syncreta.com).

Box 13.1

BOX 13.1

Embrace your inner lancelet

A debate raged in biological circles in the late 1800s about the place of lancelets in vertebrate evolution. Hundreds of papers about lancelet anatomy and embryology were published, largely motivated by a debate among three influential German biologists, Ernst Haeckel, Karl Semper, and Anton Dorn. Sempel and Dorn proposed that vertebrates evolved from some wormlike ancestor, whereas Haeckel saw the ancestors of the lancelets as our most likely ancestors. Haeckel based his conclusions on similarities (presumed homologies) between lancelets and fishes, including the perforated pharynx, segmented axial muscles, a notochord, a dorsal hollow nerve cord, and a postanal tail (Stokes & Holland 1998).

Haeckel wrote that we should regard lancelets, "with special veneration" because of their place in our ancestry; Sempel, Dorn, and religious authorities countered that reverence for lancelets caused the "dignity of humanity to be trodden underfoot". Haeckel's homologies and views have proven correct, brought about by a resurgence in interest in lancelet embryology and application of new analytical technologies (Stokes & Holland 1998). The lancelet's mucus-secreting feeding structure, the endostyle, is now considered a homolog of the vertebrate thyroid gland. Lancelet nephridia are simple versions of the vertebrate kidney, and a photosensitive, pigmented structure in the anterior portion of the lancelet nerve cord may be homologous to vertebrate eyes. Significantly, several developmental genes that code for particular somites in the lancelet embryo – specifically *Hox-1* and *Hox-3* – code for the same body sections in the vertebrates, including neural structures in the head (i.e., our brain). Finally, a cladistic analysis based on ribosomal DNA sequences places lancelets as the sister group to vertebrates, with a common ancestor in *Pikaia* or a related form.

are sometimes called **acraniates**. Lancelets also lack vertebrae, scales, genital ducts, a heart, red blood cells, hemoglobin, and specialized respiratory structures (gills), and have only one cell layer in the epidermis. Lancelets have up to 25 pairs of gonads as compared to one in lampreys and hagfish and two in most other fishes. The number of internal gill clefts increases throughout life in lancelets, whereas in fishes the number is fixed at birth. The notochord, a definitive chordate structure, extends beyond the anterior end of the dorsal nerve tube (e.g., beyond the "brain"), to the anterior end of the body.

Lancelets are economically valuable in two respects. *Branchiostoma lanceolatum*, a European and Mediterranean species, is the "amphioxus" commonly used in biology laboratories as a study animal. Besides its utility as an example of primitive chordate features, it is morphologically convergent with the ammocoete larva of the lampreys (see below), thus providing comparative material and popular questions for laboratory practicals. Lancelets are also targeted by a seasonal fishery in southern China, where they are dredged from the bottom with scoops at a rate of about 30,000 kg, or 1 billion lancelets, annually.

The fossil record for cephalochordates is limited, but recent findings suggest ancestry among the cephalochordate-like yunnanozoans (*Haikouella* and *Yunnanozoon*) of the Lower Cambrian, or perhaps in *Pikaia* from the Middle Cambrian Burgess Shale of British Columbia, which had a dorsal nerve cord and notochord (see Chapter 11, Jawless fishes). A recognizable cephalochordate fossil has been found in Early Permian deposits in South Africa (Oelofsen & Loock 1981). The evolutionary importance of the lancelets lies in their presumed place as ancestors of advanced chordates, as revealed in their embryology (Box 13.1).

Two lancelet families are recognized, each containing one eponymous genus (Branchiostomatidae, *Branchiostoma*; Epigonichthyidae, *Epigonichthyes*). A third family, the Amphioxididae, was previously recognized but has since proven to be the larva of a *Branchiostoma* species that remains planktonic after metamorphosis (Boschung & Shaw 1988). Traditionally, species have been designated on the basis of myomere and fin chamber counts, position of atriopore and anus, gonadal characteristics, and notochord and caudal fin shape. More recently, statistical analysis has revealed considerable meristic variation in such taxonomic features (Poss & Boschung 1996). Additionally, genetic analysis using 12S rRNA gene comparisons and mitochondrial DNA sequences indicates the existence of previously undetected species and lack of monophyly in recognized genera (Nohara et al. 2005; Xu et al. 2005). The coming years will undoubtedly reveal that cephalochordates are richer in biological information and species than has been traditionally held.

Hagfishes and lampreys: evolutionary relationships

Ancestor–descendant relationships of jawless fishes are fraught with controversy. Just about every conceivable permutation on relationship among hagfishes, lampreys, and jawed fishes has been proposed at some time, including hagfishes, lampreys, or gnathostomes as ancestral to the other groups (see Hardisty 1982). The possible ancestors of jawless fishes are well represented in the Silurian and Devonian (see Chapter 11). But the extinct groups are very different from one another, as are extant jawless fishes from presumed ancestral groups and from each other.

Although traditionally treated as related orders in the subclass **Cyclostomata** ("round mouths") – an hypothesis supported by recent molecular studies (see Nelson 2006) – similarities in the body morphology of modern hagfishes and lampreys are thought to reflect convergent evolution. It is probably wisest to deal with them individually and independently, and appreciate them for the unique yet primitive organisms that they are. Similarly, the "**Agnatha**", previously given superclass status, is now recognized as being paraphyletic; the term is still used as an informal adjective for jawless fishes. Hagfishes are considered a more primitive, separate, non-vertebrate group in their own superclass, the Myxinomorphi, constituting the sister group of vertebrates and the basal craniate taxon (Nelson 2006). Lampreys are placed in the infraphylum Vertebrata with all six superclasses of extinct and extant jawless and jawed fishes except the hagfishes. Vertebrates possess essential traits in common, especially dermal skeletal elements (secondarily lost in lampreys) and neural crest tissue (the embryonic nerve cord tissue that develops into gill arches, connective tissue, and bone), among others (see Chapter 11, Subphylum Craniata, Infraphylum Vertebrata).

Lampreys and hagfishes share a host of anatomical, physiological, and biochemical traits but have an even greater number of differences. Although both groups are scaleless, lampreys lack the mucus-producing capability of hagfishes. Lampreys have one or two dorsal fins supported by radial muscles and cartilage, whereas hagfishes have a single continuous caudal fin. Lampreys have a terminal mouth, hagfishes a subterminal mouth. Lampreys have a larval stage, hagfishes have direct development. In adult lampreys the external opening of the nasohypophysis is dorsal and the tract ends internally in a blind sac above the branchial region; in hagfishes, the external opening is terminal and the internal opening is into the pharynx. Lampreys have two semicircular canals, hagfishes only one. Lampreys have a pineal organ and functional eyes, hagfishes possess neither.

A major similarity between the two groups involves their immune responses. All gnathostomes, including fishes, have immune systems that involve immunoglobulin-type antigen receptors that produce pathogen-specific antibodies in response to infectious agents such as microbes. Lampreys and hagfishes also produce pathogen-specific defensive substances, but instead of antibody proteins, jawless fishes produce different kinds of proteins called **variable lymphocyte receptors**. Hence, "two strikingly different modes of antigen recognition . . . have evolved in the jawless and jawed vertebrates" (Alder et al. 2005, p. 1970).

Among the differences between the groups, lampreys possess lateral line neuromasts that are touch sensitive; these are lacking in hagfishes. All lampreys have seven gill openings, hagfishes vary between one and 16. Although the tongue possesses keratinous (horny), replaceable teeth in both groups, it is anatomically and functionally different. Myxinoids use the tongue for biting and tearing, whereas lampreys use it for rasping and suction. These and other differences in embryological, skeletal, neuromuscular, respiratory, cardiovascular, endocrine, osmoregulatory, chromosomal, and reproductive features all point out the disparate nature of the two groups (Hardisty 1982; Fernholm 1998; Nelson 2006).

Myxiniforms

Hagfishes, otherwise known as slime eels or slime hags, derive their alternative names from the copious mucus they produce via 70–200 ventrolateral pairs of slime glands (Fig. 13.2). Mucus production is the combined result of these holocrine slime glands as well as merocrine exudates from the epidermis itself (Spitzer & Koch 1998). The slime glands contain both mucous cells and thread cells, the latter being a unique trait in hagfishes that may strengthen the slime. Each slime gland is surrounded by connective tissue and striated muscle fibers that help exude the slime upon stimulation. The mucus itself consists of a protein plus a carbohydrate that binds to water and expands to form a loose jelly. A 50 cm hagfish is capable of filling an 8 L bucket with slime in a matter of minutes (Fig. 13.3).

Not surprisingly, slime production may serve multiple functions, some speculative. Authors have suggested: (i) that hagfishes produce slime when attacking dying fish, perhaps hastening suffocation of the prey by clogging its gills; (ii) that mucus could protect the hagfish from digestive enzymes when feeding inside the body of a prey animal; (iii) that mucus is repulsive to other scavengers such as sharks or invertebrates and thus serves to overcome competition; and (iv) that slime stabilizes burrow walls in the muddy bottoms in which hagfishes live (Bigelow & Schroeder 1948a; Brodal & Fange 1963; Hardisty 1979; Smith 1985a). Martini (1998), among the few to actually observe hagfishes in both the field and lab, found no evidence that burrow walls were stabilized with mucus or any other substance.

Hagfishes typically produce slime in response to being disturbed or handled. Mucus undoubtedly serves some anti-

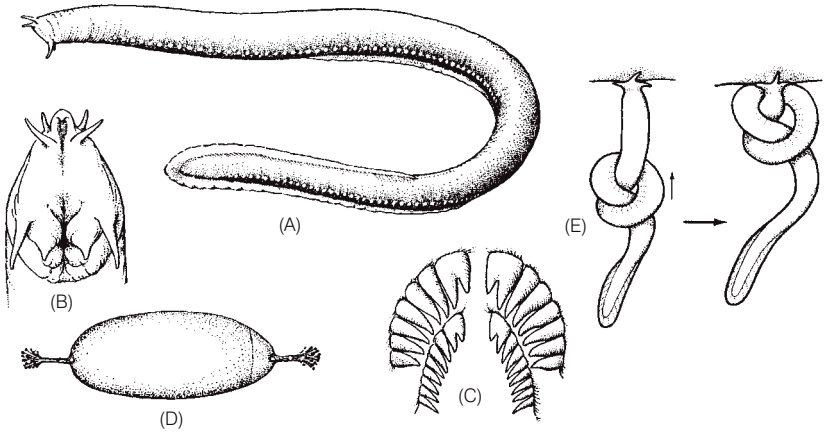

Figure 13.2
Hagfishes. (A) Adult Atlantic Hagfish, *Myxine glutinosa*, 38 cm long. Portholelike structures along the side are mucous glands. (B) Ventral view of the head region of an Atlantic Hagfish. The upper orifice is the nasal opening, and the lower orifice is the mouth. (C) The lingual (tongue) teeth of a hagfish. (D) Hagfish egg, approximately 40 mm long. (E) A hagfish pressing a knot against the side of its prey to gain leverage when tearing off flesh. (A–D) from Bigelow and Schroeder (1948a), used with permission; (E) after Jensen (1966).

Figure 13.3
A single hagfish can produce prodigious quantities of slime when disturbed. Photo by J. Meyer.

predator function, perhaps by making the fish too slippery to handle or by clogging the gills of a potential predator and threatening it with suffocation. Slime has its drawbacks however. A hagfish covered in its own slime will suffocate after a few minutes. Hagfishes rid themselves of slime by tying an overhand knot in their tail and then sliding the knot forward along the body, pushing the mucus ahead until the knot and mucus reach the anterior end and the fish can back away from the slime mass. A hagfish is also capable of backflushing its gills and nostril with water to rid them of slime (Conniff 1991).

Hagfishes are highly specialized animals belying their typification as "primitive" fishes. They possess **four rudimentary hearts**: a primary, three-chambered branchial or systemic heart posterior to the gills, and three auxiliary, single-chambered hearts located just behind the mouth (the paired cardinal heart), at midbody (the portal heart), and at the end of the tail (the paired caudal heart). These multiple pumping stations beat at different rates; the branchial and portal hearts contract via intrinsic muscles, whereas the cardinal and caudal hearts are squeezed by surrounding, extrinsic skeletal muscle. The auxiliary hearts are necessary to re-establish blood flow in venous vessels after blood leaves several sinuses where blood flow slows. The sinuses take the place of capillary beds, giving the hagfish a partially open circulatory system, more an invertebrate than a vertebrate trait. Contraction of body wall musculature during activity also aids in pushing blood from the sinuses into adjoining vessels. Hagfish blood is unique among craniates in being **isosmotic** with sea water, making it about three times saltier than the blood of bony fishes and lampreys. Hagfish kidneys are much simpler than those of other fishes, including lampreys, and may explain why hagfishes are restricted to a narrow range of salinities (Jensen 1966; Hardisty 1979, 1982; see Chapter 7, Agnathans).

Other hagfish peculiarities characterize the respiratory, digestive, immune, and sensory systems. Oxygen uptake in hagfishes occurs both at the gills and at capillary beds in the skin. Unlike most fishes, hagfishes inspire water through their nostril and then pump it via the mouth to the gill sacs. Cutaneous respiration comes into play when a hagfish has its nostril and gills buried deep in the carcass of a prey fish. Cutaneous respiration is undoubtedly facilitated by the oxygen-rich nature of the cold waters that hagfishes normally frequent, although the mud in which they bury is often anoxic. As an apparent adaptation to anoxic conditions, mud-burrowing species are exceedingly hypoxia tolerant, able to exist in anoxic conditions for hours or longer (Malte & Lomholt 1998). Low oxygen consumption

and very low basal metabolic rates appear to characterize hagfishes. Smith (1985a) calculated that Black Hagfish, *Eptatretus deani*, could obtain energy sufficient to maintain itself for 1 year after only 1.5 h of feeding on a high-energy source such as a carcass.

Hagfishes lack a true stomach, having instead an intestine that begins at the pharynx and ends at the anus, with an anterior muscular subdivision that prevents water inflow. Hagfishes do not bleed when their skin is cut, nor do such wounds become infected. Hagfishes have an immune system that produces complement-like factors instead of immunoglobulins (see above); hagfishes lack a defined thymus, spleen, or bone marrow, which are the usual sites of antibody production in vertebrates. Hagfishes also lack complete eyes, but have photosensitive receptors in their head (which contain retinal structures but no lens and are probably incapable of image formation) and cloacal region. Argument over whether the eyeless condition represents a degenerate character or whether the lineage ever possessed true eyes has been solved recently. Fossil material from the Late Carboniferous indicates that Paleozoic hagfishes possessed more developed eyes than recent forms (Bardack 1991; see below). Apparently, visual sensory input has been lost over time in the deep, dark habitats that hagfishes occupy. Food is found largely through olfaction and touch, the six barbels around the mouth serving both functions.

Hagfishes are nocturnal predators on a wide variety of small, benthic invertebrates, but are better known for their scavenging behavior (Shelton 1978; Smith 1990; Martini 1998). Hagfishes have an endearing habit of entering a dead or dying fish or other animal via some orifice or by digging through the skin and then consuming their prey from the inside, leaving only the skin and bones and making burial at sea a less-than-appealing proposition. The knot tying action that hagfishes use to deslime their bodies is also employed during feeding. A hagfish grasps a prey item by everting, retracting, and closing its toothplates. It will then pass a knot forward along its body and then press the knot against the prey as a means of levering off a piece of flesh (see Fig. 13.2B). Such knot-feeding is also seen in moray eels (see Box 19.2). Food is removed via a repeated evert–grasp–retract–release cycle of the toothplates (Martini 1998).

Reproduction in hagfishes remains something of an enigma. Both sexes contain only a single gonad, rather than the paired gonads found in most jawed fishes. In immature animals, this gonad is differentiated anteriorly as ovarian tissue, and posteriorly as testicular tissue. Upon maturation, one cell type prevails and no evidence of functional hermaphroditism has been found (spawning has never been observed). Fertilization is thought to be external since males possess no intromittent organ and females never contain fertilized eggs. Females produce eggs in batches, depositing about 20–30, 1.5–4.0 cm long, heavily yolked, sausage-shaped eggs covered by a horny shell (see Fig. 13.2D). These comparatively large eggs attach to each other and to the ocean floor. Incubation takes about 2 months, development is direct with no larval stage, and the young emerge as 45 mm long replicas of the adults. Most hagfishes show no obvious seasonality in spawning. However, actual spawning times, frequencies, places and behaviors, embryological details, ages at maturity, and reproductive life spans are unknown for most species. A cash prize for information on the reproductive habits of *Myxine glutinosa*, established in 1854 by the Royal Danish Academy of Sciences, remains unclaimed.

Hagfish species occur almost worldwide in temperate and cold temperate ocean waters above 30° latitude in both hemispheres, although hagfishes are uncommon in polar seas (Hardisty 1979). Few hagfish species occur shallower than 30 m, being limited by both the low salinities and high temperatures found at shallower depths; 34 ppt and 20°C appear to be the minimum salinity and maximum temperatures tolerated (Krejsa et al. 1990a, 1990b). The few tropical species occur in deep water, hagfishes having been captured as deep as 2700 m and photographed at 5000 m. Until recently, hagfishes had little commercial value and were largely viewed as nuisance species that scavenged on more valuable fishes (Box 13.2). Hagfishes are preyed upon by dolphins, porpoises, seals, sea lions, and octopus, sometimes accounting for 25–50% of the diet of individual predators (Martini 1998). Human consumption seems to be localized to Asia, where broiled hagfish, called "Anago-yaki" in Japan, is a marketable commodity (e.g., Honma 1998).

Hagfish taxonomy is based on the arrangement of efferent gill ducts (one vs. more excurrent openings), number of slime pores, finfolds, and tentacle and dentition patterns (Fernholm 1998). Some authors recognize two families, the Myxinidae with a single external gill aperture and the Eptatretidae with multiple external gill openings; other workers recognize two subfamilies within the Myxinidae. Maximum lengths range between 25 and 100 cm, with the exception of a recently described giant hagfish from New Zealand that attains a length of at least 127 cm and a mass of 6.2 kg (Mincarone & Stewart 2006). Ongoing analyses indicate several undescribed species in areas where only a single species was thought to occur, although disputes over the validity of some new species exist (e.g., Wisner & McMillan 1990; Nelson 2006).

The only fossil hagfish known is a small, 7 cm long specimen, found in Pennsylvanian (300 million years before present (mybp)) deposits in Illinois (Bardack 1991). This species, *Myxinikela siroka* – notable for its functional eyes, anteriorly placed gill pouches, and apparent lack of slime pores – is otherwise very similar to extant forms. Its discovery underscores the conservative nature of the hagfish lineage, a clade that may trace its ancestry into Early Paleozoic times via the conodonts (Krejsa et al. 1990a, 1990b).

Box 13.2

BOX 13.2

"Eelskin" boots

Marketing forces being what they are, it is surprising (or unsurprising) that few consumers know that the source of the popular "eelskin" wallets, purses, and briefcases is in fact hagfish. Leather workers in South Korea developed a method for tanning hagfish skin in the late 1970s (Conniff 1991). The product, often marketed as "conger eel", is a soft, supple-yet-strong, thin leather of considerable economic value: an attaché case retails for US$300, a golfbag for $1000. A substantial fishery, valued at $100 million annually, has developed off Korea, Japan, and surrounding waters. More than 1000 boats and dozens of leather processing plants were involved in the mid 1980s.

Hagfishes are caught primarily at night with baited bamboo or plastic traps at depths of 30–500 m, where the principle species captured are *Paramyxine atami*, *Myxine garmani*, and *Eptatretus burgeri* (Gorbman et al. 1990). Effort peaked in 1986, when daily catches averaged 5000 kg per boat. However, this success soon fell to less than 1000 kg/boat/day, as hagfish populations experienced overfishing pressure from the working fleet. Boats also routinely lost 200 traps per month, creating a tremendous competing "ghost fleet" that was still catching and killing hagfish. Given the low fecundity and apparent infrequent reproduction of hagfishes, and a total lack of knowledge of population size or replacement rate, an unregulated effort was bound to lead to a collapsed fishery (overfishing was apparently responsible for a fishery collapse in Japan during World War II and again in the early 1990s; Honma 1998).

In the late 1980s, Korean leather companies sought other sources of hagfish leather to feed a growing worldwide demand. Fisheries opened up along the west coast of North America and the Atlantic coast of Canada, where commercial catches were previously nonexistent. In California alone, 1989 landings of Pacific hagfish, *Eptatretus stouti*, exceeded 2,000,000 kg and involved boats from 19 different ports (Nakamura 1991). Both eastern Pacific and western Atlantic fisheries have experienced obvious signs of overfishing, including population declines and decreased catch-per-unit-effort (Martini 1998). Biological information has lagged behind the economic efforts, and regulatory legislation has been slow to develop. Moreover, eastern Pacific hagfishes produce a thinner skin of lesser quality and durability than the western species, which has affected the desirability of eelskin products (Gorbman et al. 1990).

What are the possible ecological consequences of overexploitation of hagfish populations? Hagfishes are not viewed as particularly charismatic by most people and it is unlikely that the environmental movement in any country will adopt the hagfish as a symbol of the need for preservation efforts and of loss of biodiversity. However, hagfishes can be exceedingly abundant in some areas. Densities for both Pacific and Atlantic hagfish, *E. stouti* and *Myxine glutinosa*, have been estimated at as high as 400,000–500,000/km^2 (*c*. 0.5 hagfish/m^2) (Nakamura 1991; Martini 1998). At such densities, their impacts as predators and scavengers, as bioturbators of sediment, and as recyclers of nutrients could make them a critical ecosystem component in soft-bottom benthic regions, the most abundant habitat type in the world's oceans. In addition, hagfish and Sea Lampreys are an important part of the diet of dolphins and several pinnipeds (seals and sea lions), animals of definite concern to the informed public. Substantial reductions in hagfish populations would have unpredictable ecological consequences, an unhappy situation with a familiar ring.

Petromyzontiforms

Whereas hagfishes have a bad reputation because of their scavenging habits, many lampreys are parasitic on other vertebrates. Lampreys superficially resemble hagfishes in general body form (Fig. 13.4). As with hagfishes, lampreys lack constricted vertebrae, the body being supported by a notochord. They also lack paired fins, jaws, a sympathetic nervous system, and a spleen. They too are scaleless, have a single nostril, and have horny teeth on the tongue. However, adult lampreys possess functional eyes, dorsal fins, an additional semicircular canal, a cerebellum, separate dorsal and ventral roots of the spinal nerves (an innovation among vertebrates), and a spiral-like rather than a straight intestine (Hardisty 1982).

Among the most striking differences between the two jawless fish groups is mode of reproduction. Whereas hagfishes presumably spawn repeatedly during their lives and produce a few large eggs each time, lampreys produce many small eggs and the adults die after spawning. Fecundity

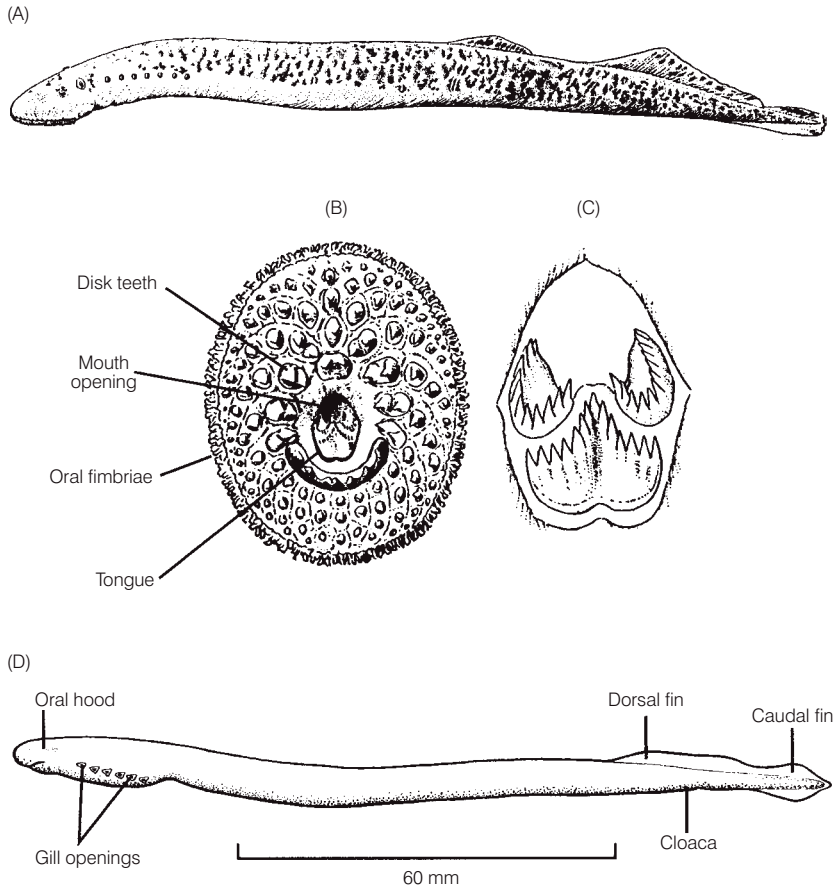

Figure 13.4
Lampreys. (A) Adult parasitic Sea Lamprey, *Petromyzon marinus*, about 45 cm long. (B) Oral disk of the Sea Lamprey showing the disk teeth used in holding on to prey. (C) Central mouth of *P. marinus*, showing the lingual (tongue) teeth used to rasp a hole in the prey. (D) Ammocoete larva of River Lamprey, *Lampetra fluviatilis*. (A–C) from Bigelow and Schroeder (1948a); (D) after Hardisty (1979).

varies from about 1000 eggs in nonparasitic species to a few hundred thousand in the larger parasitic species. Hatching in lampreys occurs after 12–14 days and young emerge as a 6 mm larval **ammocoete** (Fig. 13.4D).

In all lampreys, the free-living, blind, toothless ammocoete typically burrows into the bed of a silty stream or river. Ammocoetes, which were not definitively linked to adult lampreys until the mid-1800s, sit with their heads protruding from the bottom, filtering microscopic organisms from the water column by capturing them on mucus produced in the pharynx. This mode of feeding, possession of an **endostyle** that later develops into a thyroid gland, and the structure of the pharynx are strongly reminiscent of adult lancelets, supporting hypotheses of relationship between the groups (although lancelets move water through the pharynx via ciliary action, whereas ammocoetes pump water via pharyngeal musculature). Under favorable conditions, ammocoetes can achieve high densities, on the order of $30/m^2$ (Beamish & Youson 1987). Ammocoetes may live and feed for up to 7 years, achieving a maximum size of about 10–15 cm.

Transformation to the adult stage takes place in summer and fall in most species. In nonparasitic species, called **brook** or **dwarf lampreys**, the adult is seldom larger than the ammocoete. After an adult life span of about 6 months, during which no feeding occurs, the adult spawns and dies. In the parasitic species, free-living ammocoetes turn into parasitically feeding adults that may live for 1–3 years before spawning and dying.

Parasitic species are relatively large, up to 120 cm. Parasitic adults attach to the sides of host fishes using the toothed oral disk, rasp a hole in the skin, and live off the blood or body fluids (*Ichthyomyzon*, *Petromyzon*, *Mordacia*) or flesh (*Lampetra*, *Geotria*) of their host (Potter & Gill 2003) (Fig. 13.4B,C). Blood loss by the host can be substantial, amounting to 30% of the weight of the lamprey per day. Attachment frequently leads to death of the host. Parasitic lampreys can contribute significantly to the mortality of host species. The River Lamprey, *Lampetra ayresi*, may kill 18×10^6 kg of herring and 10% of the salmon off coastal British Columbia annually (Beamish & Youson 1987).

These natural levels of mortality may have relatively little effect on host population success under normal conditions, but where lampreys have been accidentally introduced, the effects can be catastrophic. The Sea Lamprey, *Petromyzon marinus*, invaded the upper Laurentian Great Lakes of North America via manmade canals that con-

nected the lakes with the Atlantic Ocean. Sea Lampreys have contributed to the decline or extirpation of several fish species, such as Lake Trout, whitefishes, and Blue Pike (Fuller et al. 1999; Daniels 2001). Extensive lamprey control strategies, involving chemical larvicides and various methods for trapping adults in spawning tributaries, have apparently helped reduce lamprey populations (Smith 1971; Hanson & Swink 1989; Youson 2003). Ironically, Sea Lampreys are considered imperiled in several European countries because of overfishing, migration blockage from dams, and sedimentation of spawning habitat. In France, among other nations, the species is "highly esteemed for the table" (Keith & Allardi 1996, p. 38).

Anatomical differences between lampreys and hagfishes are strongly reflected in their different foraging tactics. Unlike hagfishes, lampreys have **circumferential teeth** on the oral disk that aid in grasping live prey (see Fig. 13.4B). The olfactory and respiratory pathways are necessarily separated because lampreys feed and breathe while attached to the exterior of their prey. The nasohypophyseal opening carries water to a blind olfactory organ dorsal to the gill pouches. Attachment involves sealing the contact region between the prey and oral disk via secretion of mucus and the reduction of pressure in the buccal cavity. A vacuum is created as muscles in the mouth and pharyngeal region expel water out of the gill openings. A velar flap then seals the branchial chamber off from the buccal and pharyngeal regions, thus maintaining low pressures in the buccal cavity, allowing water to be pumped in and out of the gills for breathing purposes while also keeping food out of the branchial chamber. Negative pressure in the mouth helps maintain the hold on the prey and also promotes the flow of body fluids from the prey to the lamprey once the rasping tongue has gone to work. Uptake of blood and fluids is further aided by anticoagulants in the lamprey's saliva (Hardisty 1979).

Blood circulation in the adult lamprey differs from that of the hagfish in several respects. Although lamprey circulation is also "open" in that it is characterized by sinuses connecting arterial and venous systems, these sinuses are not as prevalent as in the hagfish. The primary lamprey sinuses are located in the branchial region and are associated with blood-gas exchange. Lampreys lack the multiple hearts of hagfishes, having instead a large, single, vagally innervated heart in a pericardial cavity, located in the typical fish position posterior to and upstream of the gills. Blood pressure is five times higher in lampreys than in hagfishes.

The reproductive biology of lampreys is well known compared to that of hagfishes. Lampreys also undergo a period of sexual intermediacy when both testicular and ovarian tissues can be found in the developing single gonad, but this period is confined to the ammocoete. During sexual maturation, lampreys undergo radical behavioral, anatomical, and physiological changes that parallel those found in salmon and anguillid eels, other families that die after reproduction (see Chapter 10, Death and senescence; Chapter 21, Lifetime reproductive opportunities). These changes cause or at least foretell an inability to live beyond the spawning period. Feeding ceases, the gut atrophies, osmoregulatory function shifts, dentition deteriorates, the body shrinks, the eyes and liver degenerate, hematopoesis (blood production) decreases, and lipid and glycogen stores are reduced. Secondary sex characters, such as thickened fins and genital papillae, are formed.

Upon maturation, adults undertake a spawning migration again reminiscent of the migrations of salmon and eels. Distances moved may range from a few kilometers in nonparasitic or landlocked species to more than 1000 km in anadromous species that move from the ocean to fresh water. Spawning locales are typically the upper regions of streams where bottom types are dominated by gravel and cobbles. These locales are often used in successive years by new generations of lampreys, although little evidence exists to suggest that lampreys return, salmonlike, to spawn in the stream of their birth. Adults on spawning migrations are attracted to suitable areas by detecting a bile acid, petromyzonol sulfate, produced by larvae (Fine et al. 2004). Males then produce a pheromone that is highly attractive to females (Johnson et al. 2006).

The spawning act begins after a male constructs a nest pit by attaching to a rock with the sucker and then carrying the rock downstream or by holding onto large cobbles and thrashing the downstream area. The pit thus created is ringed by large and small cobbles. A female will also take part in nest construction, but site selection appears to be initiated by the male. Nonparasitic species may engage in group spawning in a single nest, whereas larger, parasitic species may engage in pair spawning and male defense of the nest site. When the nest pit is finished, the female attaches to one of the large upstream cobbles, the male attaches to the anterior portion of the female, coils his body around hers, and the two thrash while the male squeezes the eggs out of the female. Spawning occurs repeatedly over 2–9 days and both sexes die within a few days after spawning. Eggs remain in the nest pit for about 2 weeks, and larvae remain in the nest for an additional week. The ammocoetes then drift downstream to areas of slow current and silty or muddy bottoms, where they burrow and begin feeding (Hardisty & Potter 1971; Hardisty 1979).

Lampreys, like hagfishes, are cool water species that seldom occur at latitudes below 30° or in water temperatures above 20°C in either hemisphere. Only two low-latitude lamprey species are known and both occur at high elevations in Mexico, forming an interesting mirror image to the submergence of tropical species among the entirely marine hagfishes. Nonparasitic forms are entirely confined to fresh water, whereas parasitic forms may occupy fresh water or may be anadromous. **Anadromous** species hatch in fresh water where they live as larvae, move into coastal

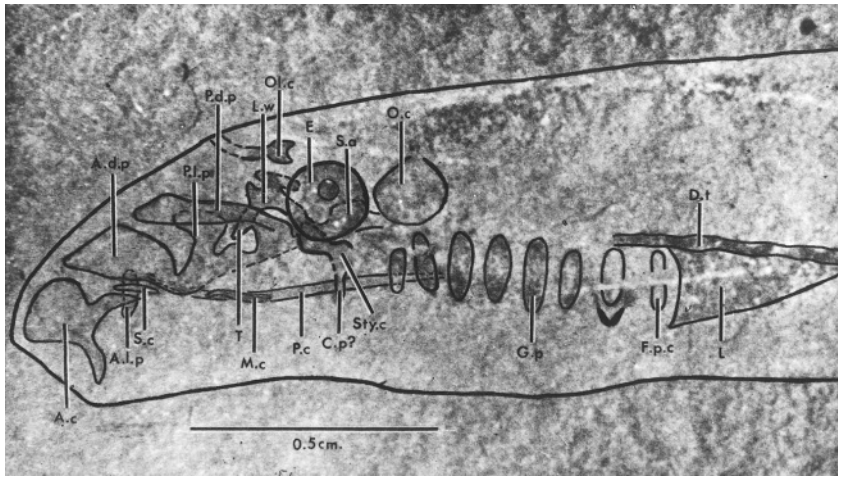

Figure 13.5

Reconstruction of the Carboniferous lamprey, *Mayomyzon pieckoensis*, from Illinois. The fossil, seen in lateral view, bears a striking resemblance to modern petromyzontid lampreys. Several recognizable relevant anatomical features are outlined in black: Ac, annular cartilage; Dt, digestive tract; E, eye; Gp, gill pouch; L, liver; Lw, lateral wall of braincase; Oc, otic capsule; Olc, olfactory capsule; Pc, piston cartilage. From Bardack and Zangerl (1971), used with permission.

marine habitats as metamorphosed adults, and then return to fresh water to spawn (Hardisty 1979, 1982; Nelson 1994).

Lamprey taxonomy is based largely on mouth, tentacle, and dentition characteristics (Gill et al. 2003). Lampreys are taxonomically unique in that they have the largest diploid chromosome number of any vertebrate, between 140 and 170 in many northern hemisphere species. The Petromyzontidae of North America and Europe form a monophyletic clade that separated early from the Geotriidae and Mordaciidae of South America, Australia, and New Zealand (Potter & Gill 2003). Two species of an extinct family, the Mayomyzontidae, have been found in 300–320-million-year-old Carboniferous deposits of North America. The more primitive *Hardistiella montanensis* had a hypocercal tail and lacked an oral sucker, whereas *Mayomyzon pieckoensis* was relatively small and lacked teeth everywhere except the tongue (Janvier et al. 2004). *Mayomyzon* is notably similar to modern petromyzontids despite its antiquity (Nelson 1994) (Fig. 13.5).

Paired species in lampreys

Lamprey evolution provides a rare glimpse of ongoing speciation processes: ancestral and derived species exist contemporaneously and often in the same river system (Salewski 2003). At least 18 nonparasitic species, or about half of all lampreys, can be matched to ancestral parasitic forms. The phenomenon has been repeated by 11 species of northern hemisphere, petromyzontid, ancestral species and even one southern hemisphere, mordaciid lamprey (*Mordacia mordax* gave rise to *M. praecox*). In some instances, a parasitic river lamprey ancestor has evidently given rise to two or even three nonparasitic brook lamprey species. In each pair, the ammocoetes are almost indistinguishable, except that nonparasitic ammocoetes may grow larger. Although adults of the nonparasitic species are smaller, both species often have the same number of myomeres. Dentition in the adults of the parasitic species is relatively constant in number and shape and in being functionally hooked and sharp. In the nonparasitic, nonfeeding adult species of a pair, dentition is variable and blunt.

Derivation of nonparasitic forms apparently occurred via extension of the larval period and a shortcutting of the metamorphosis process, both intimately linked to the thyroid gland and its hormones (Youson & Sower 2001) (Fig. 13.6). Parasitic species may spend 4 years as larvae and then take 2 years to feed and mature. A corresponding nonparasitic form has a larval period of 6 years, followed by a relatively short, 6 month or less, maturational period. Hybridization between members of a pair is exceedingly rare; this reproductive isolation is maintained largely by size differences. Nonparasitic males, being smaller, cannot coil around and squeeze parasitic females while their vents are in proximity to one another, actions that are necessary for the extrusion of eggs and proper fertilization. Adoption of a shortened, nonparasitic mode of adult existence may expand the range where a species can occur: small brooks may have abundant food resources for larvae but an insufficient supply of potential host fishes for a feeding adult.

The phenomenon of repeated, parallel evolution of such **paired** or "**satellite**" species is unique among vertebrates (Hardisty & Potter 1971; Vladykov & Kott 1979; Beamish & Neville 1992), and may result from sympatric speciation, where new species arise from old ones without geographic separation (Salewski 2003).

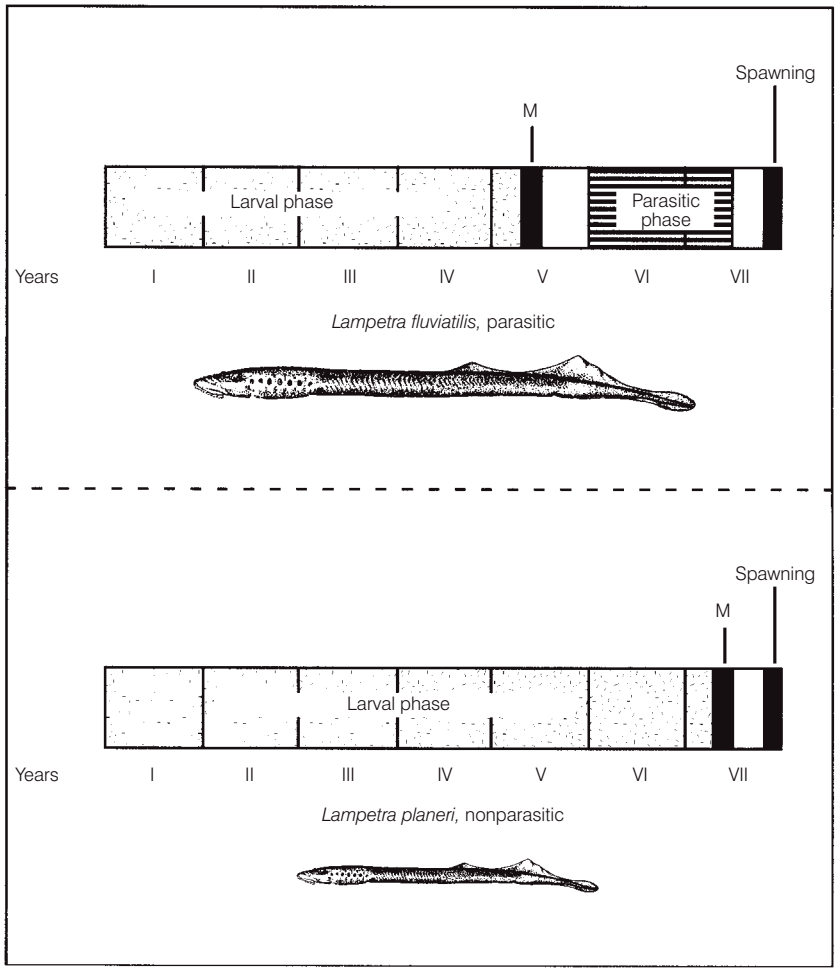

Figure 13.6

Comparative life histories of a species pair of European lampreys. (A) The parasitic ancestor, the River Lamprey *Lampetra fluviatilis*. (B) The nonparasitic derived species, the Brook Lamprey *L. planeri*. The evolution of nonparasitic from parasitic forms involves a lengthening of the larval phase and a shortening of the maturational period. The onset of metamorphosis is denoted by M; unshaded areas represent nonfeeding periods. Adapted from Hardisty (1979).

Primitive bony fishes

Subphylum Craniata
- Superclass Gnathostomata
  - Grade Teleostomi (Osteichthyes)
    - Class Sarcopterygii
      - Subclass Coelacanthimorpha (Actinistia)
        - Order Coelacanthiformes: Latimeriidae (coelacanths, two species, marine)
      - Subclass Dipnoi (Dipnotetrapodomorpha)
        - Superorder Ceratodontimorpha
          - Order Ceratodontiformes: Ceratodontidae (Australian lungfish, one species, fresh water), Lepidosirenidae (South American lungfish, one species, fresh water), Protopteridae (African lungfishes, four species, fresh water)
    - Class Actinopterygii
      - Subclass Cladistia
        - Order Polypteriformes: Polypteridae (bichirs and Reedfish, 16 species, fresh water)
      - Subclass Chondrostei
        - Order Acipenseriformes: Acipenseridae (sturgeons, 25 species, coastal and fresh water), Polyodontidae (paddlefishes, two species, fresh water)
      - Subclass Neopterygii
        - Order Lepisosteiformes: Lepisosteidae (gars, seven species, fresh and brackish water)
        - Order Amiiformes: Amiidae (Bowfin, one species, fresh water)

Subclass Coelacanthimorpha: the living coelacanths

> There can be few episodes in the history of ichthyology to rival the excitement following the announcement in the *East London Dispatch* of 20 February 1939, declaring that a coelacanth had been captured off . . . South Africa.
>
> Forey 1998, p. 1

If you open an ichthyology text published prior to World War II (e.g., Günther 1880; Jordan 1905; Norman 1931), you will find passing mention of a relatively obscure group of extinct fishes that represented a side branch of the lineage that presumably gave rise to the tetrapods. These were the coelacanths, conservative sarcopterygian fishes that had gone unchanged in many respects since the Devonian (Jarvik 1980; Forey 1998). Their fossil record stretched nearly 300 million years, from the Middle Devonian, 360 mybp, to near the end of the Cretaceous, 80 mybp, when they and then the dinosaurs disappeared.

Imagine the world's surprise when, just before Christmas 1938, a living coelacanth was trawled from a depth of 70 m off the east coast of South Africa (Smith 1939, 1956; Weinberg 2000). ***Latimeria chalumnae***, described by J. L. B. Smith, retains many of the characteristics that had defined the coelacanths since the establishment of their lineage: a thin bony layer encasing the vertebral spines and fin rays (the name *coel-acanth*, meaning "hollow spines", refers to the hollow nature of the fin rays that support the tail); an unconstricted and unossified notochord, modified as a strong-walled elastic tube; fleshy, lobed pectoral, pelvic, anal, and second dorsal fins (= Sarcopterygii); a symmetrical, three-lobed, diphycercal tail with an epicaudal fringe portion extending beyond the midline; relatively large, thick, bony scales; a double gular plate under the lower jaw; a dorsal intracranial articulation (a joint in the braincase that functions to increase gape size); and numerous other osteological features (Fig. 13.7).

The first and subsequent specimens also confirmed speculation about other aspects of coelacanth biology, including reproductive mode. One paleontological finding of a Jurassic species showed skeletal impressions of small coelacanths inside a larger one, suggesting that coelacanths were viviparous (Watson 1927). A later fossil indicated eggs inside a coelacanth, suggesting oviparity and implicating cannibalism in the case of Watson's specimen. More recently, dissections of a gravid female *Latimeria* have revealed 5–26 well-developed young with yolk sacs or yolk sac scars (Smith et al. 1975; Bruton et al. 1992). *Latimeria* is a lecithotrophic live-bearer: young develop in the oviducts from the largest eggs of any known bony fish (9 cm diameter,

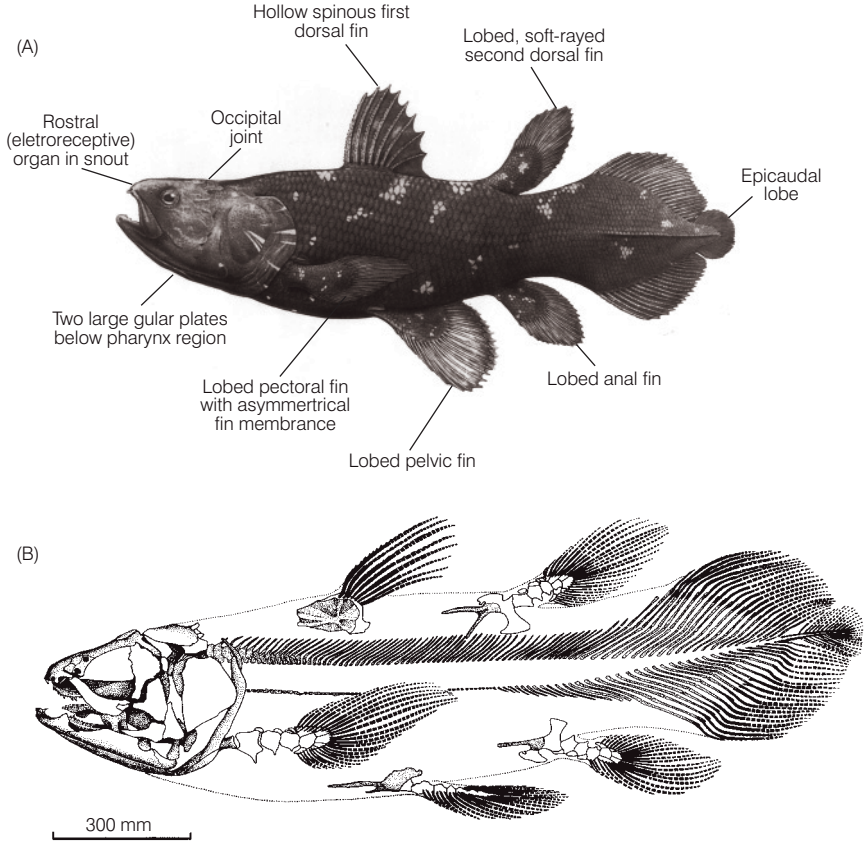

Figure 13.7
The living African Coelacanth, *Latimeria chalumnae*, an extant member of a group thought to be extinct for 65 million years. Discovered by science in 1938, the two known species occur in small populations restricted to volcanic slopes off East Africa and northern Indonesia. Both are recognized internationally as endangered. (A) External anatomy; some traits that distinguish coelacanths from other living fishes are noted. (B) Skeletal anatomy; note skull joint, arrangement of bones of the fins, and the unconstricted notochord. (A) drawing by S. Landry, from Musick et al. (1991); (B) from Forey (1998), used with permission.

>300 g) and gain all their nutrition from the large, attached yolk sac (Fricke & Frahm 1992). Watson's original interpretation was correct.

Latimeria, and coelacanths by extension, are not ancestral to the tetrapods but represent an offshoot lineage within the sarcopterygians (see Chapter 11). The elpistostegalian tetrapodomorphs are the most likely ancestral group. Elpistostegalians apparently had well-developed lungs, as befits a tetrapod ancestor. In contrast, *Latimeria* has a fat-filled gas bladder that is no more than a vestigial outpocket of the gut. It is obviously used for hydrostatic control and is not a functional "lung", not surprising for a fish that lives between 100 and 250 m depth and seldom if ever ventures near the surface. The blood vessel that drains the gas bladder returns blood to the sinus venosus at the back of the heart, as in other fishes. In tetrapods, this vein carries oxygenated blood to the left side of the heart and then to the rest of the body. The coelacanth heart itself is characteristically fishlike in that it has no divisions into left and right sides. The gut has a spiral valve, also typical of primitive fishes and not found in tetrapods; the spiral valve in *Latimeria* has parallel spiral cones rather than a scroll valve as found in ancestral gnathostomes. *Latimeria* lacks internal choanae (nostrils with an excurrent opening into the roof of the mouth); tetrapods possess internal choanae.

Recent behavioral findings have further clarified our understanding of *Latimeria*'s ecology. J. L. B. Smith (1956) called the coelacanth "Old Four Legs", in reference to the leglike appearance of the paired fins. This led to speculation that *Latimeria* literally walked along the bottom on its pectoral and pelvic fins. Motion pictures taken from small submarines indicate that *Latimeria* almost never touches the bottom (Fricke et al. 1987, 1991b). It instead drifts in the water column with the currents, sculling with its paired fins in an alternating diagonal pattern: when the left pectoral and right pelvic fins are moved anteriorly, the right pectoral and left pelvic fins move posteriorly. This is the pattern of locomotion shown by tetrapods, and interestingly, also by the lungfish *Protopterus* when moving across the bottom with its paired fins (Greenwood 1987).

Latimeria is highly electrosensitive – as are most primitive fishes – detecting weak electric currents via a unique series of pits and tubes in the snout called the **rostral organ**. This structure bears similarities to the enlarged ampullae of Lorenzini of sharks (Bemis & Hetherington 1982; Balon et al. 1988). During underwater observations, weak electric currents were induced in a rod placed near drifting *Latimeria*, and the fish responded by orienting in a vertical, head-down manner. As is characteristic of many nocturnally active fishes, the living coelacanth forms daytime resting aggregations, with as many as 17 fish occurring together in a single small cave. The fish have large, overlapping home ranges, and return to the same caves repeatedly (Fricke et al. 1991b). These observations suggest that the electrical sense of *Latimeria* could serve not only for prey detection, but also for nocturnal navigation while moving through the complex lava slopes that these fishes inhabit (Bemis & Hetherington 1982).

Coelacanths have an extensive, well-studied fossil record, dating back to the Middle Devonian (see Fig. 11.11). As many as 121 different species have been described, of which 83 are probably valid, constituting 24 genera and perhaps nine families (Cloutier & Forey 1991; Forey 1998). Diversity was maximal during the Early Triassic, when 16 described species existed in both marine and fresh water.

The living coelacanths, at least for now

When Marjorie Courtenay-Latimer went down to the docks of East London, South Africa, to wish the crew of the trawler *Nerine* a happy Christmas, she could not have had a notion of how this friendly gesture would completely change her life and the course of 20th century natural science. Captain Goosen had saved several fishes from his recent catch that he thought she might want for the East London Museum's collections. Included in the pile was a curious, 1.5 m long fish that was ". . . pale mauvy blue with iridescent silver markings. . . . Was it a lungfish gone balmy?" (Courtenay-Latimer 1979, p. 7).

Ms. Courtenay-Latimer sent a rough drawing and description of the fish to Dr. J. L. B. Smith, a South African chemist turned ichthyologist (Fig. 13.8). The Christmas mail and summer rains delayed communication between Courtenay-Latimer and Smith and it was almost 2 weeks before a telegram arrived from Smith desperately urging Courtenay-Latimer to preserve as much of the fish as possible. Smith suspected the fish was a coelacanth, but it seemed so implausible. Unfortunately, the size of the fish, the summer heat, and bad luck conspired against them and only the skin was preserved and mounted by a taxidermist. On February 16, 1939, Smith finally managed to drive to East London and view the mount and confirm that the fish was without doubt, "scale by scale, bone by bone, fin by fin . . . a true Coelacanth" (Smith 1956, p. 41). Smith named the fish *Latimeria chalumnae* in honor of Ms. Courtenay-Latimer and the Chalumna River off which the fish was captured. The hunt for a second, more complete specimen began immediately.

Despite a sizable promised reward, intensive collecting efforts along much of the eastern coastline of Africa, and deepsea trawling around the world, a second specimen was not obtained for 14 years. The second coelacanth was slightly different in that it lacked a first dorsal fin and a caudal fringe, probably having lost them to a shark. Smith erected a new genus, *Malania*, in honor of the then Prime Minister of South Africa, D. F. Malan, who loaned Smith a plane to fly to the capture locale and snatch the fish away from French authorities. As Malan was also the architect of the racial separation doctrine of apartheid in South Africa, Smith's "patronymic" was viewed as a distasteful

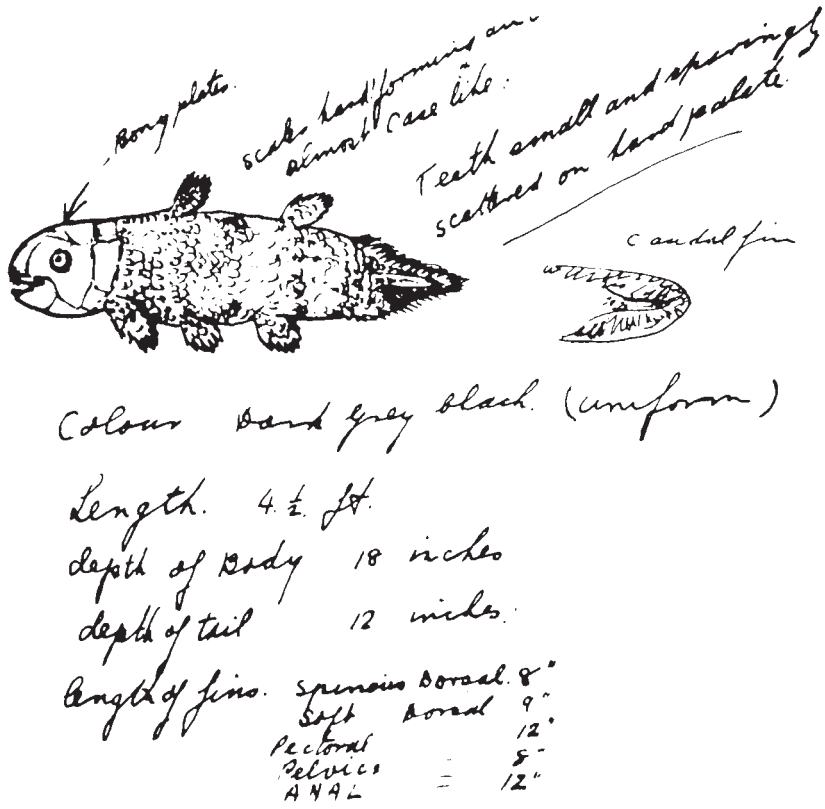

Figure 13.8

Marjorie Courtenay-Latimer's drawing and description of the first coelacanth, as sent to J. L. B. Smith. Key features pointed out by Courtenay-Latimer included bony plates on the head and the extra median lobe in the caudal fin. From Smith (1956), used with permission.

political expediency by many outsiders. Later analysis and additional specimens confirmed that only one coelacanth species existed: *Malania* was abolished in favor of *Latimeria*.

The second and all but a half dozen of the known 175 specimens of *L. chalumnae* have been caught off the coast of the Comoros Islands (now the Republic of Comores), a small island group in the Indian Ocean that lies between the island of Madagascar and Mozambique in East Africa. The fish have been captured by hook-and-line fishermen off the western coasts of two islands, Grand Comoro and Anjouan. The fish are usually captured as bycatch of the fishery for Oilfish (*Ruvettus pretiosus*, Gempylidae). The coelacanth has the native name "**Gombessa**" and is not a desirable food fish (the often-cited fact that the scales are used for roughening bicycle tire tubes is erroneous; Stobbs 1988). The fish are limited to areas of relatively recent, steep lava flows that are perforated with small caves. By day the fish rest in caves at depths between 180 and 250 m (Fricke et al. 1991b). In the evening, they move into deeper water (200–500 m) to feed on small fishes, which they capture via a suction–inhalation mechanism, much like a Giant Sea Bass (Fricke & Hissmann 1994). The relatively restricted depth range may relate to temperature preferences of 18–23°C and reflect the oxygen saturation properties of coelacanth blood, which functions poorly in warmer, less oxygen-rich surface waters (Hughes & Itazawa 1972).

Specimens range in size from 42 to 183 cm in length and weigh from 1 to 95 kg, the largest individuals being female (Bruton & Coutouvidis 1991). Age estimates indicate that coelacanths live from 20 to as much as 40–50 years (Bruton & Armstrong 1991). Females do not mature until 15 years old, and gestation may require 3 years, the longest of any known vertebrate (Froese & Palomares 2000). Intensive efforts have yet to reveal other populations around the Comoros Islands, although individual animals have been caught in trawls and gillnets off Mozambique, southern Madagascar, Kenya, and the Tanzanian coast (De Vos & Oyugi 2002; www.dinofish.com). An alarming 29 fish – including six in one night – were captured off Tanzania between 2003 and 2006 (Tony Ribbink, pers. comm.). In 2000, a second East African population was discovered by divers off the KwaZulu-Natal, South Africa coast (Venter et al. 2000; www.acep.co.za). Even more exciting was the discovery of another coelacanth species in Indonesia in 1997 (Box 13.3).

The world took notice of *Latimeria* in a big way, perhaps too big. The hype and publicity surrounding the Comoran coelacanths have posed a serious threat to their continued existence. The total Comoran population is estimated at 200–600 individuals and is thought to be declining (Fricke et al. 1991a; Fricke & Hissmann 1994; Hissmann et al. 1998). Small clutch size and late maturation indicate a slow reproduction rate, which means individuals are replaced

Box 13.3

BOX 13.3

Another coelacanth!

The intrigue and melodrama surrounding the discovery, naming, and further pursuit of *Latimeria chalumnae* have continued into recent times. In September 1997, Mark and Arnaz Erdmann spotted a coelacanth in a fish market in Sulawesi, northern Indonesia, fully 10,000 km east of the Comoros locale. Targeted fishing produced another specimen in July 1998 at depths and habitat types similar to those in the Comoros (Erdmann et al. 1999), and additional fish have been found to the west and southwest. While Erdmann and colleagues were engaged in a detailed anatomical and biochemical analysis, tissue samples from the 1998 specimen were literally hijacked and used in describing the Indonesian fish as a new species, *L. manadoensis* (Pouyaud et al. 1999b). Subsequent, thorough studies – by Erdmann and colleagues – confirmed the uniqueness of *L. manadoensis* (Holder et al. 1999). More recent comparisons of the mitochondrial genome of the two species indicate the lineages may have separated as long as 30–40 million years ago (Inoue et al. 2005).

Lost in the shuffle here are the "stealth and subterfuge" that went into the naming of the new species (Holden 1999, p 23). Unfortunately, the Principle of Priority in the Zoological Code (see Chapter 2) does not disqualify names on account of piracy, so the Pouyaud et al. description stands as first published (see also Weinberg (2000) for a readable account of these shenanigans and much more).

slowly in a population. Between 1952 and 1992, at least 173 individuals were captured, most as research and display material for museums (Bruton & Coutouvidis 1991). Unfortunately, a black market for coelacanths also developed because of the animal's freak appeal (Stobbs 1988; Bruton & Stobbs 1991). Celebrity transformed a bycatch fishery into a directed fishery; a single coelacanth was worth US$150, or about 3–5 years' income to a fisherman. The fish eventually sold for $500–2000 on the open market. This directed fishery was eliminated when the Comoran goverment outlawed the capture of coelacanths, but incidental captures still occur at the rate of 5–10 fish per year, which could represent as much as 5% of the adult population captured annually (H. Fricke, pers. comm.).

All these circumstances – slow growth and maturation, small clutch size, limited habitat and geographic range, limited recruitment, small and perhaps decreasing population size, intense exploitation – indicate that coelacanths are particularly vulnerable and threatened by extinction. International conservation efforts were initiated: the coelacanth was listed as Critically Endangered by the International Union for the Conservation of Nature (IUCN) and placed in Appendix I of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES), thereby outlawing commercial trade by signatory nations. A Coelacanth Conservation Council was formed to coordinate and promote research on and conservation of coelacanths; this organization evolved into the African Coelacanth Ecosystem Programme (www.acep.co.za; anyone can join). Efforts have also focused on providing alternative fishing methods and species for Comoran fishers (see Coelacanth Rescue Mission, www.dinofish.com) and to discourage ongoing, well-financed efforts at capturing live specimens for display in public aquaria.

The Coelacanth Conservation Council proposed that the coelacanth be adopted as the international symbol of aquatic conservation, equivalent to the panda's status for terrestrial conservation, because ". . . Coelacanths occupy a unique place in the consciousness of man: they represent a level of tenacity and immortality which man will never achieve during his short stay on earth" (Balon et al. 1988, p. 274) (Fig. 13.9).

Subclass Dipnoi, Order Ceratodontiformes: the lungfishes

Lungfishes, commonly referred to as "dipnoans" because of their two methods of breathing, are well represented in the fossil record on all major continents, including Antarctica. They arose early in the Devonian and were widespread and diverse until the Late Triassic. Today, they are represented by three genera that date back to the Cretaceous, with six remaining species in South America, Africa, and Australia. All extant lungfishes occupy freshwater habitats, although most of the 60 described fossil genera were marine.

Lungfishes possess a mosaic of ancestral and derived traits that initially clouded their taxonomic position (Conant 1987). The South American species, *Lepidosiren paradoxa*, reveals in its specific name some of the confusion its mixture

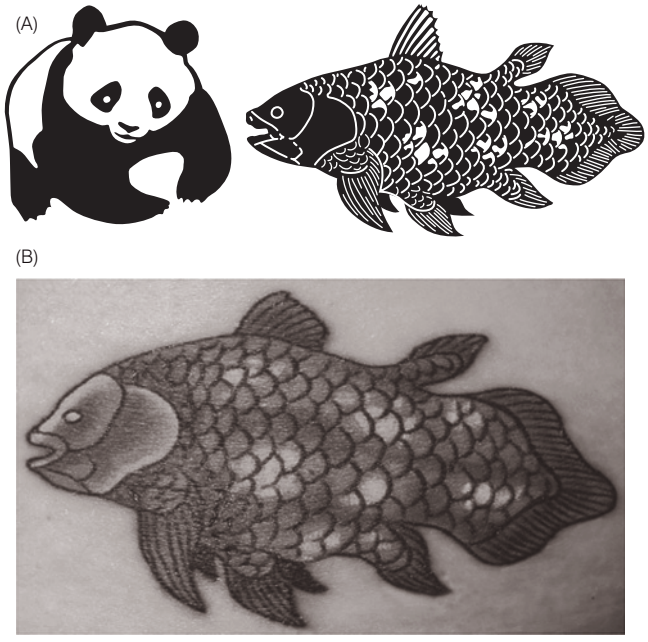

Figure 13.9

Coelacanths are as cuddly as pandas. (A) The Coelacanth Conservation Council's (CCC) image of a coelacanth, proposed to serve as the World Wildlife Fund's symbol for marine conservation, the panda representing terrestrial conservation. (B) An ichthyology student was moved by the plight of the coelacanth and had the CCC image tattooed on her hip. Photo by G. Helfman, courtesy of G. Hendsbee.

of traits must have caused. It was first described in 1836 and thought to be a reptile because of the structure of its lung and the placement of the nostrils near the lip. An African species, *Protopterus annectens*, was discovered the next year and proclaimed to be an amphibian based on its heart structure. Both species were very different from fossil lungfishes and relationships between extant and extinct forms were not obvious. After about 30 years of debate, the systematic position of lungfishes among the Sarcopterygii was generally accepted, with recognition that lungfishes had "singularly embarrassed taxonomists" (Duvernoy 1846, in Conant 1987). Ironically, recent cladistic analyses indicate that tetrapods are another subclass within the Sarcopterygii, i.e., a "divergent sideline within the fishes". This makes lungfishes in fact phylogenetically closer to tetrapods – and hence to amphibians – than to most other bony fishes (see Chapter 11).

A general and distinctive characteristic of lungfishes is the existence and location of massive **toothplates**. Teeth are not attached to the jaw margins as in most other living fishes, but instead occur only on interior bones (Bemis 1987). These toothplates are often quite large and apparently function in crushing aquatic insects, crustaceans, and particularly mollusks; the toothplates are better developed in the Australian than in the South American and African species. It is the toothplates that most commonly fossilize and which form the basis of much of our understanding of evolution in the group (see Fig. 11.12).

The living African and South American lungfishes are placed in the families **Lepidosirenidae** and **Protopteridae** (Fig. 13.10A–C). The four African species of the genus *Protopterus* are widely distributed through Central and South Africa, occurring in both lentic (still) and lotic (flowing) habitats of major river systems, including a variety of swamp habitats (Greenwood 1987). Maximum sizes range from 44 cm (*Protopterus amphibius*) to 180 cm (*P. aethiopicus*). Young fishes are active by night, adults by day, and food includes a variety of hard-bodied invertebrate taxa, with mollusks predominating (Bemis 1987). Protopterids are obligate air breathers throughout their postjuvenile life, obtaining 90% of their oxygen uptake via the pulmonary route.

African lungfishes are best known for their ability to survive desiccation of their habitats during the African dry season. Such **estivation** behavior, as described for *P. annectens*, involves construction of a subterranean mud cocoon (Greenwood 1987). As water levels fall, the lungfish constructs a vertical burrow by biting mouthfuls of mud from the bottom, digging as deep as 25 cm into the mud. As the swamp dries, the lungfish ceases taking breaths from the water surface, coils up in the burrow with its head pointing upwards, and fills the chamber with secreted mucus. This mucus dries, forming a closely fitting cocoon, and the fish becomes dormant (Fig. 13.11). This dormant period normally lasts 7 or 8 months, but can be extended experimentally for as much as 4 years in *P. aethiopicus*. During estivation, lungfish rely entirely on air breathing, the heart rate drops, they retain high concentrations of urea and other metabolites in the body tissues, metabolize body proteins, and lose weight. With the return of rains, the lungfish emerges from the burrow and resumes activity, which includes cannibalizing smaller lungfish that have also just emerged from their burrows.

African lungfishes build burrow-shaped nests, often tunneling into the swamp bottom or bank. Eggs and young are guarded by one parent, presumably the male. The male has no specialized structures to aid in oxygenating the water in the nest as reported for *Lepidosiren* (see below), although male *P. annectens* have been observed "tail lashing" near the nest, which may serve the same purpose. Young African lungfishes have external gills (Fig. 13.12), one of the traits that caused many 19th century biologists to consider them amphibians.

The South American species, *L. paradoxa* (see Fig. 13.10C), is considered to be the most recently derived member of the family (Greenwood 1987). Surprisingly little is known of its natural history compared to the African and Australian species. It occurs in swampy regions of the Amazon and Parana river basins (Thomson 1969a) and grows to about 1 m in length. As with *Protopterus*, adults have reduced gills and are obligate air breathers. Estivation

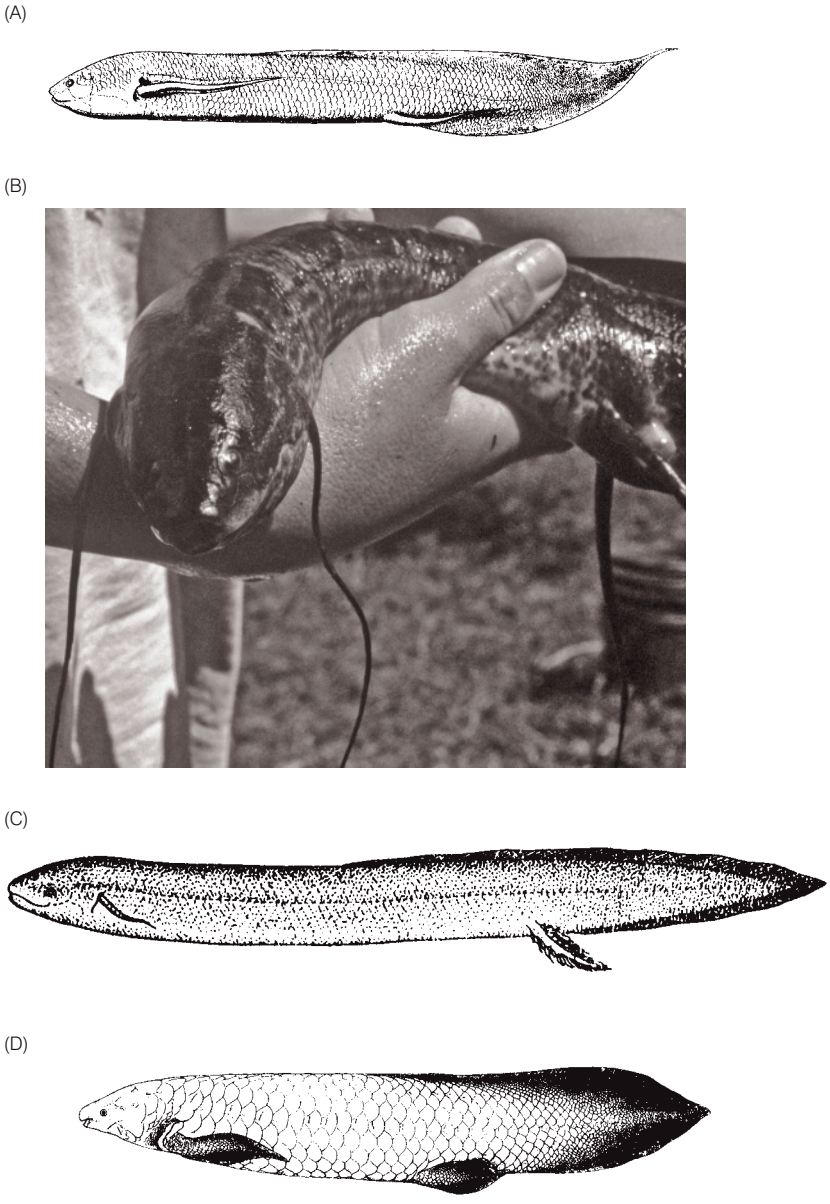

Figure 13.10

Modern lungfishes. (A) An African lungfish, *Protopterus annectens*, one of four species in the genus. (B) A live *Protopterus*; note the filamentous pectoral and pelvic fins. (C) The South American Lungfish, *Lepidosiren paradoxa*, showing the vascularized pelvic fins that develop on males during the breeding season. (D) The Australian lungfish, *Neoceratodus forsteri*. (A, D) from Jarvik 1980; (B) courtesy of L. and C. Chapman; (C) from Norman (1931), used with permission.

in burrows occurs but is poorly documented. *Lepidosiren* is best known for its reproductive behavior, although conjecture exceeds information. Eggs are deposited in a burrow nest as in *Protopterus* and guarded by the male. During the breeding season, after egg deposition, the male's pelvic fins develop vascularized filaments, in apparent response to increased testosterone levels in the male's bloodstream (Cunningham & Reid 1932; Urist 1973). These sexually dimorphic structures are purportedly used to supplement the respiratory needs of the young in the burrow, although actual behaviors and measurements during breeding have yet to be detailed. Young lepidosirenid lungfishes are not obligate air breathers, a trait that may reduce their exposure to a variety of predators while they are small and exceedingly vulnerable.

The Australian species, *Neoceratodus forsteri* (Fig. 13.10D) was the last lungfish to be described scientifically, in 1870 (but see Box 13.4). It has a very limited native distribution, restricted primarily to the Burnett, Fitzroy, and Mary river systems of northeastern Australia, with transplanted populations in the Brisbane River and several small reservoirs (Kemp 1987; Pusey et al. 2004). Among living lungfishes, *Neoceratodus* is closest to the ancestral forms in many anatomical respects, including a large (up to 150 cm long), relatively stout body (to 20 kg); large cycloid scales covering the entire body; flipperlike "archipterygial" fins; a pectoral fin inserted low on the body; a broad diphycercal tail; and a single lung. Fossilized toothplates undistinguishable from those belonging to *N. forsteri* have been found in Early Cretaceous deposits of New South

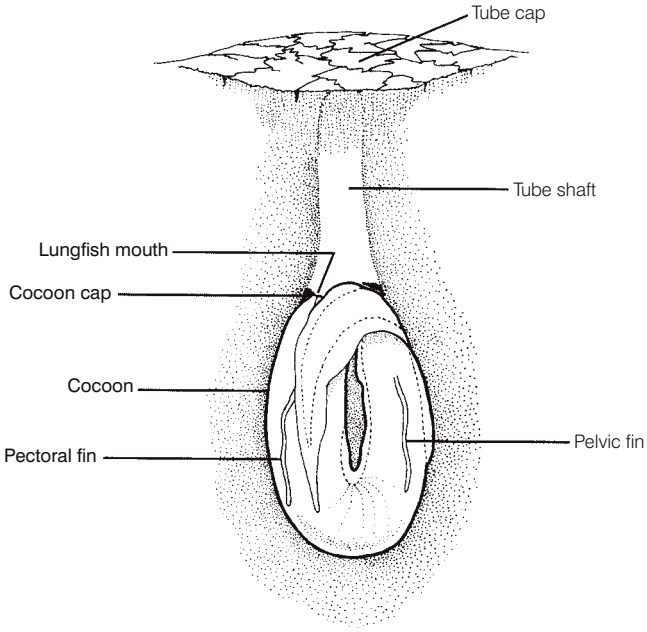

Figure 13.11
An African lungfish estivating in its mud and mucus cocoon, viewed from the ventral surface of the fish. Redrawn from Greenwood (1987).

Figure 13.12
A young African lungfish. The arrow indicates the external gills that misleadingly caused lungfishes to be classified as amphibians. From Herald (1961), used with permission of Chanticleer Press, Inc., New York.

Wales, indicating the species is at least 140 million years old. This makes *Neoceratodus* not only the oldest living lungfish but perhaps "the world's oldest living vertebrate species" (Pusey et al. 2004, p. 59).

Neoceratodus feeds in the late afternoon and maintains activity during the night, capturing benthic crustaceans, mollusks, and small fishes that it crushes with its distinctive toothplates. It is able to locate live animals by detecting the electric field emitted by the prey, adding it to the list of primitive fishes that are highly electrosensitive (Watt et al. 1999; see Chapter 6). Unlike the South American and African species, *Neoceratodus* is a **facultative air breather** that relies on gill respiration under normal circumstances. Its lung may in fact serve more as a hydrostatic than a respiratory organ (Thomson 1969a). Uptake of oxygen through the skin occurs, at least in juveniles. No special adaptations to avoid desiccation have been observed, and the fish must be kept moist and covered by wet vegetation or mud to survive out of water.

Sexes show only slight dimorphic coloration during the breeding season and are otherwise indistinguishable. In the native riverine habitat, spawning is rather unspecialized, involving deposition of eggs on aquatic plants in clean, flowing water at any time of the day or night. Fish spawn in pairs, when females deposit 50–100 eggs per spawning; no parental guarding occurs. Development of the young is direct and gradual, with no obvious larval stages or distinct metamorphosis. Young are born without external gills. Maturation does not occur until fish are 15–20 years old, and specimens in captivity in public aquaria have lived at least 65–70 years.

As a result of spawning and nursery habitat destruction brought about by impoundment construction, pollution, and perhaps interactions with introduced species, *Neoceratodus* populations have declined in some areas. The lungfish was granted Vulnerable status in 2003 under Australia's federal Environment Protection and Biodiversity Conservation Act. Fish have been transplanted into several Queensland rivers and reservoirs to aid the species' recovery.

Class Actinopterygii, Subclass Cladistia: bichirs and Reedfish

Taxonomic relationships among and within most relict groups, both in terms of affinities with other living fishes and identification of ancestral lineages, are reasonably well understood. Lungfishes, coelacanths, chondrosteans, gars, and Bowfin all have well-defined, relatively extensive fossil records with which modern species can be associated. In addition, derived traits are either unique to a group or shared with other groups in ways that confirm evolutionary hypotheses of relationship (Table 13.1). Although healthy debate on the details of relationship among these fishes exists, most researchers agree on the general patterns of interrelatedness.

Box 13.4

The seventh lungfish

No discussion of extant lungfishes would be complete without at least brief mention of *Ompax spatuloides*, Australia's other lungfish (Fig. 13.13). *Ompax* was described based on a 45 cm specimen served to the director of the Brisbane Museum during a trip to northern Queensland in 1872, 2 years after the scientific discovery of the first Australian lungfish. The fish was reputed to occur syntopically with *Neoceratodus* in a single water hole in the Burnett River. It had a body covered with large ganoid scales, small pectorals, and an elongate, depressed snout, "very much the form of the beak of the *Platypus*" (Castelnau 1879, p. 164). The Director had a sketch made of the fish, but ate it nonetheless. The sketch and notes were sent to a prominent regional ichthyologist, Count F. de Castelnau, who described the species and speculated that it was most closely related to the gars of North America. *Ompax* appeared in Australian faunal lists as a ceratodontid for 50 years, even though a second specimen was never found. Finally, in 1930, an anonymous report appeared in a Sydney newspaper recounting how the "fish" had been fabricated from the nose of a platypus, the head of a lungfish, the body of a mullet, and the tail of an eel (Herald 1961). Ichthyology's Piltdown Man had been unmasked.

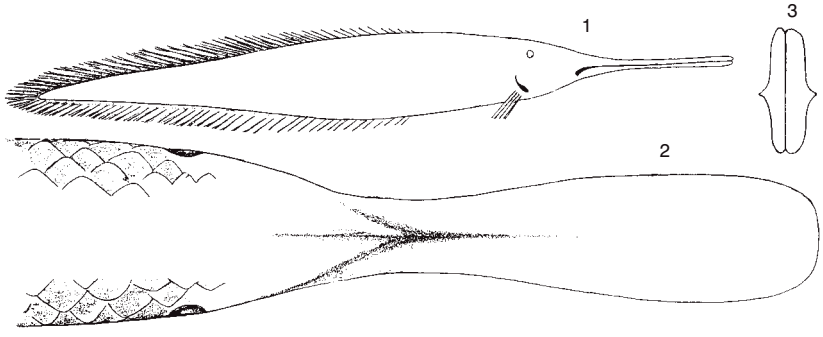

Figure 13.13
The seventh living "lungfish", *Ompax spatuloides*. This is the illustration that appeared in the original species description by Castelnau (1879). It shows (1) lateral view, (2) dorsal view of the head, and (3) presumably a cross-section of the bill, but unlabeled in the original illustration. From Castelnau (1879).

The **cladistians** stand out as an exception to this pattern of consensus. Over the years, workers have cited anatomical similarities to justify placing them variously with lungfishes, closer to the stemline sarcopterygians, or squarely amongst the Actinopterygii as another chondrostean (Patterson 1982). Other taxonomists emphasized unique characteristics and placed them in their own subclass, the Brachiopterygii. The fossil record was until recently uninformative, but fortunate discoveries in Middle–Upper Cretaceous deposits of southeastern Morocco establish definitive polypterid lineages at least as far back as 91–95 mybp (Dutheil 1999). Admittedly this is still relatively recent for what is thought to be the basal actinopterygian group (i.e., chondrosteans, thought to have arisen later, have a fossil record that goes back to the Devonian; see Chapter 11).

Modern cladistians are represented by two genera confined to west and central tropical Africa, including the Congo and Nile river basins (Fig. 13.14). Fifteen species, referred to as **bichirs** (pronounced bih-shéars), belong to the genus *Polypterus*; the remaining species is the Reedfish or Ropefish, *Erpetoichthyes* (formerly *Calamoichthyes*) *calabaricus*. Bichirs and reedfish grow to 90 cm, although most bichir species are shorter. All are predatory and inhabit shallow, vegetated, and swampy portions of lakes and rivers.

In poorly oxygenated water, bichirs are obligate air breathers and will drown if denied access to the surface. Bichirs are unique in that they use their dorsally placed spiracles to exhale (not inhale) spent air from the highly vascularized and invaginated lungs; the spiracles serve no apparent aquatic respiratory function (Abdel Magid 1966, 1967). Polypterids are additionally unique in that they inhale through their mouths by **recoil aspiration** (Brainerd et al. 1989). They use the elastic energy stored in their integumentary scale jacket during exhalation to

Table 13.1

Characteristics of extant relict fishes. Presence (+) or absence (–) of a trait, or its condition, is indicated in the body of the table. Shared characteristics among unrelated forms are strong evidence of convergent evolution, since these groups have long histories of demonstrated, separate evolution.

	Lungfishes			Chondrosteans				
Trait	**Australian**	**S. Am./Af.**	**Coelacanths**	**Sturgeons**	**Paddlefishes**	**Polypterids**	**Gars**	**Bowfin**
Scales	Cycloid	Cycloid	Cycloid[a]	Scutes[b]	–[c]	Ganoid	Ganoid	Cycloid[d]
Gular plates	–	–	2	–	–	2	–	1
Spiracle	–	–	–	+	+?	+	–	–
Larva ext gills	–	+	–	–	–	+	–	–
Lungs[e]	Sing vent	Dbl vent	Fatfill gb	Dorsal gb	Dorsal gb	Dbl vent	Vasc gb	Vasc gb
Spiral valve	+	+	+	+	+	+	+ (remnant)	+ (remnant)
Centra	–	–	–	–	–	+	+[f]	+
Tail	Diphy	Diphy	Diphy	Hetero	Hetero	Hetero[g]	Abb hetero	Abb hetero
Lobed fins	+	–	+[h]	–	–	+	–	–
Electroreceptors	+	+	+	+	+	+	–	–
Chromosome 2N	54	38/34	48[i]	112	120	36	68	46

abb, abbreviate; Af., Africa; dbl, double; diphy, diphycercal; ext, external; hetero, heterocercal; gb, gas bladder; sing, single; S. Am., South America; vasc, vascularized, cellular; vent, ventral.

[a] Coelacanths are sometimes said to have cosmoid scales, however no extant fishes have scales containing cosmine (Jarvik 1980).

[b] Sturgeons have five longitudinal rows of bony scutes, plus "dermal ossifications" scattered around the body (Vladykov & Greeley 1963, p. 25). These scutes contain ganoin and could be considered ganoid.

[c] Paddlefishes are mostly naked, with four types of scales (fulcral, rhomboid, round-based, and denticular) scattered on the head, trunk, and tail; the histology of these scales is unclear. Trunk scales are more abundant on *Psephurus* than on *Polyodon* (Grande & Bemis 1991).

[d] Bowfin "cycloid" scales are convergent not homologous with those of teleosts (Grande & Bemis 1998).

[e] Outpocketings of the esophagus are gas bladders, but are often called lungs when their primary function is breathing atmospheric air.

[f] Gar centra are opisthocoelous (concave on rear face, convex on front).

[g] Lower lobe of brachiopterygian tail created by rays coming off the ventral surface of the notochord.

[h] Coelacanth fin bases are lobed except for first dorsal.

[i] Coelacanth chromosomes are more like those of ancient frogs than of other sarcopterygians such as lungfishes (Bogart et al. 1994).

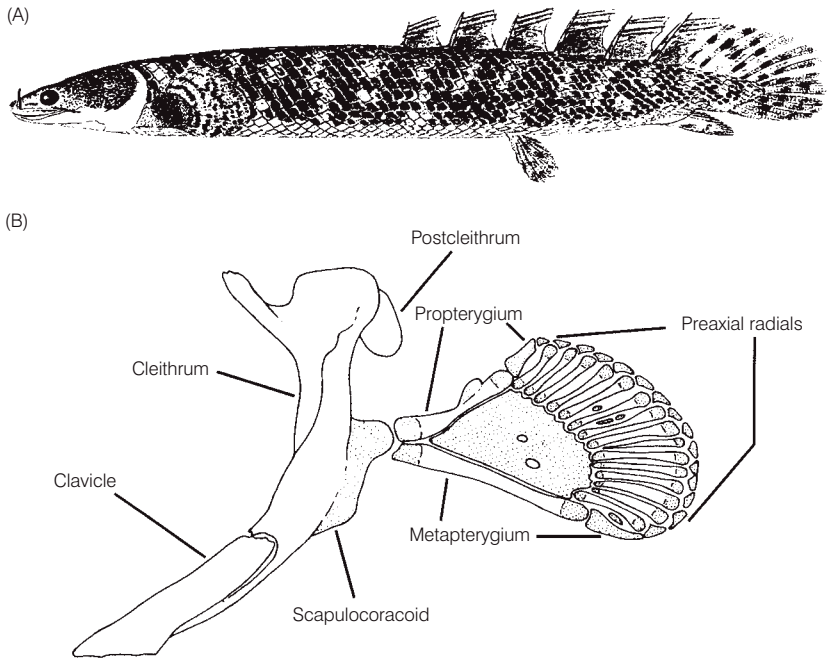

Figure 13.14

Brachiopterygians. (A) A 29 cm long bichir, *Polypterus palmas polli*, from the Ivory Coast. Note the lobelike pectoral fin base and the horizontal flaglike fin rays that extend from the distal portion of each dorsal fin spine. (B) The "peculiar and overelaborated" pectoral fin of a bichir, showing the wishbonelike basal structure (propterygium and metapterygium) that supports the radials and fin rays. (A) from Hanssens et al. (1995), used with permission; (B) from Rosen et al. (1981), courtesy of the Department of Library Services, American Museum of Natural History.

power inhalation of atmospheric air. The existence of similar bony scale rows in some Paleozoic amphibians suggests that the evolution of air breathing and perhaps eventual terrestriality may be linked to recoil aspiration that originated in fishes.

Controversy over taxonomic position arises because brachiopterygians exhibit superficial anatomical traits that have been used to justify their inclusion in almost every one of the major taxa discussed in this chapter (see Table 13.1). Cladistians possess lobelike fins (a sarcopterygian trait), ganoid scales (a palaeoniscoid or lepisosteiform trait), two gular plates (as does the coelacanth), spiracles (in common with sturgeons), feathery external gills when young and double ventral lungs (in common with lepidosirenid lungfishes), a modified heterocercal tail (as in gars and Bowfin), and a spiral valve intestine (shared by all major groups).

However, the internal structure of many of these seemingly shared primitive characteristics is very different from those of other taxa, indicating convergence on the traits and not homology. The external gills are only analogous to, not homologous with, the gills of young lungfishes. The tail is heterocercal in structure but symmetrical in external appearance; the medial and lower portions are created by rays coming off the ventral surface of the notochord, unlike any other fishes. Confusion often arises whenever we attempt to compare among living fishes, each well adapted to environmental conditions of the recent past. Many anatomical traits, in fact those most critical to systematic analyses, are retained from ancestors, whereas other traits represent recent derivations that have evolved in response to conditions greatly changed from the ancestral selection pressures. Hence we have the existence of a mosaic of primitive and derived traits in every living species, homology and analogy intertwined, with difficulty in knowing the proportions of the two. Each attempt at linking a trait in cladistians with a counterpart trait in another group becomes a possible apples-and-oranges comparison.

Cladistian autapomorphic and synapomorphic traits

The bichirs have a remarkable number of autapomorphic (unique, derived) traits. Their median and paired fins are unlike those of any other major taxon. Bichirs are also referred to as "flagfins" because the 5–18 dorsal finlets each consist of a vertical spine to which are attached horizontal rays, giving them a "flag and pole" appearance. In all other ray-finned fishes, the dorsal fin rays emerge as vertical bony elements from the body of the fish. The pectoral fin is lobe-shaped but constructed differently from the lobe fins of lungfishes and crossopterygians, or for that matter, any other fish, living or extinct. The supporting structures of the pectoral fin are shaped like a wishbone with a flat plate (Fig. 13.14B). A. S. Romer, a leader of modern vertebrate paleontology, referred to the polypterid pectoral fin as a "peculiar and overelaborated development" (Romer 1962, p. 198).

Other apparent autapomorphic traits include relatively few and small chromosomes (Denton & Howell 1973); the structure, arrangement, replacement, and differentiation of teeth (Wacker et al. 2001); and possession of only four rather than five gill arches, the fifth having been lost (Britz & Johnson 2003). And recoil aspiration breathing is performed by no other known extant group.

The placement of cladistians at the base of bony fish phylogeny is justified by a number of derived traits shared with the rest of the Actinopterygii. These characters include egg structure, nuclear DNA-coded genes, *Hox-A* gene sequences, mitochondrial DNA and amino acid sequences, and cranial skeleton morphology and function (Bartsch 1997; Bartsch & Britz 1997; Venkatesh et al. 2001; Chiu et al. 2004; Kikugawa et al. 2004). These and other synapomorphies make the Cladistia "the sister group of all other actinopterygians" (Nelson 2006, p. 88), rather than a sarcopterygian or a chondrostean. The issue appears to be settled.

Class Actinopterygii, Subclass Chondrostei, Order Acipenseriformes: sturgeons and paddlefishes

Although considered primitive actinopterygians, the extant acipenseriform sturgeons and paddlefishes are highly derived, relict species that bear little resemblance to ancestral chondrosteans. The two families probably diverged from each other during the Jurassic, but they still share a number of characteristics such as a cartilaginous skeleton, heterocercal tail, reduced squamation, more fin rays than supporting skeletal elements, unique jaw suspension, and a spiral valve intestine. Although largely cartilaginous, their skeletons are secondarily so: ancestral, Early Mesozoic chondrosteans (more correctly palaeoniscoids) were bony.

Acipenseridae

All 25 species of sturgeons are in the family Acipenseridae and are restricted to the northern hemisphere (Binkowski & Doroshov 1985; Williams & Clemmer 1991; Bemis et al. 1997; Vecsei et al. 2001; Van Winkle et al. 2002). Four genera are recognized, *Acipenser*, *Huso*, *Scaphirhynchus*, and *Pseudoscaphirhynchus*. All species spawn in fresh water, although some species move seasonally between marine and fresh water and some are technically anadromous. Species restricted to fresh water include the North American Lake Sturgeon (*Acipenser fulvescens*) and three river sturgeons (*Scaphirhynchus* spp.), the latter occurring only in larger rivers such as the Mississippi and Missouri. Anadromous species, those spending part of their lives at sea but returning to fresh water to spawn, include the Atlantic Sturgeon, *Acipenser oxyrhynchus*, the White Sturgeon, *A. transmontanus* (the largest North American freshwater fish, attaining a length of 3.6 m and a weight of 800 kg), and the beluga of eastern Europe and Asia, *Huso huso* (the largest and economically most valuable freshwater fish in the world, attaining a length of 8.6 m and a weight of 1300 kg, and not to be confused with the toothed whale of the same common name). As with other anadromous species (see Chapter 23, Diadromy), landlocked populations of sturgeons can develop.

Anatomically, sturgeons can be identified by the four barbels in front of the ventrally located mouth, five rows of bony scutes (large bony shields) on a body otherwise covered with minute ossifications, a heterocercal tail, elongate snout, a single dorsal fin situated near the tail, no branchiostegal rays, and a largely cartilaginous endoskeleton, including an unconstricted notochord (Fig. 13.15).

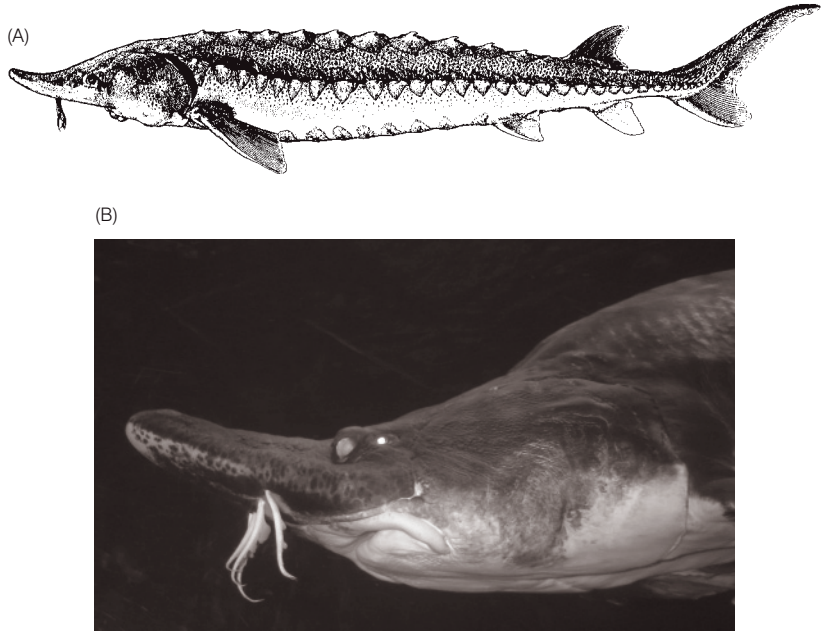

Figure 13.15
Sturgeons. (A) An Atlantic Sturgeon, *Acipenser oxyrhynchus*. Note the rows of bony scutes on the body, distinct heterocercal tail, and elongate snout with barbels preceding the ventral mouth. (B) A live Beluga sturgeon, *Huso huso*, perhaps the largest freshwater fish in the world. The bright spot is the eye, which sits just posterior to the spiracle. (A) from Vladykov and Greeley (1963), used with permission; (B) photo by G. Helfman.

Although generally slow-swimming feeders on benthic invertebrates, the protrusible mouth can be extended very rapidly, allowing larger individuals to feed on fishes (Carroll & Wainwright 2003). Vision plays at best a minimal role in prey detection, with touch, chemoreception, and probably electrolocation via rostral ampullary organs being more important (Buddington & Christofferson 1985; Gibbs & Northcutt 2004).

The life history traits of sturgeon make them unique and susceptible to overexploitation by humans. They are exceptionally long-lived: Beluga have been aged at 118 years, and White Sturgeon at 70–80 years (Nikolsky 1961; Scott & Crossman 1973; Casteel 1976). As is often the case with long-lived vertebrates, sexual maturity is attained slowly. In the Atlantic Sturgeon, both sexes mature after 5–30 years, the older ages characterizing individuals at higher latitudes. After maturation, females may only spawn every 3–5 years (Smith 1985b), and even longer intervals may characterize other sturgeon species. Fecundity is relatively high: ovaries may account for 25% of the body mass of a female, making a large female exceedingly valuable. A beluga female captured in 1924 from the Tikhaya Sosna River of Russia weighed 1227 kg and yielded 245 kg of caviar (www.guinnessworldrecords.com). High-grade caviar can sell for more than US$150/oz or $5000/kg, making the fish potentially worth in excess of $1 million.

Sturgeon are also commercially valuable as a smoked product, and the gas bladder was processed into isinglass and used for gelatin, clarifying agents, and as a commercial art glue. Natural predators beyond the juvenile stage are rare; parasitic lampreys are one of the few organisms capable of attacking an adult sturgeon (Scott & Crossman 1973). Hence natural mortality rates of adults were historically low, creating vulnerability when such species are subjected to the high mortality rates associated with commercial exploitation.

It is therefore not surprising that sturgeons worldwide have declined due to overexploitation, dam building, habitat destruction, and pollution. Large Atlantic Sturgeon were at one time sufficiently abundant in North American coastal rivers that navigation by canoes and small boats was sometimes hazardous, particularly given the fish's habit of leaping 1–2 m out of the water. Commercial landings exceeded 3 million kg annually in 1890, but 100 years later, landings were reduced by 99% (Smith 1985b).

Lake Sturgeon have been extirpated from a large part of their native range (ironically, Lake Sturgeon disappeared from the Sturgeon Falls area of the Menominee River, Wisconsin around 1969; Thuemler 1985). The Shortnose Sturgeon *Acipenser brevirostrum* of North America and the Baltic Sturgeon *Acipenser sturio* are two of the only nine fish species that appear in CITES Appendix I (www.cites.org/eng/append/appendices.pdf). Internationally, nine sturgeon stocks or subspecies are Critically Endangered, 25 are Endangered, and 13 are Vulnerable (www.redlist.org). Five US species have Endangered Species Act protection, including the Alabama Sturgeon *Scaphirhynchus suttkusi*, the most recent sturgeon to have been described (Scharpf 2000). Although sturgeon fishing is highly regulated nationally and internationally, high economic values have promoted rampant poaching and black markets, at the same time that fishery management and enforcement programs have collapsed (Vecsei 2005; Helfman 2007).

Part of the vulnerability of sturgeons results from an interaction between habitat degradation and the reproductive biology of these large, slow maturing fishes. Spawning is hampered by siltation and contamination of clean gravel and rock areas, and by dam construction that blocks migrations and limits access to spawning sites. The spawning period in several species may be very short, on the order of 3–5 days, and if environmental conditions are inappropriate, spawning may be abandoned for that year (Buckley & Kynard 1985; Williot et al. 2002). Recruitment of new fish into the population is further prevented by overharvest of mature individuals and also of fish before they reach reproductive age (sometimes as a result of incidental bycatch of juveniles in gillnets set for anadromous shad or salmon). Given late maturation and the infrequency of spawning, stocks driven to low numbers have a difficult time recovering, requiring extreme management solutions and justifying captive propagation of many species (Binkowski & Doroshov 1985; Billard & Lecointre 2001; Pikitch et al. 2005).

Acipenseroid fishes are generally regarded as highly modified descendants of palaeoniscoids that lived during the Permian and Triassic. Recognizable acipenseriforms have been found in Permian deposits in China (Lu et al. 2005), and early, recognizable sturgeon fossils date to the Upper Cretaceous of Montana (Wilimovsky 1956; Choudhury & Dick 1998). A related, extinct family, the Chondrosteidae, is known from fossils from the Lower Jurassic to Lower Cretaceous periods.

Polyodontidae

Paddlefishes also date back at least to the Early Cretaceous (Grande et al. 2002), but only two species remain, the Paddlefish of North America, *Polyodon spathula*, and the Chinese Paddlefish, *Psephurus gladius* (Fig. 13.16A, B). They have larvae similar to those of sturgeons and retain the heterocercal tail, unconstricted notochord, largely cartilaginous endoskeleton (with ossified head bones), spiracle, spiral valve intestine, and two small barbels. They differ from the acipenserids in most other respects. The bony scutes are missing and the body is essentially naked except for patches of minute scales. Paddlefishes are not benthic swimmers but instead move through the open waters of large, free-flowing rivers, feeding on zooplankton or fishes.

The North American Paddlefish, or spoonbill cat, prefers rivers with abundant zooplankton. Adult Paddlefish typically

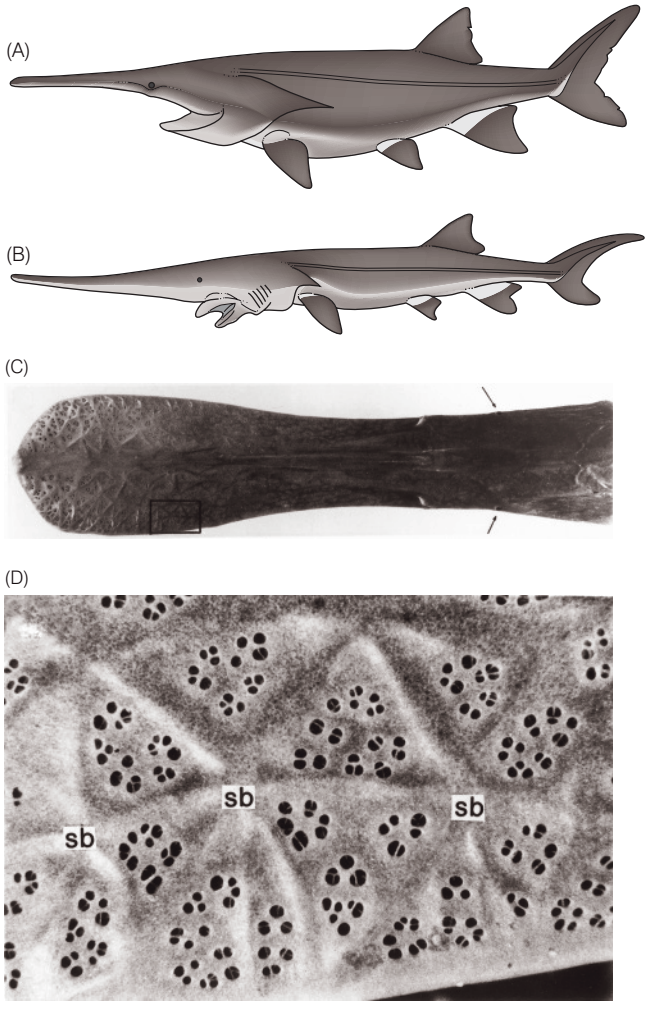

Figure 13.16

Paddlefishes. (A) The North American Paddlefish, *Polyodon spathula*. (B) The Chinese Paddlefish, *Psephurus gladius*, a poorly known, critically endangered chondrostean restricted to the Yangtze River system of China. (C) The rostral paddle of the North American Paddlefish in dorsal view; arrows indicate position of the eyes. (D) Area at lower left of (C) enlarged, showing the stellate bones (sb) that support the paddle, and the ampullary organs, which are the dark circular holes in the paddle that reportedly serve as electroreceptors. (A, B) drawings after P. Vecsei in CITES (2001); (C, D) from Grande and Bemis (1991), used with permission.

swim through the water both day and night with the non-protrusible mouth open, straining zooplankton and aquatic insect larvae indiscriminately through the numerous, fine gill rakers. Food size is limited by gill raker spacing, as small zooplankters escape the mechanical sieve of the Paddlefish's mouth (Rosen & Hales 1981). This picture of the Paddlefish as a passive filterer is confused by the occasional benthic and water column fishes, such as darters and shad, found in its stomach (Carlander 1969). Small juveniles, in which neither gill rakers nor the paddle are well developed, pick individual zooplankters out of the water column.

The function of the **rostral paddle**, which accounts for one-third of the body length in adults, remained something of a mystery until recently. It is now well established that the abundant ampullary receptors on the surface of the paddle and operculum serve to detect biologically generated electricity (Fig. 13.16C, D). Paddlefish, especially juveniles, use the ampullary receptors to detect weak electric fields created by individual plankton such as water fleas (*Daphnia*) from distances of up to 9 cm, without using vision or other senses (Wilkens et al. 2002). The paddlefish rostrum is therefore equivalent to "an electrical antenna, enabling the fish to accurately detect and capture its planktonic food in turbid river environments where vision is severely limited" (Wilkens et al. 1997, p. 1723).

North American Paddlefish may live for 30 years and attain 2.2 m length and 83 kg mass, although fish of this size are now exceedingly rare. Diminishing populations are evidenced by changes in the species' range. Although currently restricted to the Mississippi River drainage system, populations of Paddlefish historically occurred in the Laurentian Great Lakes and have been extirpated from at least four states (Gengerke 1986). Causes of population decline are similar to those affecting sturgeon. Paddlefish are long-lived but do not mature until they are 7–9 (males) or 10–12 (females) years old, and then spawn only at 2–5-year intervals. Loss of spawning habitat, which is fast-flowing, clean, gravel bottoms, is a major problem. Appropriate spawning areas are degraded by damming, which decreases water flow and leads to siltation. Paddlefish are sought commercially and recreationally for their flesh and eggs; overfishing has been frequently implicated in population declines (Russell 1986). Manmade reservoirs are productive feeding habitats for adults but do not provide appropriate spawning areas. Although not federally protected in the USA, all US states along the Missouri River have prohibited commercial fishing for it (Graham 1997b). The species has been listed in Appendix II of CITES, thus providing a mechanism to curtail overfishing and illegal trade, especially of Paddlefish caviar (Jennings & Zigler 2000).

The exceedingly rare, critically endangered, and poorly known Chinese Paddlefish, *Psephurus gladius* (see Fig. 13.16B), is the more primitive of the two species and differs primarily in head and jaw morphology and body size. The paddle is narrow and more pointed, not broad and rounded. *Psephurus* also has fewer but thicker gill rakers that resemble those of sturgeons, a protrusible mouth, and grows larger (over 3 m and 500 kg, erroneously reported to 7 m). It inhabits the Yangtze River system of central China and feeds primarily on small, water column and benthic fishes (Nichols 1943; Nikolsky 1961; Liu & Zeng 1988). Historically it also occurred in the Yellow River. Relatively little is known about its biology, including spawning habits, locales, or habitat (Liu & Zeng 1988; Grande & Bemis 1991; Birstein & Bemis 1995; Wei et al. 1997).

Psephurus is highly prized for its caviar but is now considered the most endangered fish in China because of overfishing, habitat destruction, and dam construction that blocks adults from reaching spawning grounds. It is probably anadromous, adults moving upriver to spawn and juveniles moving down to the East China Sea to grow. Gezhouba Dam on the Yangtze, completed in 1981, essentially cut the Paddlefish's habitat in half and blocked spawning migrations. The species has had full protection in China since 1983 but no recruitment to the population is thought to be occurring, and fewer than 10 adult Paddlefish have been caught annually below the dam since 1988 (Wei et al. 1997). The massive Three Gorges Dam, scheduled for completion in 2009, will likely drive the species into extinction (Fu et al. 2003). Artificial propagation has been attempted but has failed because the fish cannot be kept in captivity.

The fossil record for polyodontids is limited to four known species and some fragments, the most primitive from the Lower Cretaceous of China and the others from the Upper Cretaceous, Paleocene, and Eocene of North America (Grande & Bemis 1991; Grande et al. 2002). The jaws and gill arches of the oldest species, *Protopsephurus liui*, resemble those of *Psephurus*, indicating that piscivory is the ancestral condition and that planktivory as observed in *Polyodon* is a derived trait (Grande et al. 2002).

Subclass Neopterygii, Order Lepisosteiformes (or Semionotiformes): the gars

The gars and Bowfin are descendants of the palaeoniscoids that dominated fresh and marine waters for 200 million years from the Mid Devonian into the Mesozoic Era. Traditionally, gars and Bowfin were considered members of the order **Holostei**, which also included a variety of extinct fishes. However, most recent analyses conclude that holosteans are paraphyletic, more a grade of development than a true clade. The two modern groups differ in many important respects and their relationships to the palaeoniscoids, and position in the lineage leading to modern teleosts, are a matter of discussion. Both groups are considered neopterygian because of shared jaw, tail, and dermal armor characteristics. Most workers consider gars to be more primitive and place them in their own division (**Ginglymodii**), but some view *Amia* as the more primitive group (Normark et al. 1991; Olsen & McCune 1991; Grande & Bemis 1998).

All seven species of living gars are in the family **Lepisosteidae**, four in *Lepisosteus* and three in *Atractosteus* (Fig. 13.17). These elongate, predatory fishes are restricted to North and Central America and Cuba; five species occur east of the Rocky Mountains in North America, the remaining species occur in Central America. Gars typically inhabit backwater areas of lakes and rivers, such as oxbows and bayous. Oxygen tension in such habitats is often low and gars must breath atmospheric air at these times, using their compartmentalized, highly vascularized gas bladder as a lung (Smatresk & Cameron 1982; Smith & Kramer 1986).

Gars have entirely ossified skeletons. Their primitiveness is evident in their hinged, diamond-shaped, interlocking ganoidlike scales and abbreviate heterocercal caudal fin. Ganoin is an enamel-like material on the upper surface of the scale and characterized the squamation of the Paleozoic and Early Mesozoic palaeoniscoids, which are thought to be ancestral to (or a sister group of) modern teleostean groups. The gars have retained this primitive trait. The same logic applies to the caudal skeleton. Abbreviate

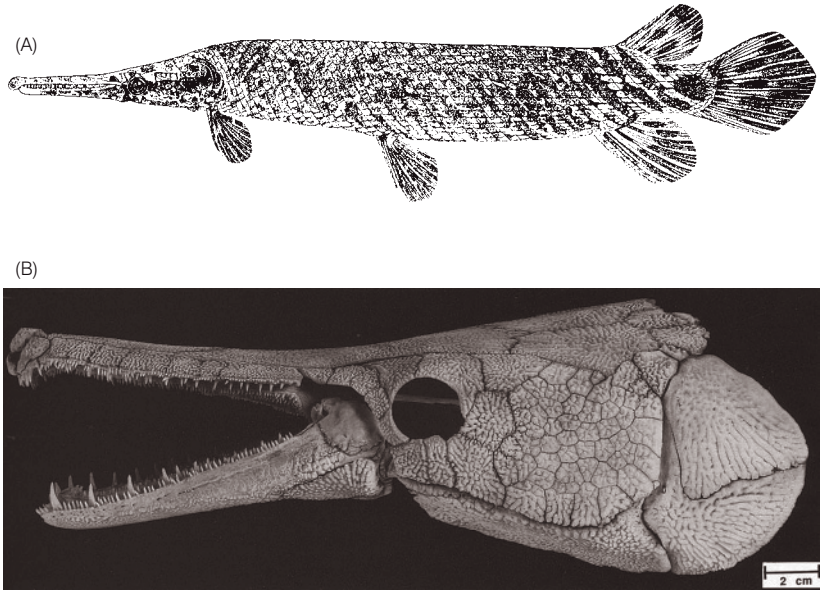

Figure 13.17
Gars. (A) A Florida Gar, *Lepisosteus platyrhincus*, showing the distinctive elongate, tooth-studded snout and posteriorly placed dorsal and anal fins characteristic of this family of North and Central American predators. (B) Head of the large Alligator Gar, *Atractosteus spatula*. Note the numerous bones in the head and cheek and the myriad needlelike teeth. (A) from Suttkus (1963), used with permission; (B) from Grande and Bemis (1998), used with permission.

Figure 13.18
A large Alligator Gar caught in Texas. Photo courtesy of Jean-Francois Healias, www.anglingthailand.com.

heterocercal tails characterized the later "holosteans" but have given way to the homocercal tail of the teleosts. A constricted and ossified notochord may be a derived innovation in lepisosteids rather than an indication of ancestral status to teleosts, since lepisosteid vertebral centra are essentially unique among living fishes. Gar centra are **opisthocoelous**, being concave on their posterior surface and convex on the anterior surface, allowing for a "ball-and-socket" articulation (most fishes have **amphicoelous** vertebrae in which both surfaces are concave; only one blenny species, some tailed amphibians, and a few birds have opisthocoelous vertebrae) (Suttkus 1963; Wiley 1976). The name Ginglymodii refers to the hinged articulation between the vertebrae.

The Alligator Gar, *Atractosteus spatula*, is the largest member of the family and one of the largest freshwater fishes in North America (Fig. 13.18). It attains a length of 3 m and a weight of 140 kg (Suttkus 1963). Although most gars are considered water column predators on other fishes and often hover just below the surface, Alligator Gars also feed extensively on bottom-dwelling fishes and invertebrates, and scavenge on benthic food (Seidensticker 1987). Alligator Gars, as well as other species, frequently enter estuarine regions (Suttkus 1963).

Comparatively little is known about the life history and general biology of gars. This is unfortunate because they are ecologically important in many fish assemblages, often becoming quite abundant in rivers and backwaters. Gars are additionally interesting in that they are the only freshwater fishes in North America with toxic eggs. The eggs are distinctly green in color and can cause sickness and even death when eaten by chickens and mice. However, the possible ecological function of this toxicity, and whether it actually affects fish or invertebrates that might feed on the eggs, remains undetermined (Netsch & Witt 1962).

Seven fossil species of gars are recognized, dating back to the Lower Cretaceous of North America, Europe, Africa, and India, and indicating a widespread Pangean distribution (Wiley 1976; Stiassny et al. 2004).

Order Amiiformes: the Bowfin

The Bowfin, *Amia calva*, is generally considered more derived than the gars (Fig. 13.19). *Amia* and its extinct relatives in two other orders make up the subdivision **Halecomorphi**, which is the sister taxon to the division Teleostei (Halecomorphi + Teleostei = **Halecostomi**). *Amia* retains the abbreviate heterocercal tail and rudimentary spiral valve intestine of more primitive groups, but has teleost-like amphicoelous vertebrae as well as cycloid scales, a scale type in which the ganoid and dentine layers have been lost, leaving only a reduced bony layer. The Bowfin's cycloid scales resemble those in teleosts but are probably convergent and not homologous with teleostean cycloid scales (Jarvik 1980; Stiassny et al. 2004). The Bowfin's head is exceptionally bony, invested in massive dermal bones that are greatly reduced in teleosts.

The Bowfin is distinct among all living fishes in possessing a single, median **gular plate** on the underside of the head (Fig. 13.19D). It is the only non-teleostean fish to swim via undulations of its long dorsal fin, which allows it to move slowly both forward and backward with stealth. Rapid swimming is accomplished by more conventional body and tail movements (Scott & Crossman 1973; Becker 1983).

The Bowfin is widely distributed throughout much of the eastern half of North America from southern Quebec and

Figure 13.19

(A) The Bowfin, *Amia calva*, a member of a monotypic order endemic to North America. (B) Entire skeleton; note the elongate dorsal fin used in slow forward and backward locomotion and the upturned caudal vertebrae forming the abbreviate heterocercal fin. (C) Skull showing the multiplicity of bones that are later lost or fused in teleosts. (D) Anterior view looking into the mouth; the abundant, large teeth are evident, as is the single gular plate on the underside of the head. From Grande and Bemis (1998), used with permission.

Ontario to eastern Texas. It is most common in vegetated lakes and backwater areas of large rivers, occupying deeper waters by day and moving into shallows at night to feed. It has abundant, sharp, conical, slightly curved teeth on both the jaws and palate (the internal structure of the teeth is unique among vertebrates); strong jaw musculature; large size (to 1 m and 9 kg); and opportunistic, predatory habits. Bowfin feed on invertebrates, fishes, frogs, turtles, snakes, and small mammals, which they engulf via suction, whereas gar impale food on their small, sharp teeth (Lauder 1980).

Bowfin males build nests in shallow water by clearing a circular depression on the bottom about 0.5 m across. The males also engage in parental care, guarding the young vigorously until they are relatively large (10 cm). The male has a distinct black spot at the base of its caudal fin; such nonseasonal sexual dimorphism does not occur in other living primitive bony fishes, although males and females differ in many teleosts.

Amia is incapable of surviving in warm, deoxygenated water without access to atmospheric oxygen. As in gars, Bowfin gulp air and pass it to a highly vascularized gas bladder. Some controversy has developed over whether Bowfin are capable of lungfishlike estivation in drying conditions. Anecdotal evidence suggests that Bowfin can bury in mud and survive for periods of weeks (e.g., Green 1966), whereas experimental laboratory findings suggest that Bowfin are physiologically incapable of surviving more than 3–5 days of air exposure (McKenzie & Randall 1990). Definitive field manipulations have yet to be performed.

Amiiform fishes have been distinct since the Early Jurassic, amiids appeared in the Late Jurassic, and the genus *Amia* dates back at least to the Early Eocene (Grande & Bemis 1998). The fossil record reveals 11 genera and 27 other amiid species, including three other species in the genus *Amia*; representatives occurred in North and South America, Europe, Asia, and Africa (Grande & Bemis 1998). Many were marine fishes and almost all were piscivorous, as evidenced by fish remains in their stomachs. One Eocene giant, *Maliamia gigas*, from West Africa may have attained a length of 3.5 m (Patterson & Longbottom 1989).

Conclusions

Trends in the characteristics of the living members of ancient groups, and comparisons with the recently successful teleosts, raise a number of intriguing questions. As anatomically and taxonomically diverse as these relict fishes are, certain convergent similarities in morphology, behavior, and ecology suggest interesting evolutionary patterns that may have characterized the evolution of major fish groups (see Table 13.1). The success of extant lungfishes, gars, the Bowfin, and the enigmatic bichirs in swampy, seasonally evaporating, tropical or semitropical environments underscores the question of evolutionary succession among major fish lineages.

Are we dealing here with relegation of these remnant, competitively inferior groups to marginal habitats, or are we faced instead with the continued superiority of ancient groups in the habitats where they originally evolved and in which they had an evolutionary headstart? What explains retention or independent evolution of the spiral valve in most of these primitive groups and the Chondrichthyes, but its replacement in higher bony fishes with a linear intestine? The same can be asked about electroreception. Why is it retained in primitive groups (except *Amia* and the gars) but lost in most modern higher taxa, except for a few which have independently re-evolved and elaborated the electrical sense (see Chapter 6)? Are the trends that characterize fish evolution in general (see Table 11.1) – reduction in bony armor, development of the pipette mouth and pharyngeal dentition, elaboration of the dorsal fin, relocation of pelvic and pectoral girdles, an increasingly symmetrical caudal fin – necessarily improvements on the primitive design? If so, how have the relict species managed to hold on in the face of what should be superior competition and predation by the "more" successful, improved teleosts? And finally, why have these few species, among the thousands of ancestral species and their derivatives, survived so long while their relatives succumbed to the ultimate fate of all organisms?

Summary

SUMMARY

1. Teleosts are the most successful fishes alive today, but a few highly derived species of several primitive groups represent the successful fishes of the past. These are the lancelets, hagfishes, lampreys, coelacanths, lungfishes, sturgeons, paddlefishes, bichirs, gars, and Bowfin.
2. Cephalochordate lancelets are arguably fishes that lack most chordate structures. They are filter-feeding bottom dwellers. Lampreys and hagfishes are jawless fishes that are probably convergently similar. Differences in mouth position, tooth and tongue morphology, embryology, pineal complex, and gill structure suggest separate ancestries. Hagfishes are entirely marine, high-latitude predators and scavengers that lack larvae but produce copious slime and can tie themselves into knots. Commercial "eelskin" comes from hagfishes. Lampreys are primarily freshwater, temperate, often parasitic fishes with complex life cycles. Numerous nonparasitic species have evolved from parasitic ancestors.
3. Coelacanths were thought to have gone extinct about 80 mybp, until a live one was captured in 1938 off South Africa. Today, a small, endangered population of 200–600 fish exists in the Comores Islands, and additional populations of unknown size have been located in Indonesia (a different species), South Africa, Madagascar, and along eastern Africa. The living coelacanths are very much like their Paleozoic ancestors, with lobe fins, diphycercal tail, hollow spines, a specialized notochord, jointed skull, young born alive, and tetrapod-like locomotion.
4. Living lungfishes are a small subset of a widely distributed, diverse Paleozoic and Mesozoic subclass. The Australian lungfish is most like earlier species; the South American and African species are highly derived in many respects. Lungfishes lack jaw teeth but have unusual toothplates on the mouth roof and floor. African lungfishes can estivate in dried mud for up to 4 years.
5. The most primitive actinopterygian fishes are the highly derived, relict, chondrostean sturgeons and paddlefishes. They share many traits (cartilaginous skeleton, heterocercal tail, few scales, numerous fin supports, unique jaw suspension), but differ in most respects. Sturgeons are large, freshwater and anadromous, long-lived fishes of North America, Europe and Asia that are highly prized for their eggs (caviar) and have been heavily overfished. Two species of paddlefishes occur in large rivers of North America and China. Paddlefishes have a long snout that may be used to detect weak electric fields.
6. The bichirs and Reedfish of Africa have been variously placed with the lungfishes, lobefins, and rayfins

because they have larvae with gills, lobelike fins, ganoid scales, and a modified heterocercal tail. But they have uniquely constructed median, caudal, and paired fins and an unusual chromosomal arrangement, causing most taxonomists to place them in their own subclass, the Cladistia or Brachiopterygia.

7 Two living orders represent close ancestors of teleosts. The lepisosteiform gars are predaceous fishes that occur in North and Central America, where they occupy backwaters and swamps. They breath atmospheric oxygen via a highly vascularized gas bladder. Unusual traits include interlocking ganoid scales, opisthocoelous vertebral centra (convex anteriorly, concave posteriorly), an abbreviate heterocercal tail, and poisonous eggs. Closer to the teleosts is the monotypic Bowfin (Amiiformes). Bowfin are restricted to eastern North America. They can also breath atmospheric air and are predaceous. Bowfin have cycloid scales, biconcave vertebra, a large gular plate, an elongate dorsal fin, and the males guard the young for an extended period.

Supplementary reading

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Chapter 14

Teleosts at last I: bonytongues through anglerfishes

Chapter contents

CHAPTER CONTENTS

By far the dominant living fishes are members of the division Teleostei. The name **teleost** means roughly "perfect bone", referring to their evolutionary position as the most advanced of the living, bony fishes. Bone mass in teleosts is reduced from the pre-teleostean condition, but internal cross-struts in the bone give it exceptional strength without great mass. Teleosts account for 96% of all living fishes, including most major fishery species. They inhabit the widest range of habitat types and show the greatest variation in body plans and foraging and reproductive habits of any fishes. By comparison, all the more primitive extant groups introduced in Chapter 12 and 13 are carnivorous and occur in a limited number of habitats. Elasmobranchs are 99% marine, whereas lungfishes, gars, Bowfin, and sturgeons are largely big river or swamp dwellers.

Teleosts in contrast occur in every imaginable freshwater and marine habitat, from ocean trenches to high mountain lakes and streams, from polar oceans at –2°C to alkaline hot springs at 41°C, from torrential rivers and wave tossed coastlines to stagnant pools. There are flying, walking, and immobile teleosts, and annual teleosts that emerge from resting eggs when it rains and then breed and die. Some teleosts brood their eggs and young in their mouths, others lay eggs inside mussels, and some jump out of the water to lay eggs on the undersides of terrestrial plant leaves and periodically splash them to keep them moist. Trophically, teleosts feed on other fishes, carrion, invertebrates, mammals including man, scales, eyes, eggs, and zooplankton. But the teleosts are the only group of fishes that utilize plant material in all its forms, including phytoplankton, cyanobacteria, algae, detritus, and vascular plants and their seeds. The only truly endoparasitic vertebrates are teleosts. Some teleosts produce either light or electricity. Teleosts are the most diverse and diversified taxon of all the vertebrates, having radiated into more niches and adaptive zones than all the other vertebrate groups combined.

It is obvious that detailed information cannot be given on even a subset of the approximately 27,000 living teleostean species. Our objectives in this chapter are to provide a feeling for: (i) what characterizes a teleost and separates it from the more primitive fishes discussed earlier; (ii) what characteristics separate different taxa within the teleosts and represent evolutionary advances within the division; (iii) what groups have been successful in what regions and habitat types; and (iv) what are some of the more interesting species and adaptations in this exceptionally successful group. Our focus is on living fishes, but it should be recalled that teleosts have existed since the Mesozoic and that the taxonomy of many of these groups is strongly influenced by characteristics of relatives known only from fossils.

Teleostean phylogeny

Teleosts per se arose in the Middle Mesozoic (probably Late Triassic, *c.* 200 million years ago), from a neopterygian

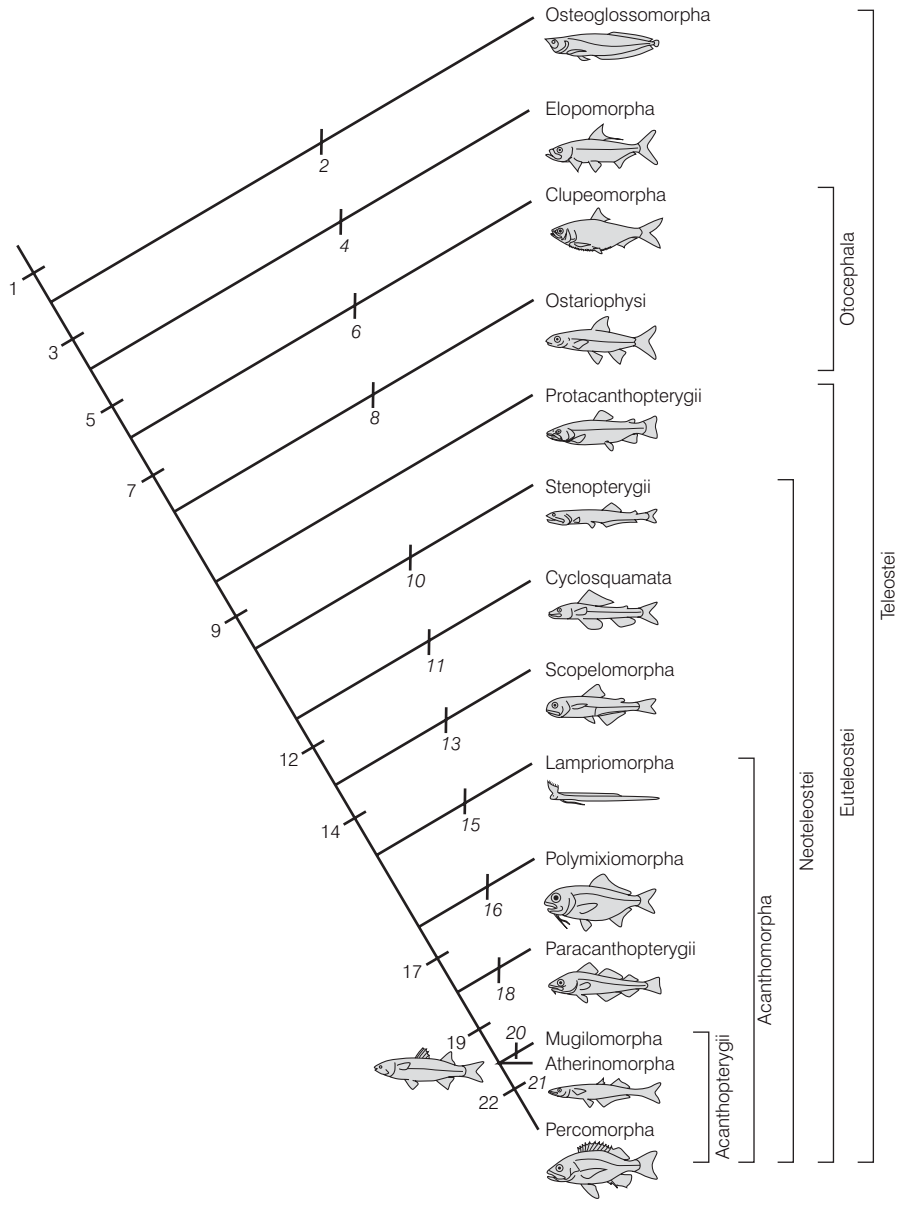

Figure 14.1

Phylogenetic relationships among living teleosts. The numbered characteristics defining the branching points (synapomorphies) are selected from a much larger list; groups after a branch point share the traits (although traits may be secondarily lost), groups before a branch do not share the trait. Italicized numbers are unique derived traits (autapomorphies) particular to a group and not shared by other taxa. Characteristics 1–7 largely repeat characters 11–18 in the cladogram of Fig. 11.23. Monophyly and definition of some groups are a matter of debate and no synapomorphies are given (i.e., the Protacanthopterygii (osmeriform smelts, salmoniform salmons) remain a problematic group that lacks well-defined, unifying characteristics). Additional details can be found in Lauder and Liem (1983), Nelson (1994), Pough et al. (2005), and papers cited in those publications.

1, mobile premaxilla, posterior neural arches (uroneurals) elongate, ventral pharyngeal toothplates unpaired; particular combination of skull bones present (basihyal, four pharyngobranchials, three hypobranchials); *2*, toothplate on tongue bites against roof of mouth; intestine lies to the left of stomach; 3, two uroneural bones extend over the second tail centrum; epipleural intermuscular bones abundant in abdominal and caudal region; *4*, ribbon-shaped (leptocephalus) larva; 5, neural arch of first tail vertebra reduced or missing; upper pharyngeal jaws fused to gill arch elements, jaw joint with unique articulation and ossification; *6*, specialized ear-to-gas-bladder connection; 7, dorsal adipose fin and nuptial tubercles on head and body; first uroneural bones of tail have paired anterior membranous outgrowth; *8*, anterior vertebrae and ribs modified to connect gas bladder to inner ear (Weberian apparatus); epidermal cells produce alarm substance; 9, first vertebra articulates with three bones of the skull (basioccipital and the two exoccipitals), retractor dorsalis muscle connects vertebral column with upper pharyngeal jaws, hinged jaw teeth capable of depression posteriorly; *10*, unique photophore histology and tooth attachment; *11*, unique gill arch structure involving second and third pharyngobranchials; 12, fifth upper pharyngeal toothplate and associated internal levator muscle missing; *13*, upper pharyngeal jaw dominated by third pharyngobranchial; 14, configuration of rostral cartilage and its ligamentous connection to premaxilla; lateral ethmoids joined to vomer; *15*, uniquely protrusible upper jaw; *16*, ligament connecting palatine and premaxilla in a unique position; 17, expanded premaxillary processes; *18*, dorsal (neural) spine attached to second preural vertebra; 19, branchial retractor muscle (retractor dorsalis) inserts only on third pharyngobranchial; well-developed ascending process of premaxilla allows increased jaw mobility; ligament supporting pectoral girdle (Baudelot's ligament) originates on basioccipital of skull rather than on first vertebra; *20*, no direct connection between pelvic girdle and cleithrum of pectoral girdle; *21*, jaw protrusion occurs without ball-and-socket joint between palatine and maxilla; fourth pharyngobranchial lost; *22*, pelvic girdle attached to pectoral girdle; anterior pelvic process displaced ventrally; pelvic fins have one spine and five soft rays. Additional characteristics are given in this and the following chapters. Fish drawings from Nelson (2006), used with permission.

ancestor, possibly a pachycormiform (see Chapter 11, Subclass Neopterygii). The earliest teleosts were probably pholidophoroids or leptolepoids, groups that consisted of several families and that may have been ancestral to more than one of the main lineages of teleosts, including the osteoglossomorphs and elopomorphs. The important point to remember, reiterating the phylogenetic account given in Chapter 11, is that modern teleosts arose during four major radiations that produced the subdivisions **Osteoglossomorpha**, **Elopomorpha**, **Otocephala**, and **Euteleostei**, the latter being by far the largest.

A listing of teleostean families is unavoidable, in part to appreciate their tremendous diversity but also because most fishes encountered anywhere in the world will belong to one of the 40 orders and 448 families (and 4278 genera) of teleosts. Despite their amazing diversity, teleosts share a number of characters that indicate **common ancestry**, particularly in the more advanced subdivision of the euteleosts or "true teleosts" (see below). The primary shared derived (synapomorphic) characters that unite the teleosts involve numerous bones of the tail and skull (Fig. 14.1). Importantly, the ural neural arches of the tail are elongated into **uroneural** bones. This means that in the tail base region, the neural arches that sit dorsal to the vertebral column fuse into elongate bones termed uroneurals. These new bones serve as basal supports for the rays that form the upper lobe of the tail fin and thus help stiffen it; their number and shape change during teleostean phylogeny. In the skull, among other characters, teleosts have a **mobile premaxillary** bone rather than having the premaxilla fused to the braincase. A mobile premaxilla is essential for upper jaw protrusion and allows a fish to shoot its mouth forward during prey capture, creating suction pressures and also overtaking prey.

In sum, major changes that define the teleosts contributed to the advances in locomotion and feeding that apparently led to their success, as detailed in Chapter 11. Most of the characteristics described here are discussed in more detail in Wheeler (1975), Berra (1981, 2001), Carroll (1988), and Nelson (1994, 2006). The overall classification followed, many of the characteristics described, and the numbers of species provided for different orders are based on Nelson (2006) with exceptions as noted.

A survey of living teleostean fishes

Subdivision Osteoglossomorpha

The **osteoglossomorph** bonytongues and their relatives are generally considered the most primitive living teleosts (Fig. 14.2). They occur in fresh water on all major continents except Europe, although only Africa has more than a few species (see Chapter 16, Archaic freshwater fish distributions). Although chiefly a tropical group, two species (the Mooneye, *Hiodon tergisus*, and Goldeye, *H. alosoides*) occur in major river systems of northern North America. The Arapaima or Pirarucu of South America (*Arapaima gigas*) is one of the world's largest freshwater fishes, reaching a length of 2.5 m. Arapaima have been stocked in lakes and reservoirs in Southeast Asia, where they are actively sought as sport fish. Anatomically, the group gets its common name from well-developed **teeth on the tongue** that occlude (bite) against similarly toothed bones (parasphenoid, mesopterygoid, ectopterygoid) in the roof of the mouth.

The South American Arawana (*Osteoglossum bicirrhosum*), the African Butterflyfish, *Pantodon buchholzi*, the notopterid featherfins or Old World knifefishes, and the mormyrid elephantfishes are popular aquarium species. The Asian Arawana or Golden Dragonfish, *Scleropages formosus* (Fig. 14.3), has been depleted in the wild due to overcollecting and is now protected in Appendix I of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES). Mormyrids, the most speciose family in the subdivision with >200 species, and the related *Gymnarchus niloticus*, possess a highly evolved electrical sense that involves both the production and detection of weak electric fields, an appropriate sense for fishes that are nocturnally active and typically occur in turbid waters. The electrical sense is used to localize objects and is also important during social interactions (see Chapter 6, Electroreception; Chapter 22, Electrical communication); analysis of electric organ discharges suggests that many cryptic species exist that are only separable on the basis of the wave patterns of their electric discharges (e.g., Arnegard & Hopkins 2003). Mormyrids have the largest cerebellum of any fish and a brain size : body weight ratio comparable to that of humans; the **mormyrocerebellum** is the neural center for coordinating electrical input. Mormyrids have a large learning capacity and are reported to engage in play behavior, a rarity among fishes, although not as unusual as might be expected (Burghardt 2005). Mormyrids are also important food fishes in Africa, with some attaining a length of 1.5 m.

Subdivision Osteoglossomorpha
- Order Hiodontiformes (two species): Hiodontidae (mooneyes)
- Order Osteoglossiformes (218 species): Osteoglossidae (bonytongues and butterflyfish), Notopteridae (featherfin knifefishes), Mormyridae (elephantfishes), Gymnarchidae (Aba)

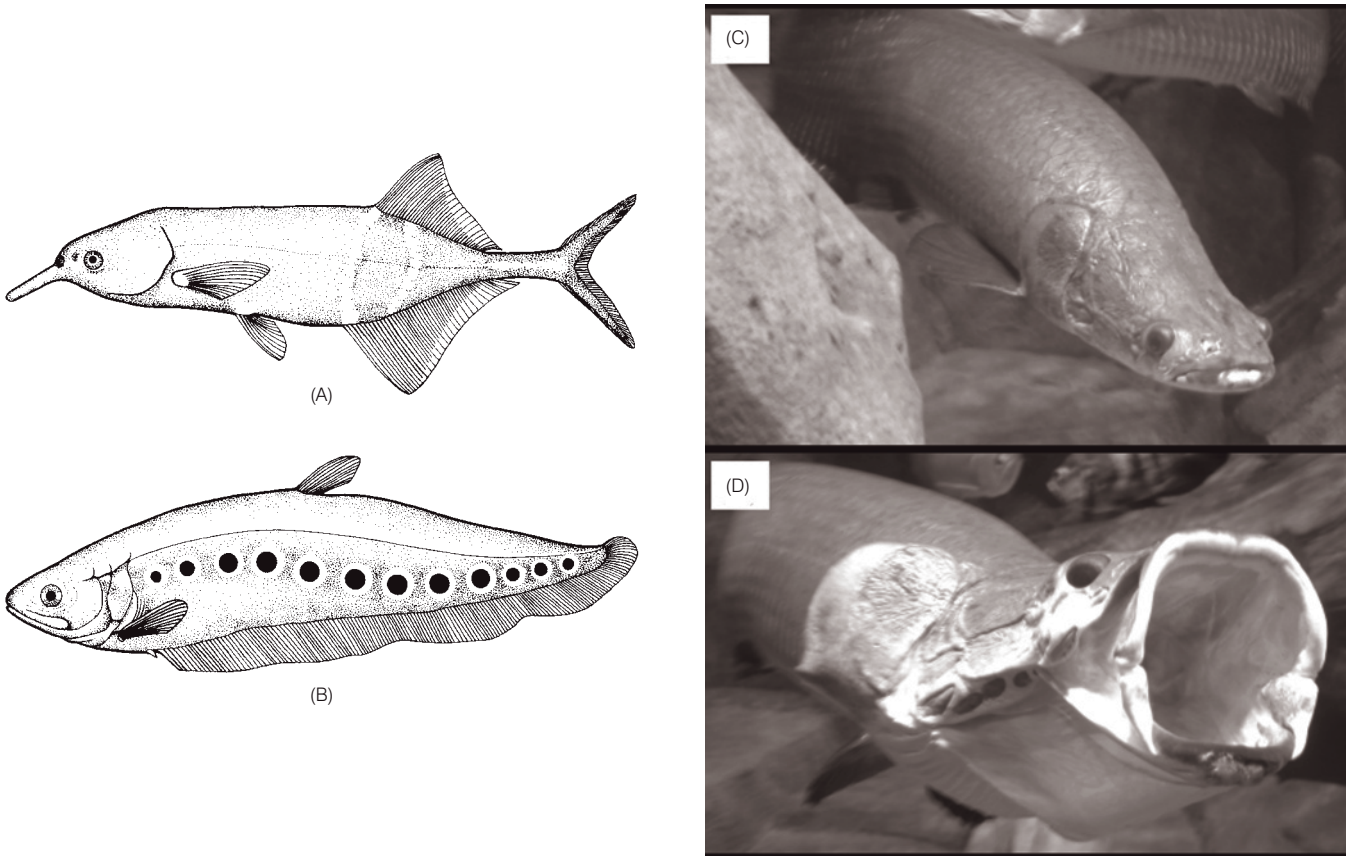

Figure 14.2

Osteoglossomorphs. (A) A mormyrid elephantfish, *Gnathonemus petersi*, from Africa. (B) A notopterid featherfin or knifefish, *Chitala chitala*, from Asia. (C, D) The South American Arapaima or Pirarucu, *Arapaima gigas*, a large predator. (A, B) after Paxton and Eschmeyer (1994); (C, D) photos by G. Helfman.

Figure 14.3

The Asian Arawana or Golden Dragonfish, *Scleropages formosus*. Overcollecting for the aquarium trade pushed this species to the brink of extinction, desirable color morphs fetching up to $5000. Photo by Marcel Burkhard, Wikimedia Commons, http://en.wikipedia.org/wiki/Image:Arowanacele4.jpg#file.

Subdivision Elopomorpha

A distinct pelagic larval form, termed a **leptocephalus** ("pointed head"), unites this speciose marine group (Fig. 14.4). Leptocephali are typically willowleaf- or ribbon-shaped and many of them shrink during metamorphosis to the juvenile form. For many years, the link between larval and adult species was not made and hence the two life history stages were placed in very different taxa (see Chapter 9, Larval morphology and taxonomy). The leptocephali of elopiform tarpons and bonefishes have a forked tail, whereas eel larvae have a pointed tail. Leptocephali are exceedingly long-lived, remaining as larvae for as long as 2–3 years in some anguillid species (see Chapter 23, Catadromy). During this time, they are dispersed by currents over large oceanic expanses, feeding perhaps on dissolved organic matter that they absorb through their skin or feeding on gelatinous zooplankton (e.g., Mochioka & Iwamizu 1996). They are thin and fragile in appearance, this effect heightened by a lack of red blood cells, which makes them translucent.

Subdivision Elopomorpha (804 species)
- Order Elopiformes (eight species): Elopidae (tenpounders, ladyfishes), Megalopidae (tarpons)
- Order Albuliformes (30 species): Albulidae (bonefishes), Halosauridae (halosaurs), Notacanthidae (spiny eels)
- Order Anguilliformes (738 species): Anguillidae (freshwater eels), Heterenchylidae (mud eels), Moringuidae (spaghetti eels), Chlopsidae (false morays), Myrocongridae (myroconger eels), Muraenidae (moray eels), Synaphobranchidae (cutthroat eels), Ophichthidae (snake eels, worm eels), Colocongridae (shorttail eels), Derichthyidae (longneck eels), Muraenesocidae (pike congers), Nemichthyidae (snipe eels), Congridae (conger eels), Nettastomatidae (duckbill eels), Serrivomeridae (sawtooth eels)
- Order Saccopharyngiformes (28 species): Cyematidae (bobtail snipe eels), Saccopharyngidae (swallowers), Eurypharyngidae (gulpers, pelican eels), Monognathidae (onejaw gulpers)

Elopomorphs are also distinguished by a reduction in the number of uroneural bones in the tail as compared to osteoglossomorphs, and by the development of thin, riblike epipleural intermuscular bones that extend from the vertebral column into the surrounding trunk musculature. These are the small bones in the meat of primitive teleosts (conger eels, herrings, carps, trouts) that make them difficult to filet and eat. Long epipleural and epineural ribs become less common in higher teleosts such as paracanthopterygians and acanthopterygians, which rely more on stouter, more firmly attached zygapophyses. These differences make both cleaning and eating easier.

The **elopiform** ladyfishes and tarpons retain a primitive characteristic, namely a **gular** bone or splint on the underside of the throat; this structure is well developed in the more primitive Bowfin, coelacanths, and bichirs but is lost in all other teleosts (except perhaps for an anabantoid, the Pikehead). Other justifications for considering elopiforms as primitive teleosts include: (i) a large number of branchiostegal rays in the throat (10–35 vs. 5–7 in many higher teleosts); (ii) inclusion of the maxilla in the gape, giving them two biting bones in the upper jaw rather than one; and (iii) heavy, bony scales that contain ganoin, a bone layer otherwise only found in gars and bichirs. The Atlantic

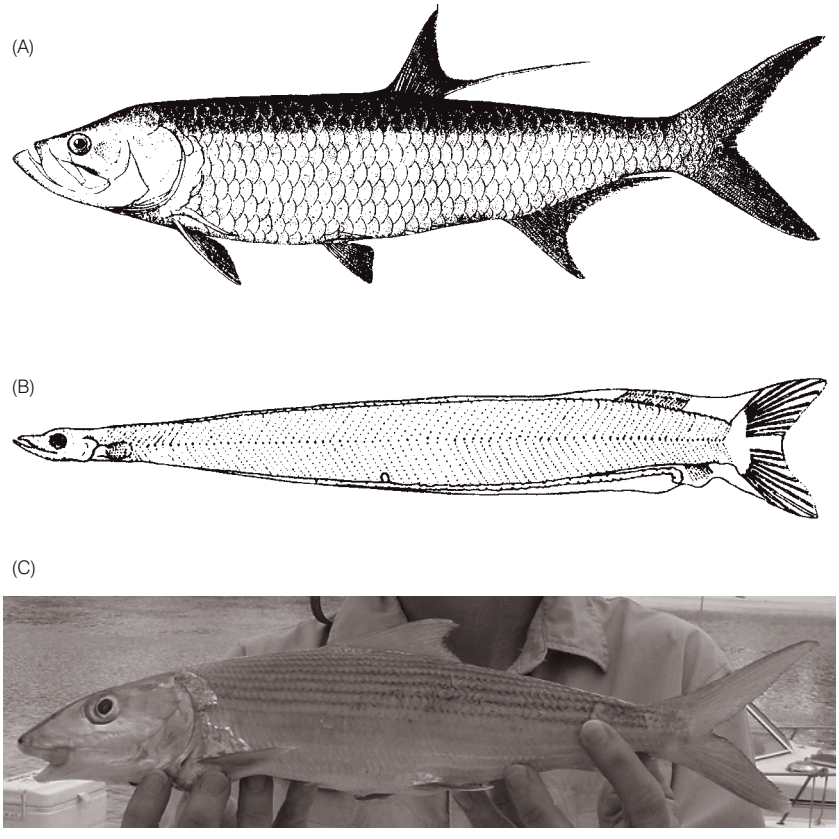

Figure 14.4
Elopomorphs. (A) A Tarpon, *Megalops atlanticus*. (B) A 7 cm long leptocephalus larva of a ladyfish, *Elops saurus*. (C) An Atlantic Bonefish, *Albula vulpes*. (A, B) from Hildebrand (1963), used with permission; (C) photo by G. Helfman.

Tarpon, *Megalops atlanticus*, is a legendary gamefish that reaches a length of 2.5 m and a mass of 150 kg. A large (65 kg) female may contain more than 12 million eggs, making tarpon one of the most fecund fishes.

Albuliform bonefishes are also popular gamefishes that occupy sandy flats in shallow tropical waters; recent molecular studies suggest eight or 10 species exist where historically only one was recognized (see Chapter 17, Cryptic evolutionary diversity: the case of the bonefishes). The notacanthoids (halosaurs and spiny eels) are an offshoot suborder between the albuliforms and the anguilliforms; they develop from leptocephalus larvae but otherwise stand in marked anatomical and ecological contrast to other members of the albuliforms. These deepsea, benthic eels occur down to 5000 m, making them among the deepest living fishes known.

The 15 families of **anguilliforms** are "true" eels, i.e., those with a leptocephalus larva, as distinguished from the approximately 45 other families of "eel-like" fishes that have converged on an elongate body and other anatomical and behavioral traits (see Box 19.2; Chapter 24, Habitat use and choice). An eel-like body facilitates forwards and backwards movement into and out of tight places and soft bottoms. Some anguilliforms are open water, pelagic forms, despite the relatively slow locomotion imposed by an anguilliform swimming mode (see Chapter 8, Locomotory types). Anguilliforms are distinguished by loss of the pelvic girdle and by a modified upper jaw that is formed by fusion of the premaxilla, vomer, and ethmoid bones. The 15 species of anguillid eels are catadromous, spawning at sea but spending most of their lives feeding and growing in fresh water.

Muraenid moray eels and their relatives (185 species) are largely marine, tropical and warm temperate species best known from coral reefs. Their sinister appearance results in part because their sedentary habits require them to hold their fang-studded jaws open while actively pumping water over their gills and out a constricted opercular opening. Although capable of inflicting serious wounds, morays are more dangerous as agents of ciguatera food poisoning, a toxin that originates in a dinoflagellate alga and is magnified in piscivores that eat prey contaminated with the toxin. The congroid eels (491 species) include fossorial (burrowing) forms such as garden eels, worm eels, and snake eels, the latter burrowing into sediments backwards with a hardened, pointed tail. Benthic conger eels are similar ecologically to morays. Other deepsea mesopelagic and bathypelagic congroids include longneck eels, snipe eels, and sawtooth eels. One family of congroids, the synaphobranchid cutthroat eels, contains a facultative parasitic species, the Snubnose Parasitic Eel, *Simenchelys parasiticus*. Although often a scavenger, *Simenchelys* sometimes burrows into the flesh of bottom-living fishes such as halibut. Two 20 cm long individuals were found lodged in the heart of a longline-captured, 500 kg Shortfin Mako Shark, where they had been feeding on blood. Histological features of the inhabited heart suggested that these eels had possibly been living in the shark's heart prior to its capture, pointing to a truly parasitic relationship (Caira et al. 1997).

The last order of elopomorphs are the truly bizarre **saccopharyngiform** deepsea gulper and swallower eels and their relatives (see Chapter 18, The deep sea) (Fig. 14.5). These species are distinguished not only by elaborate, extreme specializations of the head and tail, including an extremely long jaw, but also for a lack of features normally found in teleosts. Among the structures missing from different species are the symplectic and opercular bones, branchiostegals, maxilla and premaxilla, vomer and parasphenoid, scales, pelvic or pectoral fins, ribs, pyloric caeca, and gas bladder. Some early authors argued that saccopharyngoids were not really bony fishes. Nelson (1994, p. 115) considered the saccopharyngoids "perhaps the most anatomically modified of all vertebrate species". Another saccopharyngoid family, the monognathids, contains species with rostral fangs and apparent venom glands, a unique feature among fishes (Bertelsen & Nielsen 1987).

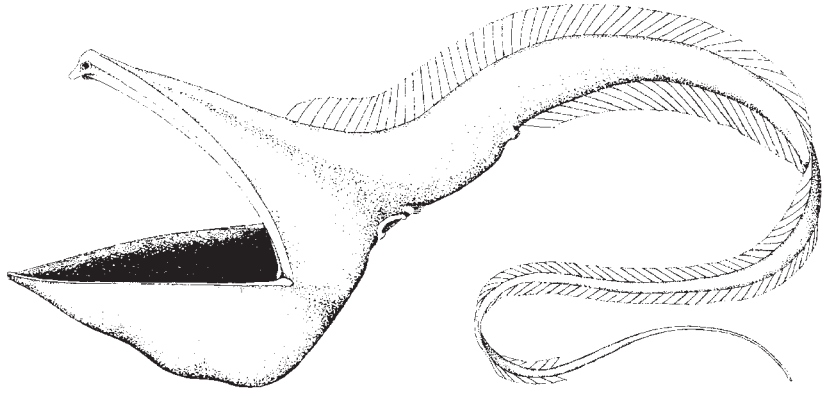

Figure 14.5
A Gulper or Pelican Eel, *Eurypharynx pelecanoides*. Ironically, this highly specialized, 40 cm long bathypelagic fish feeds on surprisingly small prey which they capture by opening their huge, dark mouths that probably generate little suction pressure. The related swallower eels feed on prey larger than themselves. Gulper Eels are unique among teleosts because they have five gill arches and six visceral clefts (Nelson 2006). From Briggs (1974), used with permission of McGraw-Hill.

Subdivision Otocephala (= Ostarioclupeomorpha), Superorder Clupeomorpha

Subdivision Otocephala (= Ostarioclupeomorpha)
Superorder Clupeomorpha
Order Clupeiformes (364 species): Denticipitidae (denticle herrings), Pristigasteridae (longfin herrings), Engraulidae (anchovies), Chirocentridae (wolf herrings), Clupeidae (herrings)

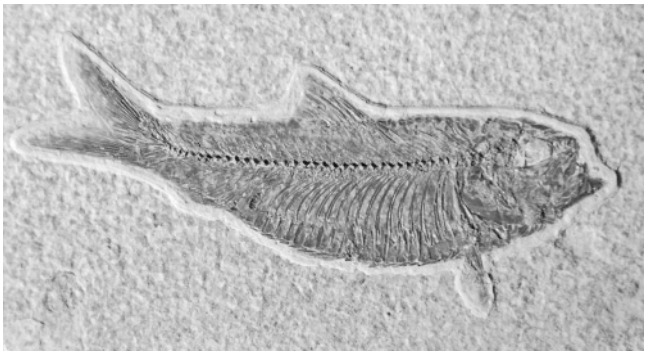

Figure 14.6
Knightia alta, an Eocene herring from the Green River formation of Wyoming (actual length 12 cm). Excellent fossils of *Knightia*, such as this one in which the characteristic abdominal scutes of clupeids are clearly visible, are abundant and are sold as curios. Photo by G. Helfman.

The past decade has seen considerable reanalysis of relationships among teleosts more advanced than the two primitive subdivisions of bonytongues and tarpon/eels. It is now widely agreed that herrings and minnowlike fishes, earlier separated, belong in the same subdivision, the **Otocephala** (or its tongue-twisting but descriptive synonym Ostarioclupeomorpha) (Johnson & Patterson 1996; Arratia 1997).

Among the most abundant and commercially important of the world's fishes are the herringlike **clupeiforms**; large fisheries exist (or existed) for California Sardines, Peruvian Anchoveta, Atlantic and Gulf Menhaden, Atlantic Herring, and South African Sardine and Anchovy (Hutchings 2000a, 2000b; Hilborn 2005). Almost all are open water, pelagic, schooling forms, 80% of which are marine. Clupeomorphs are distinguished by a gas bladder that extends anteriorly up into the braincase and contacts the utriculus of the inner ear and in some extends posteriorly to the anus; the air bladder also has extensions to the lateral line canals. This **otophysic** ("ear-to-gas-bladder") condition apparently increases the hearing ability of these fishes by increasing their sensitivity to low-frequency (1–1000 Hz) sounds as compared to other fishes. Low-frequency sounds of 3–20 Hz are typically those produced by tail beats of other fishes, such as neighbors in a school and attacking predators (Blaxter & Hunter 1982). Clupeomorphs also typically possess a series of sharp, bony scutes along their ventral edge and some also have scutes anterior to the dorsal fin. These scutes may make these fishes harder for predators to capture and swallow, although direct proof is lacking. Of phylogenetic significance, the superorder Clupeomorpha (modern clupeiforms and extinct, related orders) possess evolutionary advances over elopomorphs in terms of a modified joint at the posterior angle of the jaw (angular fused to articular rather than to retroarticular) and caudal skeleton reduction (reduced first ural centrum and reduction to six in number of hypural bones). These derived traits foreshadow the continued changes in jaw and tail structures that occurred during the evolution of higher teleostean groups.

The engraulid anchovies are relatively elongate zooplanktivorous clupeoids with large mouths made possible by an elongate maxillary that extends considerably behind the eye. Anchovies range in size from a minute Brazilian species (*Amazonsprattus*, 2 cm) to a piscivorous riverine New Guinea anchovy (*Thryssa scratchleyi*, 37 cm). The largest clupeids are the chirocentrid wolf herrings, *Chirocentris dorab* and *C. nudus*, with an Indo-Pacific to South Africa distribution. Wolf herrings are herrings gone mad. They reach a length of 1 m (the next largest clupeoid is a 60 cm Indian clupeid) and have fanglike jaw teeth plus smaller teeth on the tongue and palate which they use to capture other fishes.

The largest family in the superorder is the Clupeidae, which includes 188 species of herrings, round herrings, shads, alewives, sprats, sardines, pilchards, and menhadens. Clupeids can be marine, fresh water, or anadromous, with landlocked forms common (e.g., anadromous shads, alewives, and herrings have become established in lakes and reservoirs and in rivers trapped between dams). Whereas herrings, sardines, and menhaden are important commercially, some of the larger shads are popular sportfish (e.g., the American Shad, *Alosa sapidissima*; McPhee 2002). Probably the best known fish fossil in the world is †*Knightia*, a freshwater Eocene herring from the Green River shale formations of Wyoming (Fig. 14.6).

Subdivision Otocephala (= Ostarioclupeomorpha), Superorder Ostariophysi

Subdivision Otocephala (= Ostarioclupeomorpha)
- Superorder Ostariophysi
  - Series Anotophysi
    - Order Gonorhynchiformes (37 species): Chanidae (milkfishes), Gonorhynchidae (beaked sandfishes), Kneriidae (knerias), Phractolaemidae (snake mudheads)
  - Series Otophysi
    - Order Cypriniformes (3268 species): Cyprinidae (minnows, barbs, carps), Psilorhynchidae (mountain carps), Gyrinocheilidae (algae eaters), Catostomidae (suckers), Cobitidae (loaches), Balitoridae (river loaches)
    - Order Characiformes (1674 species): Distichodontidae (distichodontids), Citharinidae (citharinids), Parodontidae (parodontids), Curimatidae (toothless characiforms), Prochilodontidae (flannel-mouth characiforms), Anostomidae (toothed headstanders), Chilodontidae (headstanders), Crenuchidae (South American darters), Hemiodontidae (hemiodontids), Alestiidae (African tetras), Gasteropelecidae (freshwater hatchetfishes), Characidae (characins), Acestrorhynchidae (acestrorhynchids), Cynodontidae (cynodontids), Erythrinidae (trahiras), Lebiasinidae (pencil fishes), Ctenoluciidae (pike characids), Hepsetidae (African pikes)
    - Order Siluriformes (2867 species): Diplomystidae (velvet catfishes), Cetopsidae (whalelike catfishes), Amphiliidae (loach catfishes), Trichomycteridae (pencil or parasitic catfishes), Nematogenyidae (mountain catfishes), Callichthyidae (callichthyid armored catfishes), Scoloplacidae (spiny dwarf catfishes), Astroblepidae (climbing catfishes), Loricariidae (suckermouth armored catfishes), Amblycipitidae (torrent catfishes), Akysidae (stream catfishes), Sisoridae (sisorid catfishes), Erethistidae (erethistid catfishes), Aspredinidae (banjo catfishes), Pseudopimelodidae (bumblebee catfishes), Heptapteridae (heptapterids), Cranoglanididae (armorhead catfishes), Ictaluridae (North American freshwater catfishes), Mochokidae (squeakers, upside-down catfishes), Doradidae (thorny catfishes), Auchenipteridae (driftwood catfishes), Siluridae (sheatfishes), Malapteruridae (electric catfishes), Auchenoglanididae (auchenoglanidids), Chacidae (squarehead, angler, or frogmouth catfishes), Plotosidae (eeltail catfishes), Clariidae (airbreathing catfishes), Heteropneustidae (airsac catfishes), Austroglanidae (austroglanids), Claroteidae (claroteids), Ariidae (sea catfishes), Schilbeidae (schilbeid catfishes), Pangasiidae (shark catfishes), Bagridae (bagrid catfishes), Pimelodidae (long-whiskered catfishes) [Lacantaniidae, Chiapas Catfish][a]
    - Order Gymnotiformes (134 species): Gymnotidae[b] (naked-back knifefishes), Rhamphichthyidae (sand knifefishes), Hypopomidae (bluntnose knifefishes), Sternopygidae (glass knifefishes), Apteronotidae (ghost knifefishes)

[a] A recently Discovered Mexican species and family, *Lacantunia enigmatica*, Lacantaniidae, Chiapas Catfish, awaits placement in the phylogeny (Rodiles-Hernández et al. 2005), but is enticingly thought to be a sister taxon to the African claroteids (Lundberg et al. 2007).

[b] The Electric Eel or electric knifefish, *Electrophorus electricus*, now considered a gymnotid, was previously placed in its own family, the Electrophoridae.

Freshwater habitats worldwide are dominated in terms of numbers of both species and individuals by ostariophysans, which account for about 68% of all freshwater species. Ostariophysans include such disparate taxa as milkfish, minnows, carps, barbs, suckers, loaches, piranhas, tetras, catfishes, and electric eels, but two unique traits characterize most members of this massive taxon. With the exception of the gonorhynchiforms, ostariophysans possess a unique series of bones that connect the gas bladder with the inner ear, an **otophysic** condition. This **Weberian apparatus**, named after the German anatomist who first described it, involves a set of bones derived from the four or five anterior (cervical) vertebrae and their neural arches, ribs, ligaments, and muscles (see Fig. 6.4). The superorder gets its name from this complex structure (*ostar* = small bone, *physa* = a bladder; "otophysic" basically means "ear" and "bladder"); ostariophysans with the apparatus are referred to as the **Otophysi**. When sound waves contact the fish, the gas bladder vibrates, and this vibration is passed anteriorly to the inner ear, being amplified by the intervening Weberian ossicles (see Chapter 6, Hearing). Unrelated taxa have convergently evolved connections between the gas bladder and the inner ear, either by an otophysic extension of the gas bladder anteriorly (elephantfishes, clupeoids, cods, Roosterfish, porgies, some cichlids); by a bony connection involving the pectoral girdle or skull (squirrelfishes, triggerfishes); or, in chaetodontid butterflyfishes, by connections between anterior extensions of the bladder and the lateral line canal system (Webb et al. 2006). Many of these families are known sound producers and it is assumed they derive auditory advantages via their specialized structures. Gonorhynchiforms, the **Anotophysi**, possess a primitive homolog of the

Weberian apparatus consisting of three modified anterior vertebrae associated with cephalic rib bones.

The second shared derived trait that helps define the Ostariophysi is the **alarm response**, which involves: (i) the production of an **alarm substance** (***Schreckstoff***); and (ii) a behavioral **alarm reaction** to the presence of the substance in the water (***Schreckreaktion***) (see Chapter 20, Discouraging capture and handling). The alarm substance is given off when specialized dermal club cells are ruptured, as when a predator bites down on a prey fish. Nearby individuals, most likely schoolmates, sense the chemical in the water and take a variety of coordinated escape actions, depending on the species. Possession of the alarm response was a factor contributing to the inclusion of the gonorhynchiforms within the Ostariophysi.

Some ostariophysans lack one or both parts of the response for apparently adaptive reasons. Piranhas lack the alarm reaction, which makes sense as many of their prey are also ostariophysans and it would be counterproductive for a predator to flee each time it bit into prey. Some nocturnal, non-schooling, or heavily armored ostariophysans lack both parts of the alarm response, including Blind Cave Characins, electric knifefishes, and banjo and suckermouth armored catfishes. An interesting seasonal loss of the production end of the response occurs in several North American minnows. Nest building and courtship in these fishes often involves rubbing by males against the bottom and between males and females, during which time the skin and its breeding turbercles may be broken. It would be less than helpful to the male if he produced a substance that frightened females away during these activities. Males resume the production of alarm substance in the fall, after the breeding season. As with the Weberian apparatus, convergent evolution of alarm substances and responses have evolved in other teleostean groups, including sculpins, darters, and gobies (Smith 1992).

Ostariophysans encompass two series, the Anotophysi with one order and the Otophysi with four orders. These taxa are too diverse to allow much detail here, and many aspects of their biology are treated in other chapters of this book. The most primitive order is the **Gonorhynchiformes**, which includes the Milkfish, *Chanos chanos* (series Anotophysi, family Chanidae), and three other relatively small tropical families. Milkfish are an important food fish in the Indo-Pacific region and are often cultured in brackish fishponds, where juveniles are raised to edible size on an algae diet. *C. chanos* grows to almost 2 m and 25 kg and is a popular sportfish in some areas.

The series Otophysi contains the bulk of freshwater fish species globally. The **Cypriniformes** constitutes the largest order and probably contains the most familiar species of the superorder. The Cyprinidae, the largest family of freshwater fishes and the second largest family (after the gobies) of all fishes, contains 2200 of the >3200 cypriniform species. Among the better known cyprinids are the minnows, shiners, carps, barbs, barbels, gudgeons, chubs, dace, pikeminnows, tench, rudd, bitterlings, and bream and such popular aquarium fishes as the Southeast Asian "sharks" (Redtail Black Shark, Bala Shark), Goldfish, Koi (domesticated common carp), Zebra Danios, and rasboras. The Zebrafish or Zebra Danio, *Danio rerio*, has become a standard laboratory animal in developmental genetics, toxicology, and medical research (Westerfield 2000; Gong & Korzh 2004; see also Zebrafish Information Network, http://zfin.org). Zoogeographically, cyprinids are most diverse in Southeast Asia, followed by Africa, North America (where there are 300 species according to Berra (2001)), and Europe. Cyprinids are absent from Australia and South America, their ecological roles filled largely by osmeriforms and atheriniforms in the former and by characins in the latter (see Chapter 16).

It is in the cyprinids that we see the first real development of pharyngeal dentition, a second set of jaws in the throat region that are derived from modified, tooth-bearing pharyngeal arches (see Chapter 8, Pharyngeal jaws). Specifically, the fifth ceratobranchial (=pharyngeal) bone occludes against an enlarged posterior process of the basioccipital bone to form the pharyngeal bite. Cyprinids are also the first teleosts to develop a highly protrusible upper jaw and to eliminate the maxillary bones from the biting bones and gape of the mouth, both trends that are increasingly developed in more advanced teleostean taxa (see Chapter 11, Division Teleostei). Exclusion from the gape of the maxilla is a characteristic of all fishes higher than the salmoniforms, although the bite of salmoniforms and their relatives involves the maxilla. The exclusion versus inclusion of the maxilla in cyprinids versus salmoniforms has led to some controversy over which group is more advanced. The bulk of the evidence favors salmoniforms as the more advanced clade ("minnows before trout"; Smith 1988); maxilla inclusion in salmoniforms may be a secondarily evolved trait.

Some cyprinids have chromosomes in the polyploid condition, an unusual occurrence among fishes. The normal diploid 2N condition of most cyprinids is 48 or 50, although tetraploid (2N = 100), hexaploid, and even octaploid species occur, as is the case for the goldfish (Buth et al. 1991). Polyploidy is linked with large size in minnows; the world's largest species are the Southeast Asian *Catlocarpio siamensis*, a tetraploid (Fig. 14.7), and the Indian Mahseer, *Tor putitora*, both of which reach 2.5–3 m in length. The largest minnow in North America is the piscivorous Colorado Pikeminnow, *Ptychocheilus lucius*. Exceptional size in cyprinids is also often accompanied by predatory habits, as implied by the scientific names of such large (>2 m) species as *Elopichthys bambusa* and *Barbus esocinus*. Most cyprinids, however, are quite small (<5 cm), and the smallest freshwater fish, and perhaps vertebrate, in the world is an Indonesian cyprinid, *Paedocypris progenetica*, that matures at 7.8 mm (see Fig. 10.9).

The superfamily Cobitoidea includes the disparate families of algae eaters, suckers, loaches, and river loaches.

Figure 14.7
"Minnows." The giant and imperiled Asian Carp, *Catlocarpio siamensis*, native to the Mekong River basin. Photo courtesy of Jean-Francois Healias, www.anglingthailand.com.

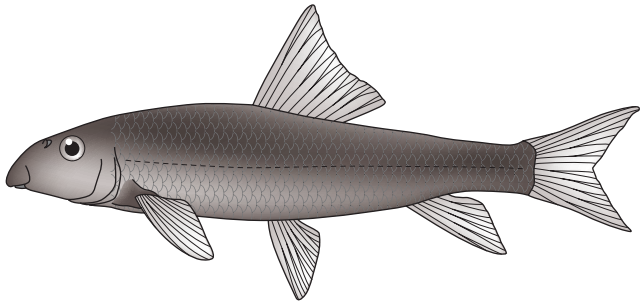

Figure 14.8
The extinct Harelip Sucker, *Moxostoma lacerum*. Once abundant in 13 eastern US states, this may have been the first American fish driven to extinction, around 1900 (see Jenkins & Burkhead 1993). Actual coloration is not known because no live fish were ever drawn or photographed; only one adult was preserved. After Trautman (1981).

Figure 14.9
A juvenile Robust Redhorse, *Moxostoma robustum*. Growing to large size (80 cm, 8 kg), this rare catostomid endemic to Atlantic slope rivers of the southeastern USA went unrecorded for over 120 years. Rediscovered in 1991, a cooperative effort among government, corporate, and nongovernmental organizations succeeded in captive propagation, release into the wild, and establishment and reproduction by propagated fish (see Helfman 2007; www.robustredhorse.com/h/reportpubs.html). Photo by G. Helfman.

Gyrinocheilid algae eaters are interesting because of modifications to the mouth and gill apparatus that allow them to scrape algae from rocks in areas of strong current. The mouth is modified into a sucking organ that helps them cling to rocks while scraping off algae. The fish breathes by inhaling water dorsally and exhaling it ventrally through small apertures in the gill opening. Suckers (Catostomidae) include about 72 species of relatively large (50–100 cm), chiefly North American fishes (Figs 14.8, 14.9). One species, the Chinese Highfin "Shark", *Myxocyprinus asiaticus*, occurs in eastern China, and another species, the Siberian Longnose Sucker, *Catostomus catostomus rostratus*, occurs in Alaska and northeastern Siberia (Scharpf 2006). Species include the buffaloes, quillback, carpsuckers, blue sucker, redhorses, jumprocks, and the extinct Harelip (Fig. 14.8) and Snake River Suckers. Most suckers are benthic feeders in flowing water with inferior mouths and plicate or papillate lips. Exceptional are some lake suckers in the western

USA (e.g., *Chasmistes*) that are midwater planktivores with more terminal mouths. Suckers can be quite confusing taxonomically because they frequently hybridize. Potential confusion is not helped by the scientific and common name combinations in this family, such as the Quillback, *Carpiodes cyprinus*, and the River Carpsucker, *Carpiodes carpio*, which can be mixed up with the Common Carp, *Cyprinus carpio*, which is a cyprinid.

Loaches (Cobitidae) constitute 177 species of predominantly Eurasian fishes that have their highest diversity in Southeast Asia. Included are such popular aquarium fishes as the Kuhli, Clown, and Skunk loaches, the weatherfishes, and the Golden Dojo. Weatherfishes (*Misgurnus*) obtained their name because they become restless when atmospheric pressure drops preceding a storm. Their sensitivity to barometric fluctuations may somehow relate to their air-breathing abilities, which involve gulping atmospheric air and passing a bubble to the intestine where gaseous exchange occurs. Balitorid river or hillstream loaches are a highly diverse family (590 species), many of which are specialized for life in fast-flowing mountain streams of India and Southeast Asia. Their paired fins tend to be oriented horizontally, are enlarged, and have adhesive pads on their ventral surfaces. In addition, their bodies are depressed dorsoventrally and their mouths are ventral, all anatomical adaptations to life in swift or turbulent water (see Chapter 18). One large subfamily of balitorids, the Nemacheilinae, includes several cave-dwelling species (see Chapter 18).

The **characiforms** are another large order (*c*. 1670 species) of primarily tropical otophysans characterized (usually) by an adipose fin, well-armed mouths and replacement dentition (e.g., piranhas; see Chapter 8, Dentition), and peripheral ctenoid as opposed to the cycloid scales found in most lower groups (Fig. 14.10). This is a remarkably diverse order anatomically and ecologically, including predators, zooplanktivores, scale eaters, detritivores, and herbivores; the latter category includes fishes that feed on seeds, leaves, and fruits. Characiforms may be surface, water column, or benthic dwellers, although most species are found in midwater, many in shoals. Body sizes range from very small (13 mm adult tetras) to quite large (e.g., 1.5 m long tigerfishes) and body shapes range from long, slender, almost darterlike benthic fishes (e.g., South American darters, *Characidium*) to deep-bodied, compressed piranhas and hatchetfishes (*Gasteropelecus*). Numerous popular, colorful aquarium fishes belong to this order, including *Distichodus*, *Prochilodus*, headstanders, spraying characins, freshwater hatchetfishes, blind characins, pencilfishes, tetras (*Cheirodon*, *Hemigrammus*, *Micralestes*, *Paracheirodon*), and silver dollars, as do important food fishes (*Prochilodus*, *Colossoma*, *Brycon*). Currently, 18 families are recognized, although past classifications have recognized as few as one. The great majority of species (*c*. 1300) are South American, about 200 are African, a small number live in Central America, and one species, the Mexican Tetra, *Astyanax mexicanus*, extends naturally into southwestern Texas. Another 10 species, including piranhas, have been introduced into the USA. Because of its large size and tropical nature, the order has undergone considerable taxonomic revision, much of which is still in progress. Perhaps as many as 88 genera and 620 species are of unknown taxonomic position (see Nelson 2006).

Figure 14.10
Piranhas, *Serrasalmus* spp., are representative of the speciose tropical order of characiform fishes. Photo by G. Helfman.

The most primitive characiforms are the 100 species of African citharinoids (*Distichodus*, *Citharinus*), attesting to an African origin for the order and the connection between Africa and South America prior to the break up of Gondwanaland in the Mesozoic. African characiforms also include the advanced alestiids (about 100 species). Two of the largest characiforms are predaceous African species. The Pike Characin, *Hepsetus odoe* (Hepsetidae), is an impressive predator that reaches 65 cm in length and has fanglike teeth. It is remarkably convergent with the alestiid tigerfishes, *Hydrocynus* spp., which reach almost 2 m in length and over 50 kg in mass. Not far behind in the dentition and size categories are the cynodontid wolf characins or payara of South America (*Hydrolycus*: 1.2 m, 18 kg), a much-sought sportfish.

Apart from various popular aquarium species, certainly the best known or at least most notorious characids are the piranhas (Fig. 14.10). This subfamily, the Serrasalminae, contains about 80 species, some of which are predatory (*Serrasalmus*), others which are scale-eating opportunists and specialists (*Pygocentrus*, *Catoprion*), and some that are largely herbivorous, such as the pacus and silver dollars (*Colossoma*, *Metynnis*) (Sazima 1983; Nico & Taphorn 1988). Despite their reputation and potential for doing damage, many purported attacks on humans by piranhas actually result from postmortem scavenging on drowning victims (Sazima & Guimaraes 1987). In recent years, however, this picture has changed as a result of a prolifera-

tion of dams in southeastern Brazil that created ideal piranha spawning habitat. More than 85 attacks on bathers by nest-guarding piranhas have been reported, many resulting in serious injury (Haddad & Sazima 2003). The large, herbivorous serrasalmine species are important food fishes in the Amazon basin and are also important dispersers of seeds during the wet season, particularly because they use their massive dentition to husk seeds, which may aid germination (Goulding 1980). The Characidae overall includes 12 subfamilies, 165 genera, and at least 960 described species.

The diversity of catfishes (**Siluriformes**) amazes most everyone (Burgess 1989; Arratia et al. 2003) (Fig. 14.11). Approximately 35 families and 2900 species of catfishes are recognized and it is not surprising that catfish systematics remains active, controversial, and unsettled (see the All Catfish Species Inventory, http://silurus.acnatsci.org for regular updates and photos). Commonalities among the families include: fusion, reduction, or loss of a number of skull bones found in lower teleosts, including the maxilla; teeth on the roof bones of the mouth (vomer, pterygoid, palatine); an adipose fin, sometimes with rays or a spine; an unsegmented, spinelike ray at the front of both the dorsal and pectoral fins that in some families is covered by a toxin produced by epidermal glandular cells; the dorsal spine is often preceded by a shorter spine that helps lock the larger spine in the erect position; a lack of scales, often combined with the presence of bony plates or tubercles; small eyes (and nocturnal, benthic foraging habits); and one to four pairs of barbels associated with both the upper and lower jaws that serve both chemosensory and tactile functions.

Catfishes are known from all continents, including Antarctica during the Oligocene. They reach their greatest diversity in South America, where the largest families occur (loricariid suckermouth armored catfishes with 684 species, trichomycterid pencil catfishes with 201 species, and callichthyid armored catfishes with 177 species); the bagrids of Africa/Asia and the African mochokid upside-down catfishes are close behind with 170 to 180 species. The most

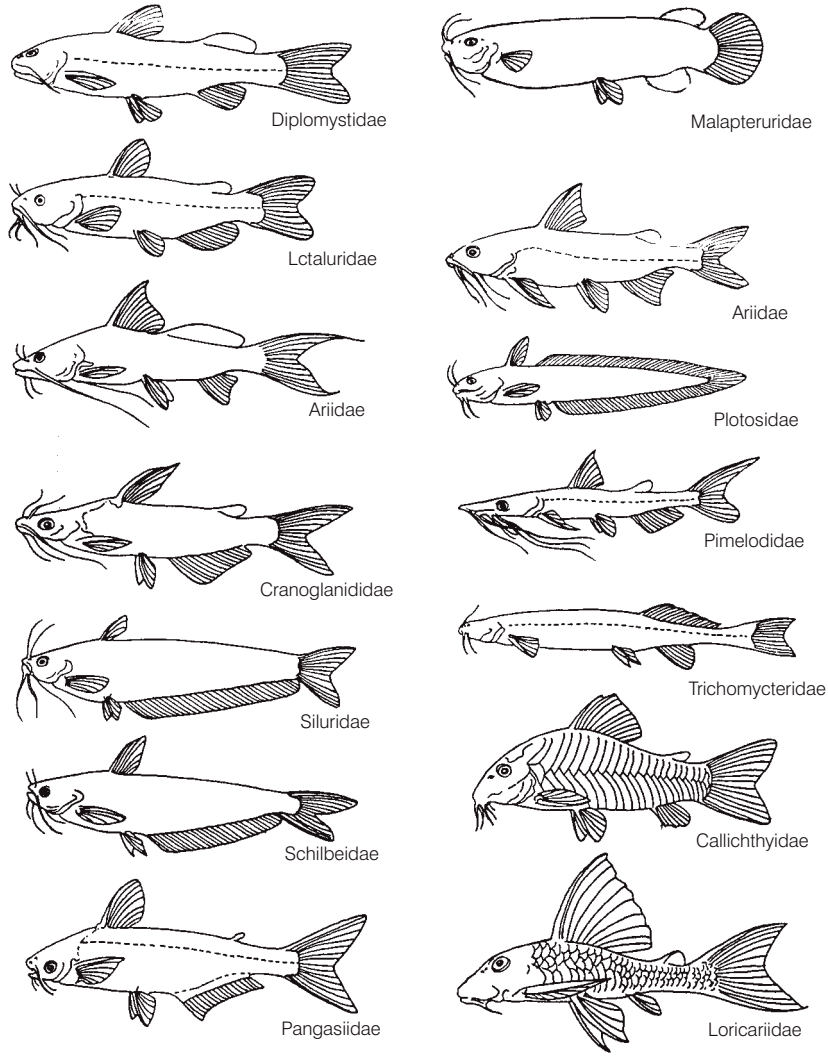

Figure 14.11

Selected catfishes, showing some of the array of body types and shared characteristics among the 35 families. Drawings by John Quinn, in Burgess (1989), used with permission of TFH Publications.

primitive catfishes are the South American diplomystids, which have a well-developed, toothed maxillary bone, a trait they share with the extinct Eocene hypsidorids. As with the vast majority of ostariophysans, most catfishes are confined to fresh water, including many cave species (e.g., Proudlove 2006). However, two families of catfishes are primarily marine, the widespread sea catfishes (Ariidae) and the highly venomous Indo-Pacific eeltail catfishes (Plotosidae). The plotosids have diversified in several respects. Juvenile lined catfishes, *Plotosus lineatus*, are tightly schooling, diurnally active fishes in contrast to the solitary, nocturnal behavior of most other families. Both families contain members that occur in fresh water, such as the plotosid tandan catfishes of Australia (*Tandanus*), which probably represents secondary evolution of the use of freshwater habitats (i.e., freshwater ancestor gave rise to a marine species which then reinvaded fresh water). Marine plotosids have highly venomous spines and relatively bold coloration, suggesting an aposematic warning function (see Chapter 20, Evading pursuit), which does not appear to deter their chief predators, the equally venomous seasnakes (Voris et al. 1978).

Most catfishes are naked, lacking true scales. But in some families, different parts of the body are covered with individual or overlapping bony plates (armorhead catfishes, loach catfishes, sea catfishes, thorny catfishes, callichthyid armored catfishes, suckermouth armored catfishes), or thornlike projections, tubercles or "odontodes" (sisorids, thorny catfishes, aspredinid banjo catfishes, spiny dwarf catfishes). The popular "plecostomus" catfishes of the aquarium trade are loricariid suckermouth armored catfishes; most are in the genus *Hypostomus* because, regrettably, *Plecostomus* is no longer a valid scientific name. Relatives in the genus *Pterygoplichthys* have become a nuisance introduction in Mexico and Florida where they undergo population explosions.

Some of the world's largest freshwater fishes are catfishes, including the predatory European wels (*Siluris glanis*, Siluridae) at 5 m and 330 kg; the herbivorous, Critically Endangered, Mekong Giant Catfish (*Pangasianodon gigas*, Pangasiidae) at 3 m and 300 kg; and the 2.8 m, 150 kg long-whiskered pimelodid Piraiba (*Brachyplatystoma filamentosum*) of South America (Fig. 14.12). Piraiba are importantly economically and ecologically in the Amazon basin and are legendary for their annual migrations (Barthem & Goulding 1997). The largest catfishes in North America are the Flathead and Blue catfishes, *Pylodictis olivaris* and *Ictalurus furcatus*, which reach about 1.5 m and 50–68 kg. Very small catfishes such as spiny dwarf catfishes (Scoloplacidae) and whalelike catfishes (Cetopsidae) are only 20–25 mm long as adults. Some small catfishes are notably unpleasant. The pencil or parasitic catfishes (Trichomycteridae) of South America include species that eat mucus and scales from other fishes or that pierce the skin or gill cavities of other fishes and feed on blood. At least one species, a candiru, *Vandellia cirrhosa*, is known to swim up the urethra of bathers and lodge itself there with its opercular spines, necessitating surgical removal (Burgess 1989; Spotte 2002). This behavior results in part because trichomycterids are positively rheophilic, which means they tend to swim "upstream" into gill cavities, or occasionally into a urethra.

Most catfishes are benthic, but some silurid sheatfishes, schilbeids, ageneiosid bottlenose catfishes, and *Hypopthalmus* lookdown catfishes normally swim above the bottom (the relatively bizarre lookdowns are probably filter feeders). Occupation of the water column has produced some striking convergences in species that hover in open space. For example, the Glass Catfish, *Kryptopterus bicirrhus*, of Southeast Asia is a 10 cm long, transparent silurid with one pair of long barbels that protrude outward from its head, a long anal fin, no adipose fin, a forked tail, and only a

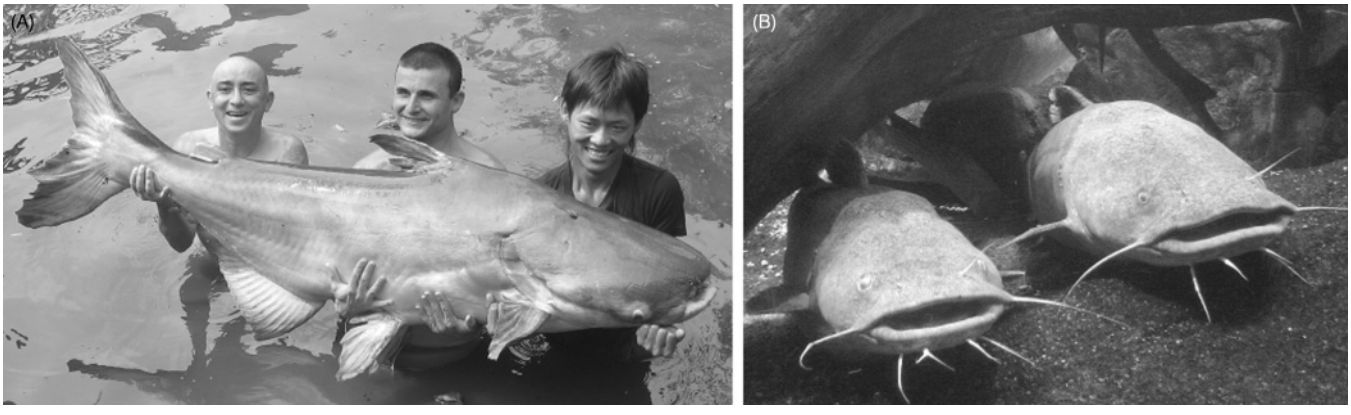

Figure 14.12

Large catfishes. (A) The Mekong Giant Catfish, one of the world's largest catfishes. This specimen was caught from a stocked population in Bung Sam Lan Lake, Thailand. (B) Two *c*. 20 kg Flathead Catfishes, North America's second largest catfish. (A) photo courtesy of Jean-Francois Healias, www.anglingthailand.com; (B) photo by G. Helfman.

single small ray in its dorsal fin (hence the name *kryptopterus* = "hidden fin"). It tends to hover tail down in the water column, often in shoals. *Parailia pellucida*, the African Glass Catfish, is a 10 cm long transparent schilbeid with four pairs of long barbels that protrude outward from its head, a long anal fin, a small adipose fin, a forked tail, and no dorsal fin. It also tends to hover tail down in the water column, often in shoals.

A number of unique modifications occur in the different families, far too many to detail here (see Burgess 1989 and several chapters in Arratia et al. 2003). Among these traits are accessory air-breathing structures and terrestrial locomotion in airbreathing catfishes, airsac catfishes, and callichthyid armored catfishes (see Chapter 5, Air-breathing fishes; Chapter 18, Deserts and other seasonally arid habitats); generation of electric impulses in the African electric and upside-down catfishes (see Chapter 6, Electroreception); climbing ability in climbing catfishes and jet propulsion in banjo catfishes (see Chapter 8, Locomotion: movement and shape); use of lures in angler catfishes (see Chapter 19, Pursuit); and mouth-brooding of large eggs in sea catfishes (see Chapter 21, Parental care).

The most advanced ostariophysans are the **gymnotiforms**, which show internal anatomical similarities to the siluriforms and probably share a common ancestor. However, gymnotiforms are distinct from catfishes and all other ostariophysans, as well as from all other teleosts except osteoglossiform mormyrids and gymnarchids, in that they produce and receive weak electric impulses. Gymnotiforms are known collectively as South American knifefishes because of their strong resemblance to the African knifefishes (Notopteridae); the latter have electrogenic relatives among the mormyrids and gymnarchids but do not produce electricity themselves.

Gymnotiforms are restricted to Central and South America and consist of 134 species in five families. Anatomically, they are characterized by an elongate, compressed body, an extremely long anal fin that reaches from the pectoral fin to the end of the body, no dorsal or caudal fin, small eyes (and nocturnal foraging), and electrogenic tissue combined with modified lateral line organs for detecting weak electric fields. The electrogenic tissue is derived from modified muscle cells in four families, and, curiously, from nerve cells in the apteronotid ghost knifefishes (Alves-Gomes 2001). Apteronotids also depart from the rest of the order by having a distinct tail fin, and include some truly bizarre species (Fig. 14.13). Electrical output in gymnotiforms is continual at high frequencies, as compared to the pulsed, low-frequency output of mormyrids. The electrical output is very weak, on the order of fractions of a volt, except in the Electric Eel (*Electrophorus*), which puts out a weak field for electrolocation purposes and strong pulses upwards of 600 volts for stunning prey or deterring predators (Fig. 14.14). Gymnotiforms range in size from 9 cm long hypopomid bluntnose knifefishes to the 2.2 m long Electric Eel.

Figure 14.13
Two individual *Orthosternarchus tamandua*, an apteronotid knifefish from the Amazon basin. The small black dot on the head is the greatly reduced eye. These predators occur at depths of 6–10 m where they feed on insect larvae (Fernandes et al. 2004). Photo courtesy of C. Cox Fernandes.

Subdivision Euteleostei

All the teleosts above the level of the ostariophysans are generally placed together in the subdivision **Euteleostei**, the "true" teleosts. This designation underscores the conclusion that teleostean phylogeny involved four major radiations, the first three producing relatively primitive and separate groups (osteoglossomorphs, elopomorphs, otocephalans), and the fourth containing a vast (346 families, 2935 genera, 17,419 species) assemblage of more advanced, euteleostean fishes.

The monophyly of the euteleosts as well as the organization of the subdivision remain an area of debate because unique shared derived characters common to all or most members are lacking (or are confused by exceptions), and evidence from different approaches (e.g., anatomical, developmental, and molecular) supports differing conclusions. Johnson and Patterson (1996) proposed a scheme, followed here, that emphasizes three shared traits:

1. Similarities in the pattern of embryonic development of the supraneural bones among euteleosts, which are the small T-shaped or rodlike bony or cartilaginous elements that lie within the musculature between the cranium and the dorsal fin.
2. The presence of an outgrowth on the stegural bone, a structure associated with the neural arches of the vertebral centra of the tail base.

Figure 14.14
Gymnotiform electric knifefishes. An accurate rendering of electric eels, *Electrophorus electricus*, in an otherwise dramatized setting. Anonymous source.

3 The presence of caudal median cartilages, cartilages that lie between the hypural bones of the caudal base.

Johnson and Patterson's analysis eliminates reliance on even more problematic structures for defining the euteleosts. Older summaries emphasized the shared existence of structures that had probably evolved convergently among taxa or that were shared with groups clearly primitive to euteleosts, or that were missing from important clades. One such trait was the presence of epidermal **breeding turbercles** and dermal **contact organs**, small bumps on the fins and bodies that develop during the breeding season in 25 families (Collette 1977; see Chapter 21, Sexual selection, dimorphism, and mate choice). Another, highly enigmatic trait was the presence of an **adipose fin**. This small, (usually) rayless fin sits posterior to the first dorsal, often just anterior to the caudal peduncle. It can be a small vertical flap or bump or it can be a long, substantial structure confluent with the caudal fin, as in many catfishes. It occurs in characiforms, catfishes, smelts, the deepsea stomiiforms, aulopiforms, and scopelomorphs, the salmoniforms (salmons, trouts, whitefishes), and trout-perches. It is generally lacking from higher fishes, particularly those with a spiny first dorsal. Its functions are a mystery.

Subdivision Euteostei, Superorder Protacanthopterygii

Subdivision Euteleostei
- Superorder Protacanthopterygii
  - Order Argentiniformes (202 species): Argentinidae (argentines or herring smelts), Opisthoproctidae (barreleyes), Microstomatidae (pencilsmelts), Platytroctidae (tubeshoulders), Bathylaconidae (bathylaconids), Alepocephalidae (slickheads)
  - Order Salmoniformes (154 species): Salmonidae (whitefishes, graylings, chars, trouts, salmons), Osmeridae (smelts), Retropinnidae (New Zealand smelts, southern graylings), Galaxiidae (galaxiids)

Protacanthopterygians as a group have undergone repeated revision, taxa being removed and added to the superorder as new information is obtained and old data are reinterpreted. The name is used here because it provides an organizational category for a series of apparently related fishes (Fig. 14.15). Nelson (2006) retained Osmeriformes as a separate order within this superorder; we have chosen to follow Johnson and Patterson (1996) and consider osmeroids a suborder within the salmoniforms. We have similarly chosen to separate the esociform pikes and mudminnows from the Protacanthopterygii, aligning them with more advanced teleostean groups (see below, Neognathi).

Argentiniforms are primarily deepsea inhabitants (see Chapter 18). The barreleyes are bizarre looking deepsea fishes with elongate tubular eyes that point upwards. The platytroctids are also deepsea fishes that exude a blue-green luminous fluid from a papilla located under the shoulder girdle, perhaps analogous to squid ink; many species also possess photophores (light organs), a convergent trait among deepsea species.

Within the **Salmoniformes** are two suborders, the **Salmonoidei** and the **Osmeroidei**. Salmonoids are an important group commercially, ecologically, and esthetically, and a fascinating group evolutionarily. They are the focus worldwide of fisheries classes and of popular and technical books. Different taxonomic treatments recognize as many as three different families (coregonid whitefishes, thymallid graylings, salmonid salmons and relatives), but we follow Nelson (2006) and treat them as subfamilies of a larger Salmonidae. Their general anatomical similarities include an adipose fin, no spiny fin rays, a triangular flap at the base of the pelvic fin **(pelvic axillary process)**, gill membranes free from the ventral side of the head, maxilla included in the gape, a physostomous gas bladder, and vertical barring (parr marks) on the sides of most young. Internally the last three vertebrae angle up toward the tail, and a myodome, or area of the skull where the extrinsic eye muscles insert, is present.

The **coregonine** whitefishes and ciscoes consist of approximately 32 species of relatively large-scaled

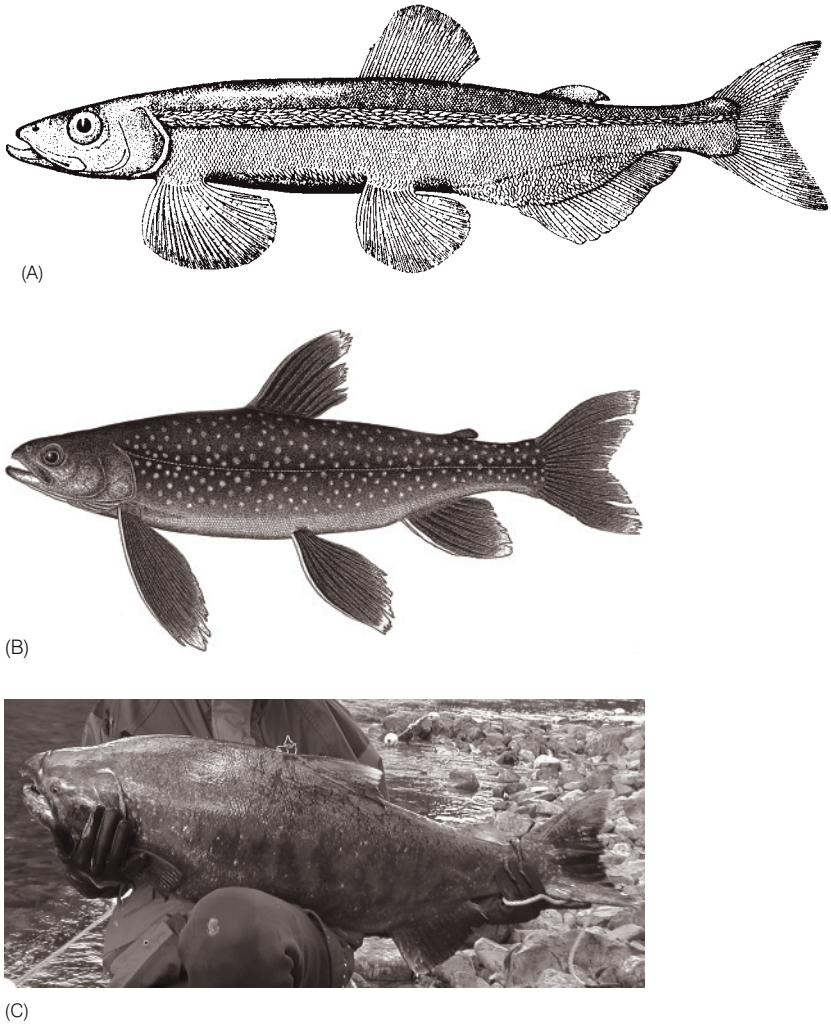

Figure 14.15

Protacanthopterygians. (A) An osmerid, the Capelin, *Mallotus villosus* (sexually mature female). (B) The Longfin Svetovidov's Char, *Salvethymus svetovidovi*, of Lake El'gygytgyn, Siberia. This long-lived, small char (30 years, 30 cm) is threatened by pollution and fishing. (C) A large Chinook Salmon, *Onchorhynchus tshawytscha*, from British Columbia. (A) from Bigelow (1963), used with permission; (B) drawing by Paul Vecsei, used with permission; (C) photo courtesy of R. Carlson.

salmonids that lack teeth on the maxillary bone. They are zooplanktivorous fishes in high-latitude lakes of North America and Eurasia that show a great deal of within-species variation and specialization, forming **species complexes** that differ from lake to lake. Kottelat (1997) documented at least five apparent extinctions and several more extirpations of unique coregonines in Europe. During the mid-20th century, two coregonines native to the Laurentian Great Lakes, the Deep Water Cisco, *Coregonus johannae*, and the Blackfin Cisco, *C. nigripinnis*, disappeared as the result of overexploitation, pollution, siltation, competition with nonindigenous species, and perhaps predation by introduced Sea Lampreys. Whitefishes exemplify the vulnerability of taxa that develop localized specializations (the Wild Salmon Center and Ecotrust maintains a website at www.stateofthesalmon.org that includes accounts of imperiled salmonids based on information from the International Union for the Conservation of Nature (IUCN)'s Salmon Specialist Group). The **thymalline** graylings, *Thymallus*, are a smaller group of about five species of northern hemisphere riverine salmonids that are easily identified by an elongate, flowing dorsal fin.

The subfamily **Salmoninae** contains seven Eurasian and North American genera (*Brachymystax*, *Acantholingua*, *Salmothymus*, *Hucho*, *Salvelinus*, *Salmo*, *Oncorhynchus*) that differ from other salmonids by having small dorsal fins, small scales, and teeth on the maxillary bone (Fig. 14.15B, C). Most species of economic importance are in the latter three genera, although the Siberian Taimen, *Hucho taimen*, is the world's largest salmonid at 2 m and 70 kg (a commercially caught individual weighed 114 kg). North American Salmoninae are currently divided into three genera and approximately 20 species, the names and relationships of which have been the subject of considerable debate (Box 14.1, Fig. 14.16). The chars (or charrs) include the Lake, Brook, and Bull trouts, Arctic Char, and Dolly Varden, all in the genus *Salvelinus*. The northernmost-living freshwater fish in the world is the Arctic Char, *Salvelinus alpinus*, of

Box 14.1

BOX 14.1

What's in a name: the saga of the Rainbow Trout

The Rainbow Trout, for better or worse, has probably been more actively stocked and cultured than practically any other fish species (Fuller et al. 1999). It is consequently one of the most thoroughly studied fishes worldwide. The species was known for most of the 20th century as *Salmo gairdnerii*. Although salmonid taxonomists have argued over the correct name of the Rainbow Trout since 1792, the general public and most of the fisheries and ichthyological communities were unaware of such controversy. Hence considerable surprise and consternation arose when the American Fisheries Society accepted a decision by its Committee on Names of Fishes in 1988 to change the scientific name of the Rainbow Trout to *Oncorhynchus mykiss*. Such a change probably ranks second to the *Brontosaurus* versus *Apatosaurus* debate in terms of number of people affected (Gould 1990). The history and justification of the Rainbow Trout name change are good examples of the dynamics of scientific nomenclature and advance (Kendall 1988; Stearley & Smith 1993), and were clearly explained to the fishery biology community by Smith and Stearley (1989).

The change resulted from the intersection of: (i) taxonomic debates concerning the application and interpretation of the rules of nomenclature; (ii) recent discoveries involving biochemical and anatomical investigations on salmonids; and (iii) how cladistic analysis has modified our view of evolutionary relationships. First, the Rainbow Trout turns out to be the same fish as an Asian species, the Kamchatka Trout, *Salmo mykiss*, which was named by Walbaum in 1792. During the early scientific explorations of the North Pacific, wide-ranging salmonids were "discovered" repeatedly, one species being assigned different names. Between 1792 and 1862, Walbaum, Richardson, and Suckley all independently described what we today recognize as the Rainbow Trout. This duplication resulted in part because salmonids are notoriously variable in anatomy, color, and behavior (especially in the Kamchatka; see Chapter 24). The confusion was not alleviated by Rainbow Trout having two very different life history patterns, a sea-run form, known as the Steelhead, and a land-locked form, known as the Rainbow Trout (and Redband Trout in some areas). Additional confusion over the geographic ranges of Rainbow and Cutthroat Trout (*O. clarkii*) only clouded the issue more, and it was not until Okazaki's (1984) analysis that vertebral and scale counts, karyotypes, and electrophoretic data were brought together to demonstrate convincingly that *S. mykiss* and *S. gairdnerii* from both sides of the Pacific were the same fish. Since the

Kamchatka Trout was described first by Walbaum, its specific name, *mykiss* (from an indigenous Kamchatkan name) has historical priority. Still unsettled was the question of which was the appropriate generic name.

The dilemma of generic names has been clarified by recent osteological (particularly skull and jaw bones) and biochemical studies of a variety of salmonids. These investigations indicate that the Pacific species of trout (Rainbow, Cutthroat, Golden, Mexican Golden, Gila, and Apache trouts) are more closely related to the Pacific salmons (*Oncorhynchus* spp.) than they are to the Atlantic salmonids, namely the Atlantic Salmon (*Salmo salar*) and the Brown Trout (*S. trutta*). Since any accurate classification should reflect the true relations among the species, the most logical choice is to put all the western and Pacific species, be they "trout" or "salmon", in one genus, and the Atlantic species in another.

This conclusion is really nothing new; Regan in 1914 proposed just such a realignment. But Regan's ideas were unfortunately rejected by later workers who focused on characters that varied between sexes, or who felt that primitive characters retained among taxa (symplesiomorphies) should form the basis for classification. However, the emergence of cladistics with its emphasis on shared derived (synapomorphic) traits as stronger indicators of evolutionary relationships has helped swing the debate. The argument boils down to an emphasis on similarities due to lack of change versus similarities due to the evolution of shared, specialized characters (see Chapter 2; Approaches to classification). Regan's original analysis, based on skull characters, is borne out by biochemistry and other osteological features, as well as by a number of life history, reproductive, coloration, and behavioral characters (Fig. 14.16). The result is that the ichthyological and fisheries communities have accepted *Salmo* as the generic name for the Atlantic species, *Oncorhynchus* for Pacific trouts and salmons, and *Oncorhynchus mykiss* as the scientific name for the Rainbow Trout.

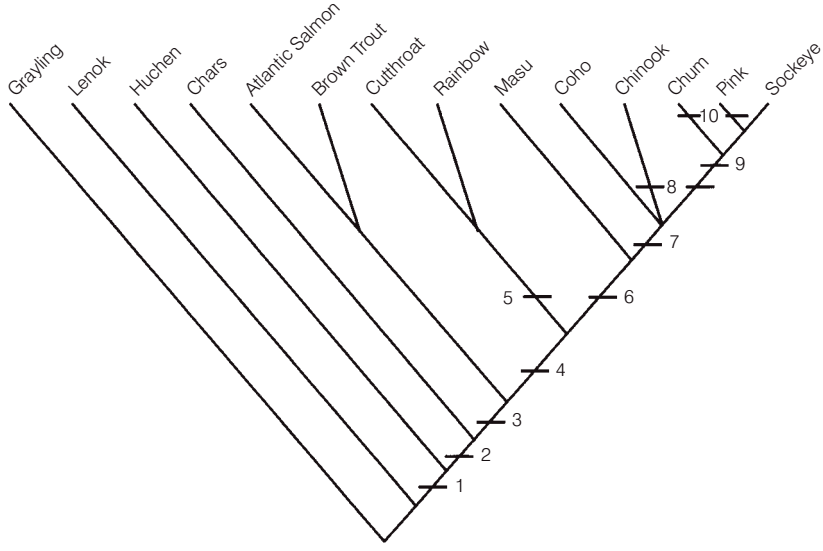

Figure 14.16

Phylogeny of the salmonids. A cladogram of most living salmonids based on life history traits shows the evolution of the various species. The same cladogram is constructed if anatomical and biochemical traits are used. The first four lineages represent separate genera (*Thymallus*, *Brachymystax*, *Hucho*, *Salvelinus*), Atlantic Salmon and Brown Trout are in the genus *Salmo*, and the remaining eight species (those above trait 4) are all in the genus *Oncorhynchus*. The more primitive coregonine whitefishes would come off to the far left of the cladogram and are not shown. The following life history and reproductive characteristics are the shared derived characters that were used to construct the cladogram. The listed characters correspond to the numbered branch points in the cladogram. Groups to the right and above the number possess the trait, those to the left do not. From Smith and Stearly (1989), used with permission.

1, egg diameter greater than 4.5 mm; females dig redds (nests); large males have hooked jaws (kype) during breeding season; 2, fall spawners; 3, commonly undergo long oceanic migrations; 4, most spawners undergo irreversible hormonal changes; 5, spring spawners; 6, anadromous forms die after spawning; 7, non-migratory individuals tend not to reproduce; 8, most smolt in first year, some go to sea as even younger fry; 9, juveniles are strong schoolers, parr are slender; 10, the freshwater phase is reduced; young migrate soon after emerging from gravel.

Lake Hazen, on Ellesmere Island in Canada (80°N); many char are anadromous, moving into the sea to feed and grow and then back into fresh water to spawn. Arctic Char in isolated lakes frequently differentiate into distinct ecomorphological types, forming functionally different ecological populations within taxonomic species (see Chapter 24, Genetic structure of populations and Fig. 24.3).

The remaining salmonines are the Atlantic basin salmon and trout (*Salmo salar*, the Atlantic Salmon; *S. trutta*, the European Brown Trout, with numerous subspecies and races; and three other European species), and the 11 species of Pacific basin trouts and salmons in the genus *Oncorhynchus* (Behnke 2002) (Fig. 14.17). Two *Oncorhynchus* species, *O. masou* and *O. rhodurus*, are endemic to Japan. Pacific trouts and salmons include narrowly distributed, landlocked forms such as Golden and Gila trouts, and species that are spectacularly anadromous, such as the Chinook, Chum, Coho, Pink, and Sockeye salmons (*O. tshawytscha*, *O. keta*, *O. kisutch*, *O. gorbuscha*, and *O. nerka*, respectively). (Latinized names of Pacific salmon defy the usually predictable logic of binomial nomenclature. The mystery is partially solved when one learns that these spellings represent Russian names transliterated into English and later converted into Latin over a 60-year period by a series of German and British ichthyologists (Moyle 2002).) Some Pacific salmon undergo oceanic migrations of thousands of kilometers before returning to their birth river to spawn and die (see Chapter 23; Representative life histories of migratory fishes). The actual number of species, subspecies, and distinct races of Pacific salmons is a matter of considerable and important debate because of the wholesale destruction of stocks in various rivers of the Pacific Northwest region of the USA (Lichatowich 1999; Williams 2006). Many of these stocks are reproductively isolated and genetically distinct and therefore are viewed as unique evolutionary taxa, termed evolutionary significant units (ESUs) for conservation purposes.

Figure 14.17

A Golden Trout, *Oncorhynchus aguabonita*, the state fish of California. Greatly depleted by introduced species and habitat destruction, Golden Trout are now the focus of restoration programs that include eradication of the European Brown Trout that were actively stocked in past decades. Photo by T. Kelsey, courtesy of E. P. Pister.

In the osmeroids is the family **Osmeridae**, which includes about 30 species of marine, freshwater, and diadromous (migrating between fresh water and the sea) species that inhabit shallow waters. Osmerids are generally small, silvery, elongate fishes that swim in the water column. They have a single, soft-rayed dorsal fin and sometimes an adipose fin. The maxilla is included in the gape, and most jaw bones possess teeth. Although their pelvic fins are abdominal, as is the case for most of the preceding teleostean groups, some osmerids have their pectorals located higher on the body than is common in the more primitive groups. Osmerids include commercially important species such as Capelins (*Mallotus*), Eulachons (*Thaleichthys*), Asian Ayu (*Plecoglossus*), and Rainbow Smelt (*Osmerus*), many of which are superficially similar to the more advanced silversides (Atherinidae).

The other osmeroids are two families that dominate cold freshwater environments of the southern hemisphere. These are the retropinnids and galaxiids. Retropinnids are small (10–35 cm), marine and anadromous (spawn in fresh water, grow in the sea) fishes of New Zealand and Australia known as southern smelts and southern graylings; they sometimes establish landlocked populations in lakes. The galaxiids occur in Australia and New Zealand but also in southern South America and Africa. Galaxiids constitute important commercial whitebait fisheries in New Zealand. Galaxiids have complex life cycles, exhibiting all major types of diadromy, including anadromy, catadromy, and amphidromy (see Chapter 23, Diadromy). Some are also semelparous, spawning only one time before dying (see Chapter 24, Life histories and reproductive ecology). Retropinnids and galaxiids as a group have suffered numerous extirpations and extinctions as a result of habitat destruction and the stocking of non-native trouts (see Chapter 26, Species introductions). One retropinnid, *Prototroctes oxyrhinchus*, is known to be extinct.

A truly unique galaxiid is the salamanderfish *Lepidogalaxias salamandroides* (Fig. 14.18). This benthic living, elongate fish inhabits seasonally dry ponds of southwestern Australia, where it buries in the mud and lives in a torpid state after ponds dry up, re-emerging with the next rains (see Chapter 18, Deserts and other seasonally arid habitats). Salamanderfish lack eye muscles but instead have a flexible neck joint that allows them to bend their neck at a right angle to the side, a very unusual ability in fishes. Neck bending is made possible by large gaps between the back of the skull and the first cervical vertebrae and between the first and second cervical vertebrae. Salamanderfish have also apparently reinvented the physostomous gas bladder, in that they lack a normal gas bladder but instead have a gas-containing structure made up of simpler mesentery-like tissue and collagen fibers (Berra & Allen 1989; Berra et al. 1989).

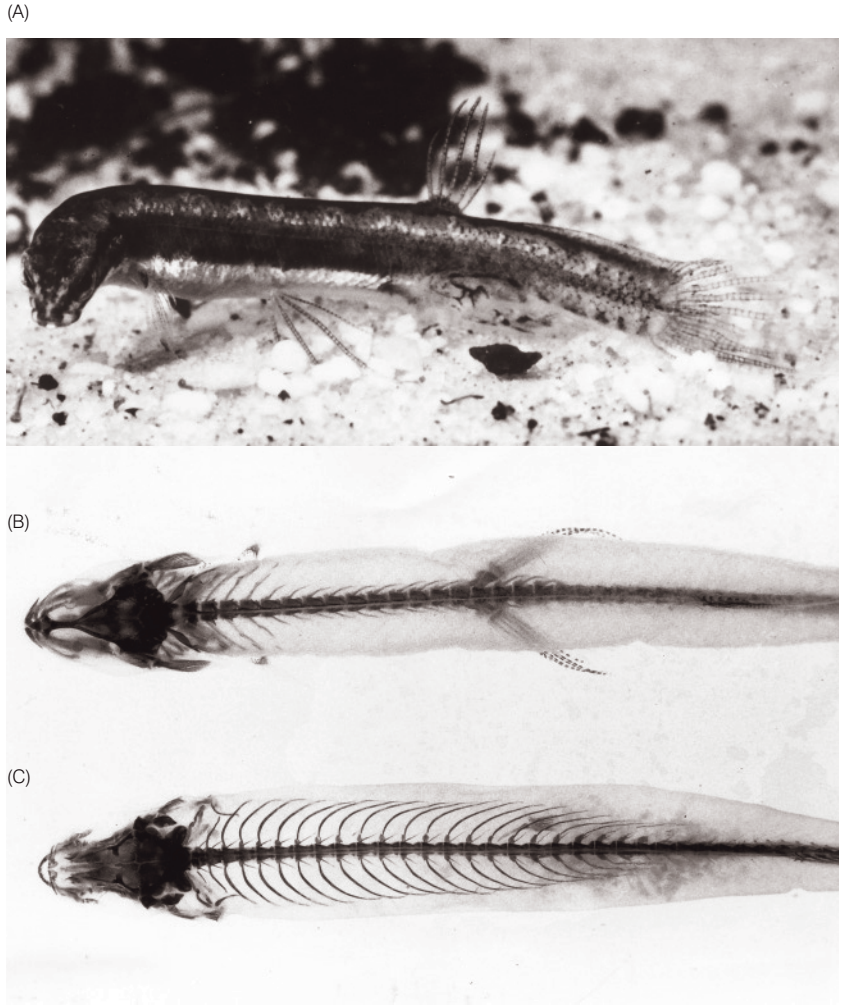

Figure 14.18
Neck flexibility in the Australian salamanderfish, *Lepidogalaxias salamandroides*. This unusual benthic fish is able to bend its neck sideways and downwards due to a unique arrangement of spaces between the skull and the cervical vertebrae. A lack of ribs throughout the vertebral column probably aids in neck bending and also allows the fish to make sinuous movements. (A) A 35 mm long salamanderfish in the bent-neck position. (B) A cleared and stained, 49 mm long salamanderfish showing intervertebral gaps and lack of ribs. (C) A comparison specimen of the related *Galaxiella munda* (Galaxiidae, 46 mm), showing the tightly coupled vertebrae and more elongate ribs. Note also the well-developed pelvic girdle of *Lepidogalaxias*, which is used as a prop during resting. From Berra and Allen (1989), used with permission.

Neognathi

The remaining Euteleosts, all 336 families and 17,000+ species, are collectively placed in the unranked taxonomic category **Neognathi**, which consists of the order Esociformes (10 species) and the **Neoteleostei**, the latter also an unranked taxonomic level. The esociform pikes and mudminnows are viewed as the sister group of all higher euteleosts because they share a distinct type of tooth attachment and a skeleton made up of acellular bone (Johnson & Patterson 1996). Consensus on this arrangement is by no means universal, with some authors contending that esociforms are protacanthopterygians and a sister taxon to salmoniforms (see Nelson 2006 for a review).

Order Esociformes

Order Esociformes (10 species): Esocidae (pikes, pickerels), Umbridae (mudminnows)

The **esociforms** consist of two temperate families of freshwater fishes in which the maxillary bone is included in the gape but is toothless, and in which the median fins are located relatively far back on the body. Esocids include the Grass, Redfin, and Chain pickerels, the Northern and Amur pikes, and the superpredatory 1.4 m Muskellunge, *Esox masquinongy* (Fig. 14.19). The Northern Pike, *E. lucius*, has the most widespread natural east–west distribution of any completely freshwater fish, occurring across the northern portions of North America, Europe, and Asia (= circumpolar distribution). The family goes back into the Cretaceous, and one Paleocene species is very similar to the Northern Pike despite a 62-million-year separation. Anatomical and behavioral convergences between pikes and barracudas, the latter a higher acanthopterygian, are fairly remarkable (see Chapter 19, Pursuit and Fig. 19.1). The mudminnows and blackfishes (Umbridae) are also scattered across northern North America, Europe, and Asia. The Central Mudminnow, *Umbra limi*, has a remarkable ability to survive in high-latitude lakes that become ice-covered and oxygen-poor through much of the winter (see Chapter 23, Seasonal cycles).

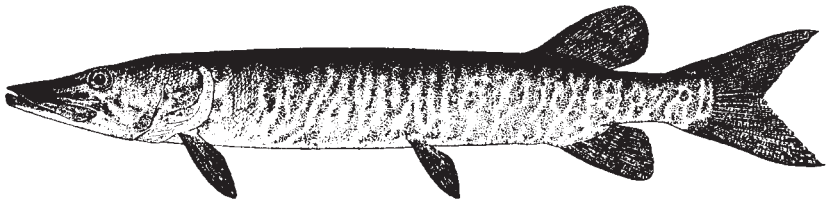

Figure 14.19
The esocid Muskellunge, *Esox masquinongy*, one of the largest freshwater predators in North America. From Scott and Crossman (1973).

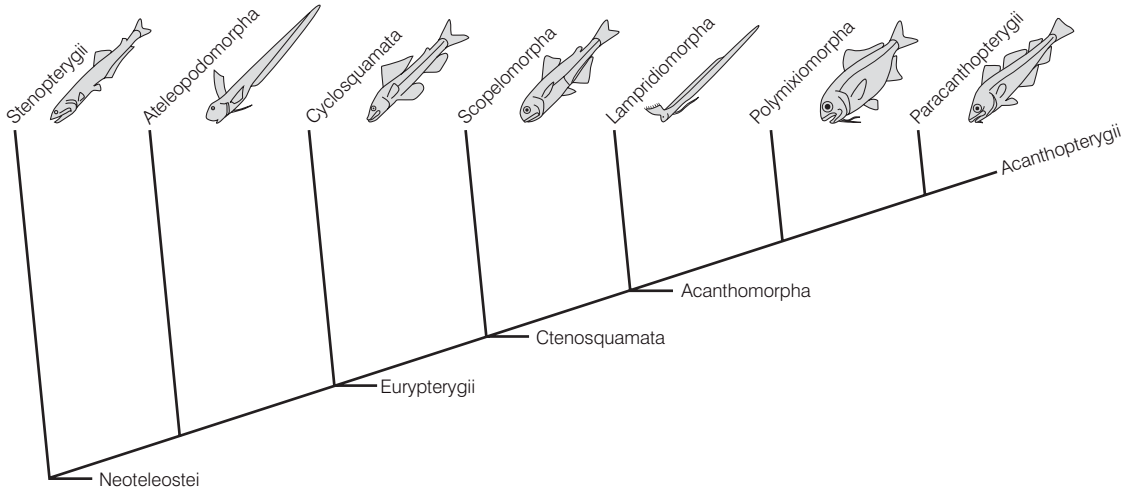

Figure 14.20
Phylogenetic relationships among formally recognized, advanced teleostean superorders above the level of the Protacanthopterygii. Along the diagonal line of the cladogram are commonly used designations that do not have formal rank but that are generally distinguishable by shared derived traits as discussed in the following accounts. After Nelson (2006).

Neoteleostei

All of the fishes above the esociforms are considered to be **neoteleosts**, a category without formal rank that lies somewhere between a subdivision and a superorder (Fig. 14.20). Eight neoteleostean superorders are recognized, including six relatively specialized deepsea and pelagic superorders (discussed at length in Chapter 18, The deep sea) and two very diverse, advanced superorders, the paracanthopterygians and acanthopterygians. Neoteleosts as a taxon are considered to be monophyletic on the basis of four skull and jaw characters possessed by the different members that are lacking in more primitive fishes:

1. The manner in which the vertebral column connects to the back of the skull changes. In the neoteleosts, the first vertebra articulates with three bones of the skull (basioccipital and the two exoccipitals), whereas in more primitive teleosts it articulates with only the unpaired basioccipital.
2. A muscle, the retractor dorsalis, connects the vertebral column with dorsal elements of the upper pharyngeal jaws and pulls those jaws posteriorly.
3. A shift occurs in the insertion position of another muscle, one of the internal levators that originates on the base of the skull and lifts the pharyngeal jaws.
4. A unique hinged manner of attaching teeth to the jaws develops, allowing the tooth to be depressed towards the back of the mouth.

In addition, a trend toward more anteriorly located pelvics and more laterally located pectorals is evident during neoteleostean phylogeny, and acellular bone (skeletal material lacking bone cells) occurs in most neoteleosts, whereas more primitive groups have bone cells (Smith 1988).

Superorder Stenopterygii

Superorder Stenopterygii
  Order Stomiiformes (391 species): Diplophidae, Gonostomatidae (bristlemouths), Sternoptychidae (marine hatchetfishes), Phosichthyidae (lightfishes), Stomiidae (barbeled dragonfishes)

Stomiiforms are all deepsea fishes of the mesopelagic and bathypelagic regions (open water, between 200 and about 4000 m depths) and are often characterized by long teeth

uniquely attached to jaw bones, large mouths, histologically unique photophores (light organs) that include a duct, and a peculiar ventral adipose fin ahead of the anal fin in some. Gonostomatid bristlemouths (*Cyclothone*) and phosichthyid lightfishes (*Vinciguerria*) may be the most abundant and widely distributed vertebrates on earth. The sternoptychid marine hatchetfishes possess several structural specializations that emphasize the vertical plane and body compression. The mouth opens vertically, the photophores point down, a preopercular spine points upwards, the pelvic bones are oriented vertically, the lateral compression of the body is heightened by an abdominal keel-like structure, and a bladelike structure preceding the dorsal fin is made up of dorsal pterygiophores that project through the back of the fish. Pterygiophores normally serve as the basal support for median fins, not as elements of a fin itself. Idiacanthine black dragonfishes have a larval form with eyes at the ends of elongated stalks. Stomiiforms show many traits common to other, unrelated deepsea fishes that are generally viewed as convergent adaptations to the light- and food-limited conditions of the deep sea (see Chapter 18, The deep sea).

Superorder Ateleopodomorpha

Superorder Ateleopodomorpha
- Order Ateleopodiformes (12 species): Ateleopodidae (jellynose fishes)

The **ateleopodiform** jellynose fishes are an unusual group of bulbous-headed, elongate species that swim just above the bottom in deep water. Their skeleton is largely cartilaginous. Their large and pointed head, exaggerated anal fin, and relatively pointed tail are all traits they share with other deep, benthopelagic fishes such as chimaeras, spiny eels, halosaurs, eucla cods, rattails, and grenadiers (see Chapter 18, The deep sea).

Superorder Cyclosquamata

Fishes more advanced than ateleopodomorphs are sometimes referred to as **eurypterygians** ("wide or broad fins"). The most primitive superorder in this group is the Cyclosquamata ("cycloid scales"), which contains one large order of almost entirely deepsea fishes. **Aulopiforms** have a surprisingly extensive fossil record (approximately six families and perhaps 20 genera) for a group that today is largely open water and deep sea. The extant deepsea groups include the truly bizarre giganturid telescope fishes (Fig. 14.21A) which undergo a spectacular metamorphosis during which the premaxillary, palatine, orbitosphenoid, parietal, symplectic, posttemporal, supratemporal, hyoid, and cleithral bones in the head region are lost, as are several gill arches, the gill rakers, and the gas bladder. The larvae possess an adipose fin, pelvic fin, and branchiostegal rays that are also lost during metamorphosis. The adults possess large tubular eyes, a huge mouth, flexible teeth, an expandable stomach, pectoral fins located exceptionally high on the body above the eyes, loose skin, and a peculiar tail with the ventral lobe extending far beyond the dorsal lobe.

Chlorophthalmid greeneyes are the first fishes encountered in this survey that are hermaphroditic, as are members of other families in this order. All of the more primitive groups so far have been distinctly gonochoristic, which means that an individual is only one sex throughout its life. Hermaphroditism of some form is surprisingly common in higher teleosts (see Chapter 10, Adults; Chapter 21, Gender roles in fishes). This dichotomy between primitive and advanced teleosts suggests that sexual lability – either in terms of initial sexual determination or of an ability to change sex later in life – represents a derived trait that became differentially retained or independently evolved after the neoteleostean or eurypterygian level of development was reached.

Included among the ipnopids are the often illustrated spiderfishes or tripodfishes, which have greatly elongated pectoral, pelvic, and caudal rays; they use the pelvics and caudal to form a tripod for resting on sediments of the deep ocean floor (Fig. 14.21.B). The best known shallow representatives of this order are the synodontid lizardfishes, which are common benthic inhabitants of coral reefs worldwide (and whose name should not be confused with the synodid upsidedown catfishes) (Fig. 14.21C). Lizardfishes are closely related to the secondarily pelagic Bombay ducks (*Harpadon*) that support an important fishery in the Indian Ocean. The order includes the alepisaurid lancetfishes, which are large (up to 2 m) mesopelagic predators on other fishes. Lancetfishes are distinguished by their large, sail-like

Superorder Cyclosquamata
- Order Aulopiformes (236 species): Paraulopidae (cucumber fishes), Aulopodidae (flagfins), Pseudotrichonotidae (sanddiving lizardfishes), Synodontidae (lizardfishes), Bathysauroididae (bathysauroidids), Chlorophthalmidae (greeneyes), Bathysauropsidae (bathysauropsids), Notosudidae (waryfishes), Ipnopidae (deepsea tripodfishes and spiderfishes), Scopelarchidae (pearleyes), Evermannellidae (sabertooth fishes), Alepisauridae (lancetfishes), Paralepididae (barracudinas and daggertooths), Bathysauridae (deepsea lizardfishes), Giganturidae (telescopefishes)

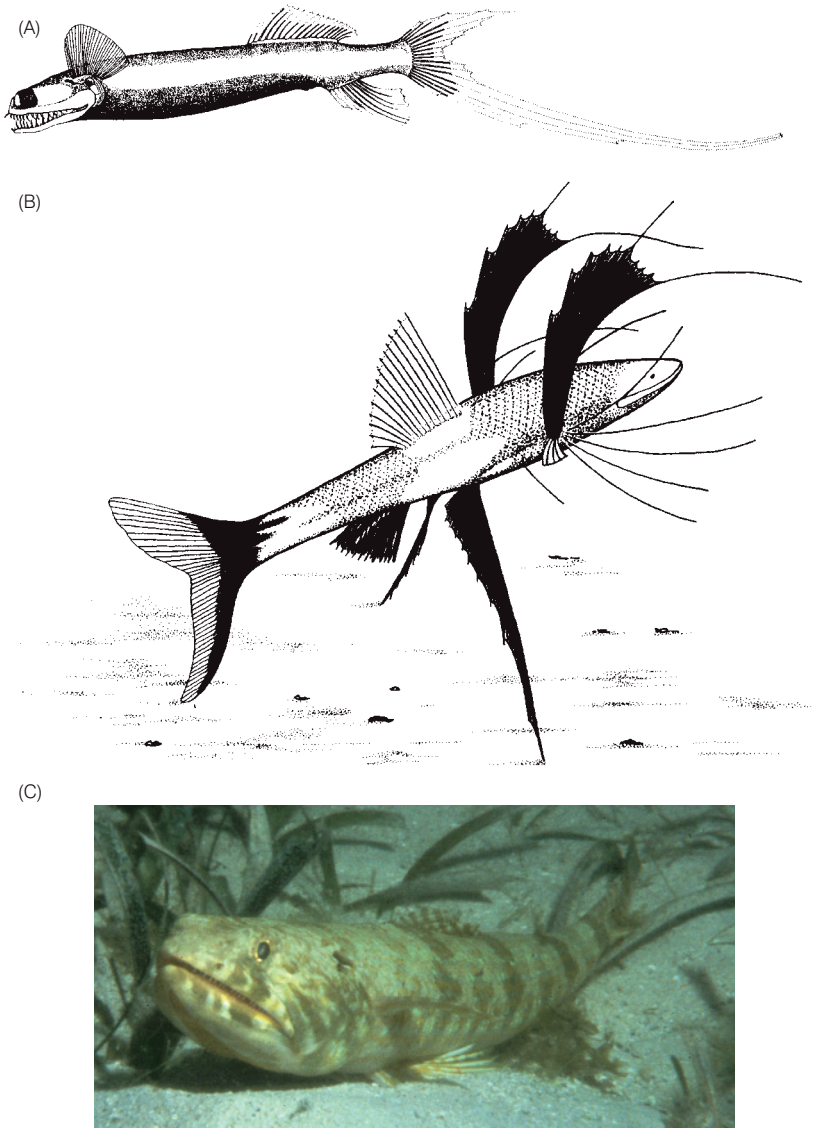

Figure 14.21
Aulopiforms, from deep and shallow water. (A) Giganturid telescopefishes are mesopelagic, water column dwellers. (B) Ipnopid spiderfishes are deepsea benthic dwellers. (C) Synodontid lizardfishes are benthic, shallow water, sand bottom, lurking predators on coral reefs and in some subtropical areas. (A) from Walters (1964); (B) after Heezen and Hollister (1971); (C) photo by G. Helfman.

dorsal fin that extends from the head almost to the caudal peduncle (function unknown). These fishes, which look very much like scombroid snake mackerels, have proven a great boon to deepsea taxonomists as several species of mesopelagic fishes have been described from the stomach contents of alepisaurids (see Chapter 18, The deep sea).

Superorder Scopelomorpha

Superorder Scopelomorpha
Myctophiformes (246 species): Neoscopelidae (blackchins), Myctophidae (lanternfishes)

All fishes above the level of the Cyclosquamata have lost the fifth pharyngeal toothplate and the muscle that lifts it (Johnson 1992). These advanced groups are often termed the **Ctenosquamata** in reference to the predominance of ctenoid scales among them. One order of deepsea fishes, the **myctophiforms**, makes up the superorder Scopelomorpha (Fig. 14.22). Myctophiforms have lost the fifth pharyngeal toothplate but most still have cycloid scales, justifying their primitive status among ctenosquamates. Their relative primitiveness is also shown in their retention of an adipose fin, but they are advanced in that the maxilla is excluded from the gape. The myctophid lanternfishes, with about 240 species, are an important group of mesopelagic deepsea fishes in terms of diversity, distribution, and numbers of individuals. They occur in all seas, from the Arctic to the Antarctic, and are the prey of numerous other fishes as well as of marine mammals. They make up a large fraction of the deep scattering layer – a diverse assemblage of fishes and invertebrates that live at mesopelagic depths

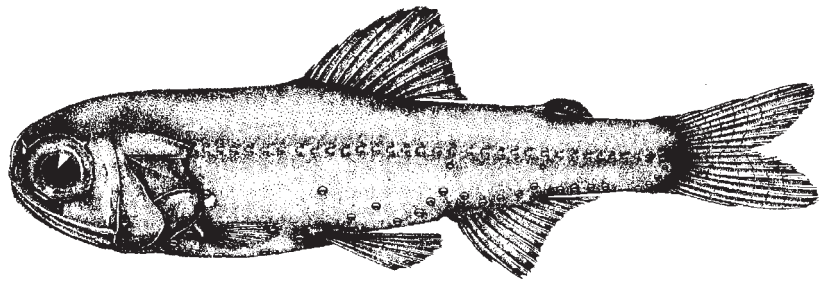

Figure 14.22
A myctophid lanternfish, *Diaphus mollis*, about 4 cm long. The round structures along the ventral half of the body are light-emitting photophores. From Nafpaktitis et al. (1977), used with permission.

(below 200 m) during the day and migrate towards the surface at dusk. Myctophid taxonomy is often based on otolith structure and species-specific patterns of photophores, characters that are even preserved in some fossils.

Acanthomorpha: the spiny teleosts

Neoteleosts above scopelomorphs possess true fin spines and are termed acanthomorphs. The appearance of true fin spines, rather than hardened segmented rays, marks a major evolutionary step in the evolution of bony fishes. True spines occur in the dorsal, anal, and pelvic fins of higher teleosts. Spines develop when the two halves of the primitively paired and jointed dermal fin rays fuse into a single, unsegmented structure. Several other characteristics, mostly associated with improved locomotion and feeding, also mark the ascendancy of teleosts above the ctenosquamate level of development (see Chapter 11, Division Teleostei). Locomotion was improved by the strengthening of vertebral accessories (zygapophyses), providing body stiffening and better attachment for muscles. These changes allowed a shift from slow, sinusoidal motion of the entire body to rapid oscillation of the tail region, driven by tendons attached to the tail base (see Chapter 8, Locomotion: movement and shape). The tail itself also underwent considerable modification. Pharyngeal teeth diversified and the maxilla shifted from a tooth-bearing bone to a structure that helps pivot the premaxilla, making mouth protrusion and suction more effective. These advances probably made possible the explosive radiation of spiny-rayed teleosts, known collectively as acanthomorphs, during the Early Cenozoic.

The acanthomorphs include the superorders Lampriomorpha, Polymixiomorpha, Paracanthopterygii, and Acanthopterygii (see Chapter 15).

Superorder Lampriomorpha

As is often the case, the most primitive members of a major taxon retain certain ancestral traits but possess others indicative of advanced status. **Lampriforms** lack true spines, but the maxilla helps move the premaxilla and bears no teeth. The connection between the two upper jaw bones and the manner in which they slide to protrude the mouth are unique, so much so that the group used to be referred to as the Allotriognathi, or "strange jaws". The seven families of lampriforms are almost all open water oceanic fishes with unusual body and fin proportions. Opahs are relatively large (up to 1.8 m, 70 kg), oval-shaped, colorful pelagic predators on squids and other fishes (Fig. 14.23A). The 30 cm long tube-eye (*Stylephorus*) is capable of an almost 40-fold enlargement of its mouth volume during feeding, which is probably a record among vertebrates (see Chapter 8, Jaw protrusion: the great leap forward). The remaining five families contain mostly large and rare, elongate, pelagic fishes with long dorsal fins. Crestfishes and radiicephalids have ink sacs that they discharge through their cloaca. In trachipterid ribbonfishes, the caudal fin is made up only of the upper lobe, which sits inclined at a right angle upward. The oarfish, *Regalecus*, reaches a confirmed length of over 7 m and perhaps as much as 11 m, making it the longest extant teleost; uncertainty arises because intact specimens are seldom found (Fig. 14.23B). Despite their size, they are apparently planktivores that hover head up in the water column, swimming via rapid undulations of the long dorsal fin. Their name comes from bladelike expansions at the end of the pelvic fins. Specimens are uncommon, many obtained after storms when the bodies of these strange-looking fishes are tossed up on beaches. The oarfish, with its bluish-silvery body, scarlet dorsal crest of elongate fin rays, and deep red fins, is likely responsible for many sea serpent sightings, particularly those referring to monsters "having the head of a horse with a flaming red mane" (Norman & Fraser 1949, p. 113).

Superorder Lampriomorpha
- Order Lampriformes (21 species): Veliferidae (velifers), Lampridae (opahs), Stylephoridae (tube-eyes or thread-tails), Lophotidae (crestfishes), Radiicephalidae (tapertails), Trachipteridae (ribbonfishes), Regalecidae (oarfishes)

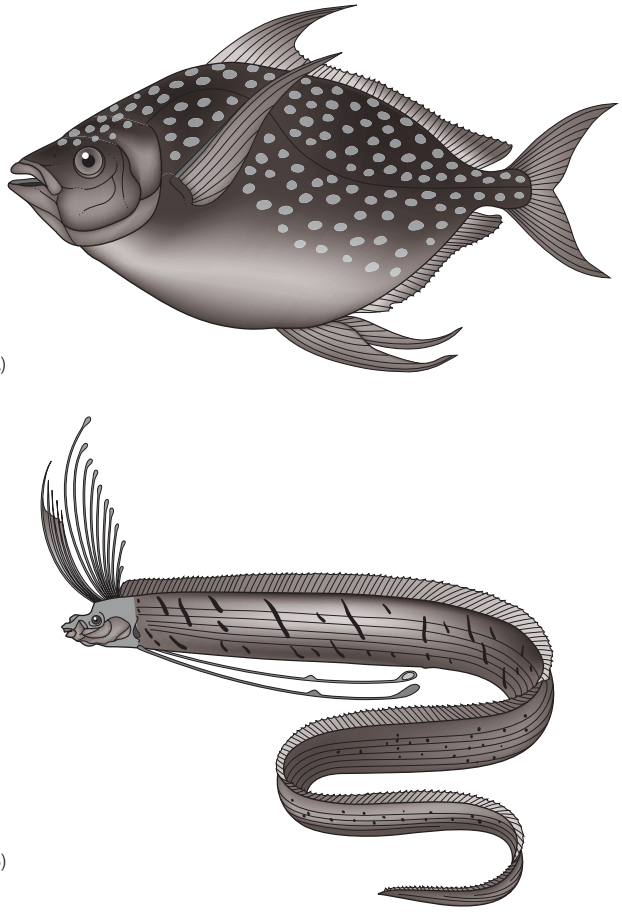

Figure 14.23
Lampriformes. (A) An opah or moonfish, *Lampris regius*. This large pelagic predator has red fins, a silvery-white body, with a bluish back. (B) The oarfish, *Regalecus glesne*, the world's longest teleost, reaching lengths of 7 m to as much as 11 m. Whole specimens are rare. (B) courtesy of T. Roberts.

Superorder Polymixiomorpha

Superorder Polymixiomorpha
- Order Polymixiiformes (10 species): Polymixiidae (beardfishes)

The taxonomic status of this enigmatic family has been the subject of considerable debate (see Johnson & Patterson 1993a, 1993b; Nelson 1994, 2006). Beardfishes possess advanced characters such as four to six true spines in the dorsal fin and four spines in the anal fin, and their pelvic fins are located fairly forward on the body. Yet they retain two sets of intermuscular bones, the epineurals and epipleurals, a characteristic of more primitive taxa, and have a unique arrangement of jaw muscle ligaments. This combination of primitive, advanced, and unique characteristics complicates determination of their relationships. At different times, they have been classified as a sister taxon to the remaining acanthomorphs, with the primitive paracanthopterygian percopsiforms (trout-perches and relatives), or with primitive acanthopterygian beryciforms (squirrelfishes and relatives). We follow Nelson (2006) and place them between lampriomorphs and paracanthopterygians, but with minimal certainty. Beardfishes have large eyes, chin barbels, are about 30 cm long, and live at moderate depths (200–600 m).

Superorder Paracanthopterygii

Superorder Paracanthopterygii
- Order Percopsiformes (nine species): Percopsidae (trout-perches), Aphredoderidae (Pirate Perch), Amblyopsidae (cavefishes)
- Order Gadiformes (555 species): Muraenolepididae (eel cods), Bregmacerotidae (codlets), Euclichthyidae (Eucla Cod), Macrouridae (grenadiers or rattails), Moridae (morid cods), Melanonidae (pelagic cods), Merlucciidae (merluccid hakes), Phycidae (phycid hakes), Gadidae (cods)
- Order Ophidiiformes (385 species): Carapidae (pearlfishes), Ophidiidae (cusk-eels), Bythitidae (viviparous brotulas), Aphyonidae (aphyonids), Parabrotulidae (false brotulas)
- Order Batrachoidiformes (78 species): Batrachoididae (toadfishes, midshipmen)
- Order Lophiiformes (313 species): Lophiidae (goosefishes), Antennariidae (frogfishes, sargassumfishes), Tetrabrachiidae (tetrabrachiid frogfishes), Lophichthyidae (lophichthid frogfishes), Brachionichthyidae (handfishes), Chaunacidae (coffinfishes, sea toads), Ogcocephalidae (batfishes), Caulophrynidae (fanfins), Neoceratiidae (toothed seadevils), Melanocetidae (black seadevils), Himantolophidae (footballfishes), Diceratiidae (double anglers), Oneirodidae (dreamers), Thaumatichthyidae (wolftrap anglers), Centrophrynidae (deepsea anglerfishes), Ceratiidae (seadevils), Gigantactinidae (whipnose anglers), Linophrynidae (leftvents)

The 36 families of recognized paracanthopterygians represent a major and contentious side branch during the evolution of advanced acanthomorphs. They are weakly defined by a number of characters, chiefly involving the caudal skeleton and holes in the skull through which cranial nerves

pass (Nelson 1994), but ". . . there is no firm basis to believe [the superorder] is monophyletic" (Nelson 2006, p. 232). Their ecological success is largely as benthic, marine fishes that are nocturnally active or live in permanently darkened waters, such as the bathypelagic region of the deep sea or in caves. Only about 20 relatively primitive paracanthopterygians, out of a total 1340 species, live in fresh water. Many paracanthopterygians have sonic muscles on their gas bladders and produce sounds.

At the base of the paracanthoptgerygians are the **percopsiforms**, small (<20 cm), freshwater fishes, eight of nine of which live in eastern North America. The Trout-perch, *Percopsis omiscomaycus*, and its Columbia River congener, *P. transmontana*, are the most advanced fishes we will encounter with an adipose fin. This seeming primitive condition is interesting given that modern percopsiforms possess several traits suggesting a reversal of the evolutionary trends of advanced teleosts, including fossil percopsiforms. The modern species have fewer fin spines, more vertebrae, and a more posteriorly located pelvic girdle than occurred in fossil forms. The aphrododerid Pirate Perch, *Aphrododerus sayanus*, is a swamp dweller with the distinction of having its anus move from just anterior of the anal fin in juveniles to the throat region of adults. Speculation abounded on the functional reasons for this anatomical anomaly. Recent observations reveal that Pirate Perch are nocturnally active fish that hide and spawn in dense vegetation and root mats (Fletcher et al. 2004; Tiemann 2004). Females push head first into such root mats to deposit eggs, and males enter the same spot shortly thereafter to deposit sperm; hence the anterior position of the anus allows deposition of eggs and sperm deep into a protected, otherwise inaccessible area (Fig. 14.24). By day, fish emerge from vegetation refuges only far enough to expose the head and anus, at which time they defecate. The jugular position of the anus would permit defecation without altering water quality in the refuge and would also minimize exposure to predators. As is so often the case, seemingly specialized traits often confer multiple functional benefits.

The amblyopsid cavefishes include six species of highly modified, often blind and scaleless forms that show numerous adaptations for cave life (see Chapter 18, Caves). Their isolated, easily disturbed habitats and bizarre appearance has made them vulnerable to both collecting and habitat disruption, and several species are threatened and hence protected nationally and internationally.

The **gadiforms** include some of the most important commercial fishes in the world such as the cods, haddocks, hakes, pollocks, and whitings (Fig. 14.25A). Gadiforms lack true spines but have experimented with fin rays. The long dorsal fin is relatively diversified compared with most primitive groups; it is often divided into two or three parts, an anterior ray that is sometimes spinous (grenadiers) or elongate and even filamentous (morid cods, codlets, eel cods). True cods (Gadinae) have three dorsal fins and two anal fins. Pelvic fins are thoracic or jugular in position and are sometimes modified into filaments with a possible sensory function (e.g., Eucla Cod, codlets, physid hakes). Many species have chin barbels (grenadiers, morid cods, eel cods, physid hakes, cods), a convergent trait in benthic or near-benthic (surpabenthic, benthopelagic) fishes. Gadiforms are northern marine fishes with the solitary exception of the Burbot, *Lota lota*, which is a lake gadid of Holarctic (high latitude, northern hemisphere) distribution. The commercially important Atlantic Cod, *Gadus morhua*, is the largest species in the order; it once reached lengths of 1.8 m and weighed over 90 kg, although fish over 10 kg are now rare due to

Fig. 14.24

Spawning behavior of the Pirate Perch, *Aphrododerus sayanus*, a fish with a jugular-positioned anus. Pirate Perch spawn in dense root mats, the female and then the male pushing into narrow canals to deposit eggs and sperm. Inset: a female in the process of laying eggs. From Fletcher et al. (2004), used with permission.

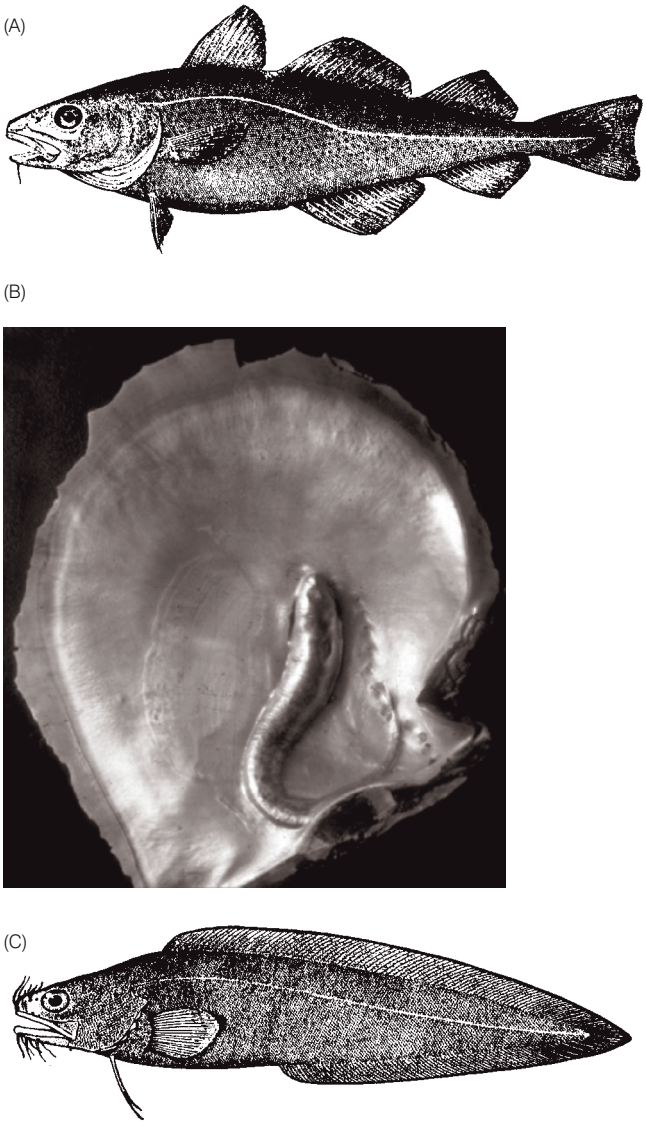

Figure 14.25

Paracanthopterygians. (A) A gadiform, the Atlantic Cod, *Gadus morhua*. (B) A Pacific Pearlfish, *Encheliophis dubius*, entombed in a black lip pearl oyster. (C) An ophidiiform, the Bearded Brotula, *Brotula barbata*. (A, C) from Jordan (1905); (B) courtesy of the Museum of Comparative Zoology and Harvard University.

extensive overfishing. Previously "inexhaustible" cod fisheries have crashed throughout much of the North Atlantic, affecting entire ocean ecosystems and the fishing economies dependent on them (Mowat 1996; Kurlansky 1997). The largest food fishery in the world in recent times has been for North Pacific Walleye Pollock, *Theragra chalcogramma*, with a harvest in excess of 6 million tons in 1989.

In **ophidiiforms** the pectoral fins are high up on the body and have a vertical orientation. The pelvic fins, when present, are located anteriorly under the head in what is termed the mental or jugular position. Pelvic fin loss in this group probably relates to their eel-like bodies; many eel-like fishes, regardless of taxonomic position, have reduced or absent pelvic fins and girdles (see Chapter 24, Habitat use and choice). Ophidiiforms inhabit what have to be viewed as marginal or at least exceptional habitats for fishes. Carapid pearlfishes are **inquilines** (tenants), living inside the body cavities of starfishes, sea cucumbers, bivalves, and sea squirts; some may be parasitic, feeding on the internal organs of their hosts. The common name originated with the discovery of the oyster's revenge, where an individual Pacific Pearlfish, *Encheliophis dubius*, became entombed in a blacklip oyster (*Pinctada mazatlantica*) (Fig. 14.24B). Pearlfishes are apparently unique among fishes in that they have two distinct larval stages, a "vexillifer" pelagic stage followed by a "tenuis" demersal stage during which they search for a host. Ophidiid and bythitid cusk-eels and brotulas include blind species in freshwater caves of the Caribbean basin and Galápagos Islands, and infaunal coral reef species that hide deep within crevices (Fig. 14.24C). The depth record for a fish is held by a neobythitine cusk-eel, *Abyssobrotula galatheae*, taken 8370 m down in the Puerto Rico Trench (see Chapter 18, The deep sea). Bythitid brotulas and parabrotulid false brotulas are live-bearers, a rare derivation among paracanthopterygians.

Batrachoidiforms are well-camouflaged, benthic marine fishes with eyes placed high on the head, flattened heads and large mouths, relatively elongate dorsal and anal fins, multiple lateral lines, and only three pairs of gills (rather than the usual five pairs). Their dorsal fins have two or three stout spines. Midshipmen (*Porichthys*) have 600–800 lateral photophores; photophores are unusual among shallow water fishes. Fishes in this order are often quite vocal, producing a variety of sounds with their gas bladders. The muscles that vibrate the swim bladder of toadfishes are the fastest contracting muscles known among vertebrates (Rome et al. 1999). Male midshipmen have been the focus of complaints by houseboat dwellers in San Francisco Bay during the (midshipmen's) breeding season, when the males produce a sustained, low-frequency "hum" (Ibara et al. 1983). In the venomous toadfishes of the advanced subfamily Thalassophryninae, dorsal and opercular spines are part of a complex system that injects a powerful venom. Toadfishes are unusual zoogeographically because they are a shallow, warm water family that is most diverse in the Americas, whereas most tropical marine families have their greatest diversity in the Indo-Australian region (Collette & Russo 1981; see Chapter 16, Marine zoogeographic regions). Three South American species are restricted to fresh water. In morphology, ecology, and venom production, toadfishes are convergent with the scorpaeniform stonefishes and perciform weeverfishes.

The most advanced order within the Paracanthopterygii is the **lophiiforms**, a diverse and often bizarre-looking group of marine fishes that are primitively benthic, shallow water dwellers but that have evolved many highly modified,

open water, deepsea forms. Many if not most of them use a modified first dorsal spine as a lure for catching smaller fish. The basal group is the lophiid goosefishes, known commercially as monkfish or poor man's lobster. Goosefishes occur on both sides of the Atlantic and also in the Pacific and Indian oceans. The western North Atlantic Goosefish, *Lophius americanus*, can exceed 1 m in length and 40 kg in mass, and has a huge mouth with long, recurved teeth that point back into the mouth. Goosefishes prey on other fishes and on diving seabirds. Antennariid frogfishes also rest on the bottom and are well-camouflaged, globose fishes that can walk across the bottom on their pectoral and pelvic fins (an old name for the lophiiforms, **Pediculati**, refers to the elbowlike bend in the pectoral and the footlike appearance of the pelvic fins). The esca or lure of frogfishes can be quite ornate, mimicking a small fish, shrimp, or worm (Fig. 14.26). When not waved in front of potential prey, the esca sits in a protective depression between the second and third dorsal spines. If the esca is bitten off, it apparently can regenerate back to its species-specific form (Pietsch & Grobecker 1987).

Geographically restricted fishes make up the family of brachionichthyid handfishes (Fig. 14.27). These small, colorful (red, orange, or pink with dark spots) benthic fishes occur only in southeastern Australia, with five of the eight known species restricted to Tasmania. Unlike the vast majority of marine fishes, handfishes lack a pelagic larval stage, fully formed juveniles emerging from eggs that are guarded by the female for 7–8 weeks. Because of their size, restricted range, attractive coloration, threats from introduced predators, and low dispersal of both young and adults, most species are considered highly imperiled. The spotted handfish, *Brachionichthys hirsutus*, has Critically Endangered status with IUCN.

The ogcocephalid batfishes are among the least fishlike fishes around (other candidates include seahorses, shrimpfishes, boxfishes, and ocean sunfishes; see next chapter). The flattened, rounded head accounts for more than half the length of the body; it tapers quickly behind the expanded pectoral fins, giving the fish the appearance of a rounded axe with a short handle. Batfishes alternate walking on their pectorals with swimming via jet propulsion of water expelled from their round, backward-facing opercular openings. As modified as the batfishes are, they are rivaled in strange appearance by the 11 families of deepsea anglerfishes, suborder Ceratioidei (Fig. 14.28). The ceratioids are the most speciose fishes of the vast bathypelagic region, comprising 160 species. Among their other derived traits, 23 species in five families have very small males that fuse to and become parasitic on the larger females, the difference in length between male and female being as much as 60-fold (Pietsch 2005; Pietsch & Orr 2007; see Chapter 18, The deep sea). Male parasitism appears to have evolved independently perhaps seven times in the suborder.

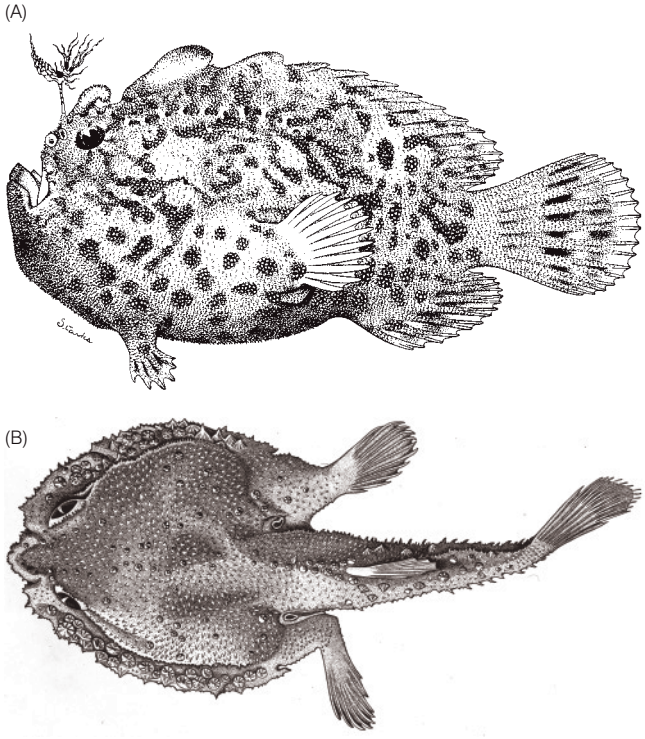

Figure 14.26
Lophiiformes. (A) A 6 cm long Bloody Frogfish, *Antennarius sanguineus*, from the Galápagos Islands. Note the elaborate esca or lure at the end of the modified first dorsal spine or illicium. (B) Dorsal view of a Batfish, *Dibranchus spinosa*. Opercular openings are the teardrop shaped holes at about midbody. (A) drawing by C. L. Starks, in Heller and Snodgrass (1903); (B) after Briggs (1974).

Figure 14.27
Brachionichthyid handfishes. A male and female Red Handfish (*Brachionichthys politus*) guarding their relatively large, yellow-brown eggs. Handfishes get their name from their pectoral fins, which are armlike appendages with an elbow and fingers. Handfishes are restricted to southeastern Australian waters, chiefly Tasmania. Photo by D. Hall, www.seaphotos.com.

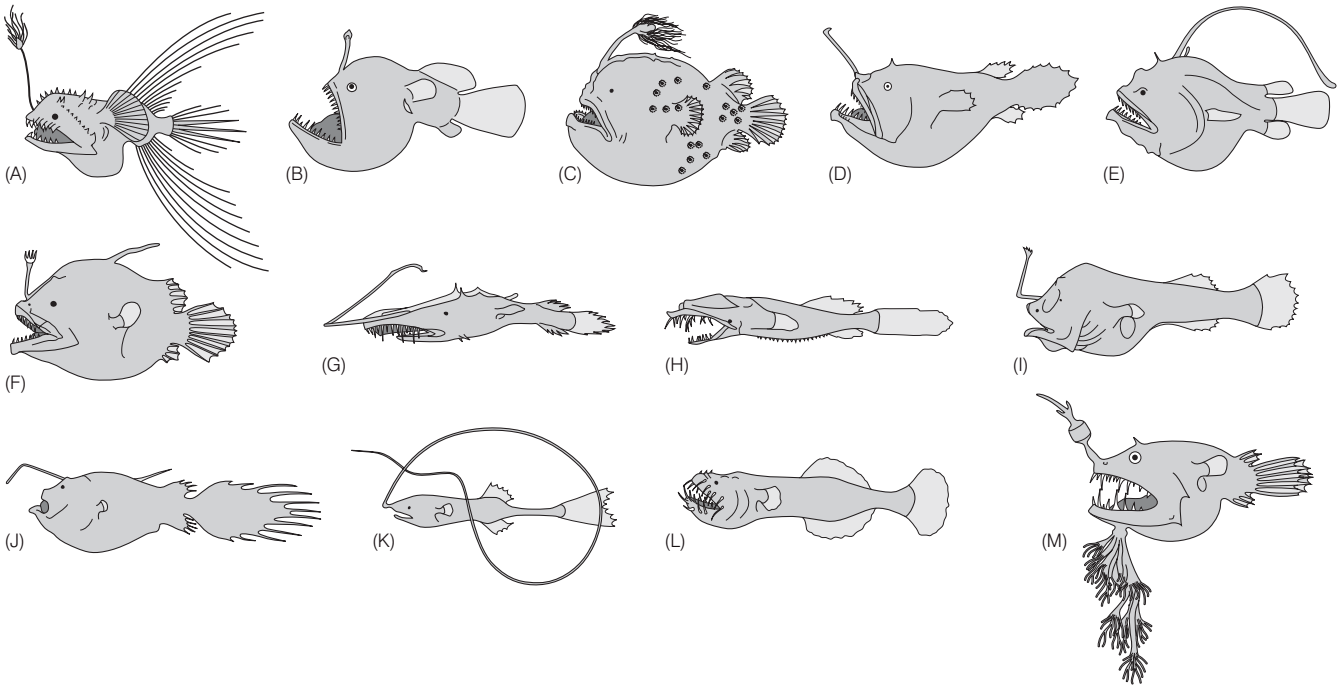

Figure 14.28

Ceratioid anglerfishes. Shown are females from the 11 ceratioid families: (A) Caulophrynidae; (B) Melanocetidae; (C) Himantolophidae; (D, E) Diceratiidae; (F) Oneirodidae; (G, H) Thaumatichthyidae; (I) Centrophrynidae; (J) Ceratiidae; (K) Gigantactinidae; (L) Neoceratiidae; (M) Linophrynidae. See Pietsch and Orr (2007) for color photos. After Pietsch (2005), used with permission.

Summary

SUMMARY

1 The 27,000 teleost species occupy almost all aquatic habitats. Teleosts arose in the Early Mesozoic and radiated as modern osteoglossomorphs, elopomorphs, otocephalans, and euteleosts. Today, 40 orders and 448 families are recognized, defined largely by skull and tail modifications that improved feeding and locomotion.

2 Osteoglossomorphs are chiefly tropical, freshwater fishes in which tongue teeth bite against the mouth roof. Some species are highly prized in the aquarium trade. The diverse African elephantfishes produce and detect weak electric fields.

3 Elopomorphs are characterized by a ribbon-shaped leptocephalus larva and include tenpounders, tarpons, bonefishes, spiny eels, and true eels. Elopomorphs are predominantly marine fishes that occur from very shallow to very great depths. The anguilliform true eels include 15 families of elongate fishes, one of which is catadromous, spawning at sea but growing in fresh water.

4 The subdivision Otocephala includes the superorders Clupeomorpha and Ostariophysi. Clupeomorphs are generally small, schooling fishes of pelagic marine and occasionally freshwater habitats. They are characterized by an otophysic ear-to-gas-bladder connection, and by bony scutes on the belly. Herrings and anchovies are exceedingly important fisheries species.

5 The species-rich Ostariophysi contains predominantly freshwater fishes such as milkfishes, minnows, suckers, characins, loaches, catfishes, and South American knifefishes. Ostariophysans have modified anterior vertebrae, making up the Weberian apparatus that aids in hearing (absent in the more primitive Anotophysi). They produce and respond to alarm substances (*Schreckstoff*). Cypriniforms possess pharyngeal jaws and dentition used in manipulating and crushing prey and vegetation. Characins are highly successful South American and African fishes such as piranhas and tetras. Siluriform catfishes

include 35 families of primarily benthic, nocturnal fishes with barbels, spines, and adipose fins. Gymnotiform knifefishes have converged with the osteoglossomorph elephantfishes in the production and detection of weak electric fields.

6 The fourth subdivision, the Euteleostei, contains three-quarters of the families and two-thirds of the species of teleosts. Protacanthopterygians are loosely related marine, freshwater, and diadromous fishes that include the deepsea argentiniforms, salmons, and smelts. Whitefishes, graylings, salmons, and trouts constitute the salmoniforms, characterized by an adipose fin, a triangular flap at the base of the pelvic fin, and the configuration of the last three vertebrae. Many salmonids undergo extensive migrations between fresh and salt water during their lives. Osmeriforms are generally small, silvery, elongate, water column dwelling fishes such as freshwater smelts, deepsea barreleyes and slickheads, and southern hemisphere Salamanderfish and galaxiids.

7 Euteleosts more advanced than protacanthopterygians are referred to as neognaths, and neognaths more advanced than the esociform pikes – the remaining 335 families and 17,000+ species – are collectively placed in the unranked taxonomic category Neoteleostei. Esociform pikes and pickerels are northern hemisphere predators. The eight superorders of neoteleosts share similarities in the articulation between the skull and first cervical vertebra, two muscles that move the pharyngeal jaws, and jaw teeth that can be depressed posteriorly. The first four superorders of neoteleosts are primarily deepsea or pelagic fishes. Stenopterygians are deepsea fishes with long teeth, large mouths, and peculiar photophores (light organs) including bristlemouths and marine hatchetfishes. Ateleopodomorph jellynose fishes swim just above the bottom and have cartilaginous skeletons. Cyclosquamates are primarily deepsea forms, such as the bizarre giganturid telescopefishes and tripodfishes, but include the shallow water lizardfishes. Scopelomorphs are primarily lanternfishes, which have species-specific photophore patterns.

8 Neoteleosts above scopelomorphs possess true fin spines and are termed acanthomorphs. Other acanthomorph advances include strengthened vertebral accessories and tail structures that improved swimming, pharyngeal tooth diversification, and improved jaw protrusion. Lampriomorphs (tube-eyes, oarfish) and polymixiomorphs (beardfishes) are primitive acanthomorphs; oarfish may exceed 8 m in length and are the world's longest teleost.

9 The superorder Paracanthopterygii consists of freshwater cavefishes and trout-perches, but mostly of marine, benthic, nocturnal fishes, including very deepsea ophidiiforms, commercially important cods, acoustically active toadfishes, anatomically specialized batfishes and handfishes, and the diverse bathypelagic lophiiform anglerfishes. Some anglerfish males are much smaller than and parasitic upon the larger females.

Supplementary reading

SUPPLEMENTARY READING

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Chapter 15

Teleosts at last II: spiny-rayed fishes

Chapter contents

CHAPTER CONTENTS

Most modern bony fishes belong to a single advanced superorder, the **Acanthopterygii**. The group is so diverse and its members so important from all standpoints that a full chapter is needed to discuss them, although no one chapter or one book can do them justice. Several genera and families, such as the sticklebacks, livebearers, darters, black basses, perches, butterflyfishes, cichlids, damselfishes, tunas, and billfishes are the subjects of one or several books themselves and so the treatment below is understandably cursory. Again, the phylogeny and taxonomy presented here as well as many of the aspects of biology of different groups are taken largely from Nelson (2006), a reference that should be consulted for additional details. And as Nelson points out repeatedly, taxonomic work on most groups is ongoing and often unsettled (Box 15.1).

Superorder Acanthopterygii: introduction

Given the remarkable diversity of the higher spiny-rayed fishes – approximately 14,800 species in 267 families – it is a tribute to their successful suite of adaptations that they are generally recognized as a coherent group (Fig. 15.2). Although controversy about relationships and taxonomic position among the various orders and families abounds, certain generalities can be made about the group as a whole and the characteristics that define it. Two primary innovations are shared by most lineages of acanthopterygians:

1. Upper jaw mobility and protrusibility are maximal in this group. This is achieved by the development of a dorsal extension of the anterior tip of the premaxilla, termed the **ascending process**. This process slides along the rostral cartilage on the snout of the fish, shooting the upper jaw forward and downward. Protrusion is aided by a camlike connection between the maxilla and premaxilla, the maxilla rotating and helping push the premaxilla forward (Lauder & Liem 1983; see Chapter 11, Division Teleostei).
2. Pharyngeal dentition and action reach their highest level of development. Improved function is aided by a redistribution of the attachments of muscles and bones in the pharyngeal apparatus. The retractor dorsalis muscle (see preceding chapter) now inserts on the third pharyngobranchial arch, and the upper pharyngeal jaws are supported principally by the second and third epibranchial bones.

Acanthopterygians also typically have: ctenoid scales (with numerous exceptions); a physoclistous gas bladder; maxilla excluded from the gape; two distinct dorsal fins,

Box 15.1

Acanthopterygian phylogenies: can't we all just get along?

> Students of ichthyology should study these works as examples of how researchers can arrive at different conclusions.
>
> Nelson (2006, p. 225)

A student or a non-systematist fish researcher, upon encountering the bewildering diversity, unfamiliar names, and labyrinthine relationships of higher teleosts, can understandably desire a straightforward presentation of the facts and a single classification to memorize and use. Ah, were it that simple.

Systematics draws on multiple sources of information to form the building blocks of a classification; traditional morphology (augmented by chemical and radiological techniques) and molecular genetics are but two such sources. Correctness often hinges as much on force of argument as on strength of data. Different authors using different techniques can draw different conclusions, as can different authors using the same data; two authors in the same paper looking at the same data may even disagree (e.g., Springer & Johnson 2004, and your present authors).

An excellent example of this sort of debate has raged (and rages) around the classification of the acanthopterygians. Figure 15.1, taken from Nelson (2006), shows two very different hypotheses, in the form of cladograms, about relationships within the acanthopterygians. The top cladogram (Fig. 15.1A) is the arrangement used here and the one followed in Nelson (2006). The lower cladogram (Fig. 15.1B) is that proposed by Johnson and Patterson (1993b) and accepted by a number of experts. Both agree on the major composition of the superorder Acanthopterygii, but important differences include the placement of the mugiliform mullets and atheriniform silversides at the base of the lineage in (A), whereas in (B) those groups are considered higher, percomorph taxa. In (B), stephanoberyciform pricklefishes and zeiform dories are considered as basal, pre-percomorph groups. Beryciform squirrelfishes and relatives are placed in the Percomorpha in (A) but are pre-percomorphs in (B). Which interpretation is correct?

We do not know. It is possible, and even likely, that neither is definitive and that with additional information, a modified or composite view will emerge. Nelson (2006), faced with the need to present an organized classification, chose the simpler view presented in (A) because it corresponded largely to what he had given in his 1994 edition of *Fishes of the world*. He lamented that, given "so much conflicting information . . . no comprehensive synthesis seemed possible" (Nelson 2006, p. 261). Because we are following Nelson's (2006) treatment through most of this book, and because students require and deserve a straightforward presentation of the facts and a single classification to learn, we present the acanthopterygian groups in the same basic arrangement as Nelson, with the same caveats and reservations. We refer an interested reader to his treatment of the debate and the original literature cited therein.

the first of which is spiny and the second of which is soft-rayed; pelvic and anal fins with spines; pelvic fins located anteriorly, containing one leading spine and five or fewer soft rays, and pectoral fins placed laterally on the body; and an externally symmetrical tail fin supported by fused basal elements. A number of other trends in feeding, locomotion, and predator protection characterize the higher spiny-rayed fishes and show progressive change during acanthopterygian phylogeny. Most of these were discussed in Chapter 11 and will only be summarized here as particularly good examples or striking exceptions are encountered among the taxa. An important point to be remembered is that these are the most advanced and diverse of today's fishes, dominating the shallow, productive habitats of the marine and many lake environments.

Series Mugilomorpha

Series Mugilomorpha
- Order Mugiliformes (72 species): Mugilidae (mullets, grey mullets)

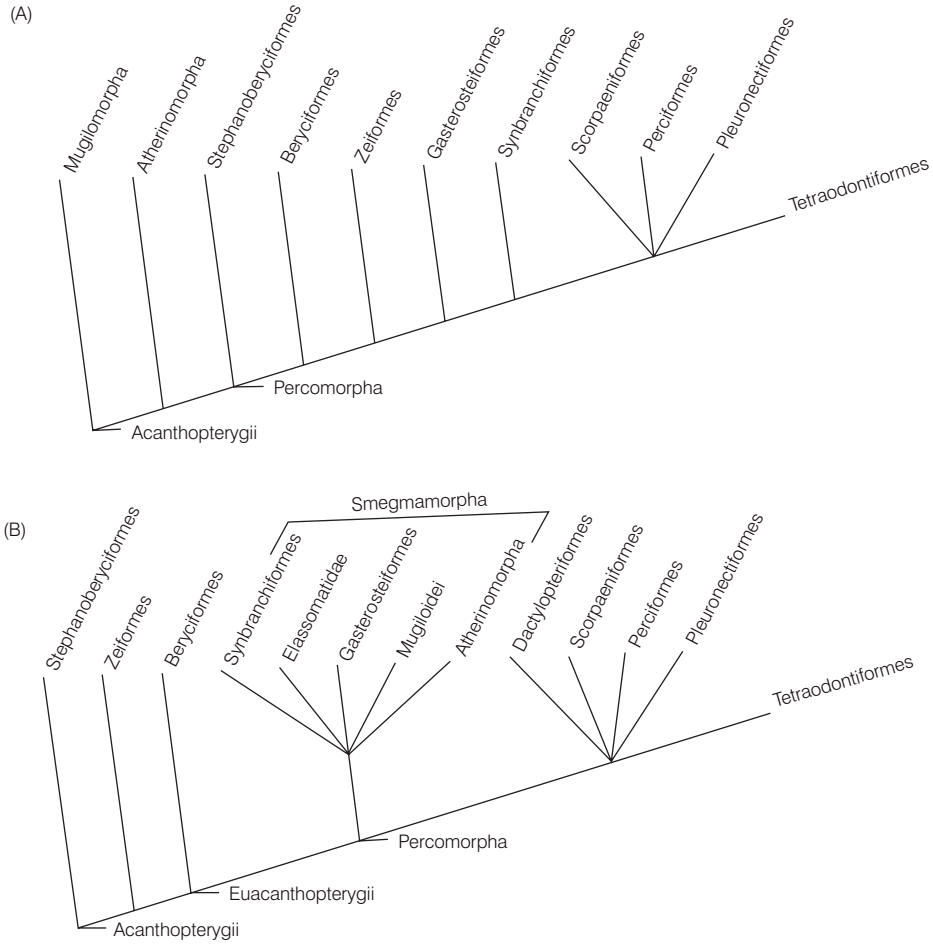


Figure 15.1
Two very different interpretations of relationships among acanthopterygian, spiny-rayed fishes: (A) from Nelson (2006) and (B) from Johnson and Patterson (1993b). From Nelson (2006), used with permission.

The **mugilid** mullets (not to be confused with the mullid goatfishes) are a family of nearshore, catadromous fishes of considerable economic importance and of some taxonomic controversy. Their distinctly separated spiny and soft dorsal fins and spines in the pelvic and anal fins in part justify their inclusion with the other acanthopterygians (Fig. 15.3). They are considered primitive in that some have cycloid scales or scales intermediate between cycloid and ctenoid, and the pelvic girdle lacks any direct ligamentous or bony connection to the cleithral region of the pectoral girdle. In most higher groups the two girdles are connected. Many mullets are detritivorous, feeding on the organic silt that covers the bottom and digesting the minute plants and animals in such ooze with a gizzardlike stomach. Mullets frequently leap from the water for inexplicable reasons; one study showed that the frequency of such jumping increases when dissolved oxygen levels are low (Hoese 1985).

Series Atherinomorpha

Series Atherinomorpha
- Order Atheriniformes (312 species): Atherinopsidae (New World silversides), Notocheiridae (surf sardines), Melanotaeniidae (rainbowfishes, blue eyes), Atherionidae (pricklenose silversides), Phallostethidae (tusked silversides, priapium-fishes), Atherinidae (Old World silversides)
- Order Beloniformes (227 species): Adrianichthyidae (adrianichthyids), Exocoetidae (flyingfishes), Hemiramphidae (halfbeaks), Belonidae (needle-fishes), Scomberesocidae (sauries), Zenarchopteridae
- Order Cyprinodontiformes (1013 species): Aplocheilidae (Asian rivulines), Nothobranchiidae (African rivulines), Rivulidae (New World rivulines), Profundulidae (Middle American killifishes), Goodeidae (goodeids, splitfins), Fundulidae (topminnows), Valenciidae (Valencia toothcarps), Cyprinodontidae (pupfishes), Anablepidae (four-eyed fishes), Poeciliidae (livebearers)

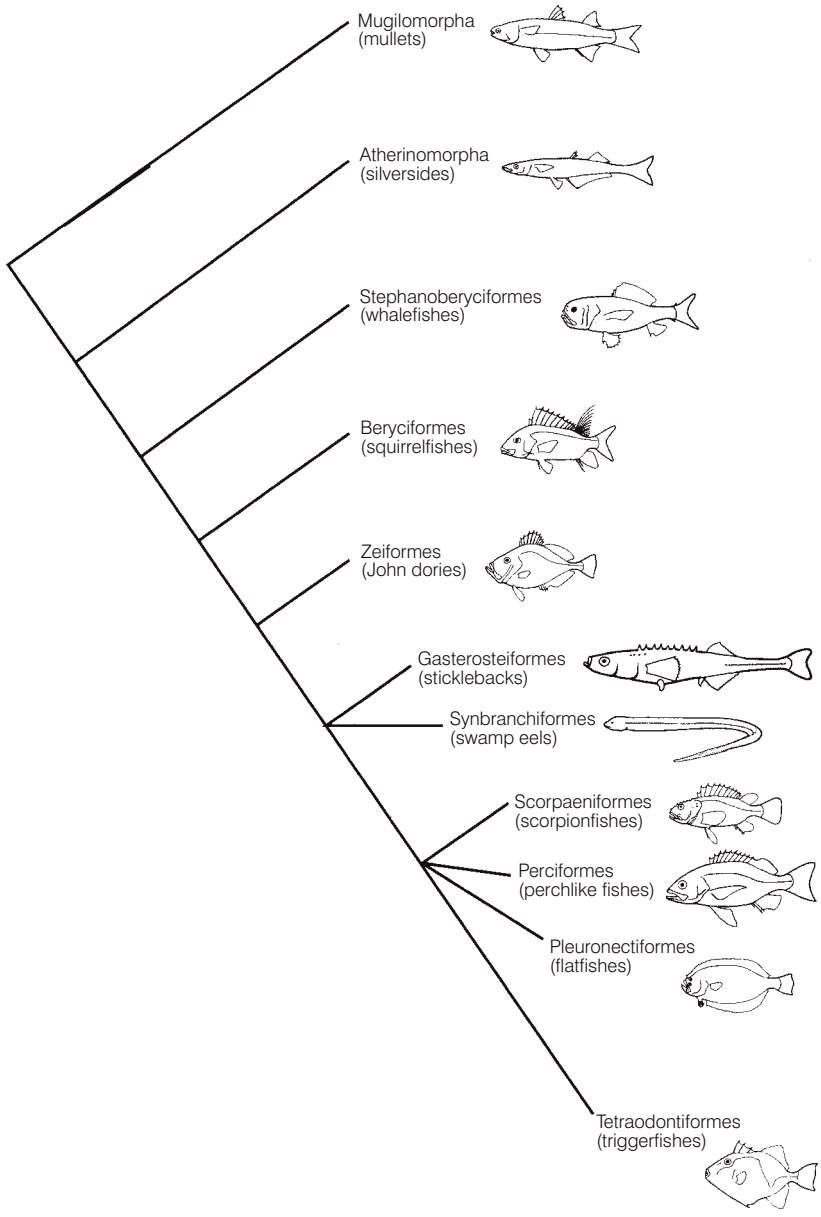


Figure 15.2
Phylogeny of acanthopterygian or higher spiny-rayed fishes. Most recognized clades are given ordinal or higher status and do not have accepted common names. The common names given are of better known representatives. This is basically the same phylogeny as shown in Fig. 15.1, except the synbranchiform swamp eels are now considered more advanced than, and not a sister group to, the gasterosteiform sticklebacks. See Fig. 14.1 for characters that define branching points in the phylogeny of the Acanthopterygii. After Nelson (2006).

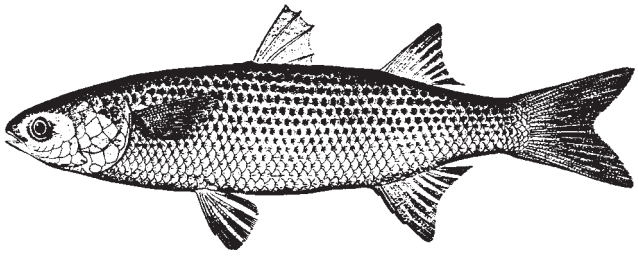


Figure 15.3
A striped mullet, *Mugil cephalus*. From Jordan (1905).

The most successful fishes at the surface layer of the ocean and of many freshwater habitats are in the three orders of the Atherinomorpha. Such well-known surface dwellers as silversides, needlefishes, sauries, flyingfishes, halfbeaks, killifishes, topminnows, and livebearers all belong to this group (Fig. 15.4). Anatomically, the atherinomorphs are set aside from the rest of the acanthopterygians in part because they have a unique way of protruding the jaw. The premaxilla does not articulate directly with the maxilla. Protrusion instead occurs by an intervening linkage between premaxilla and maxilla via the rostral cartilage. Atherinomorphs typically have terminal or superior mouths, as would be expected of surface-feeding fishes. Internal fertilization and

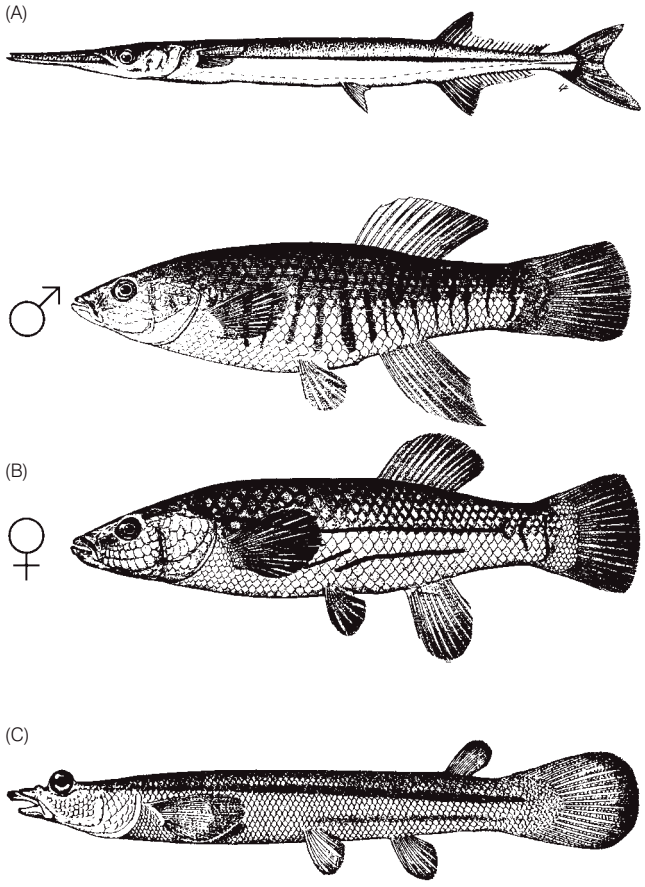


Figure 15.4

Atherinimorphs. (A) A belonid needlefish, *Tylosurus crocodilus*. (B) A fundulid Striped Killifish, *Fundulus majalis*, showing the male above, and female below. (C) The Four-eyed Fish, *Anableps*. (A) from Collette (1995), used with permission; (B) drawing by H. L. Todd, in Collette and Klein-MacPhee (2002); (C) from Jordan (1905).

live-bearing of young have evolved repeatedly within the group; many of the egg-laying families have chorionic filaments that protrude from the egg and help it attach to plants and other structures. Atherinomorphs are sexually unique in that the only known unisexual (all female) fishes are members of this group, namely populations of an atherinopsid silverside and some poeciliid livebearers.

Within the order **Atheriniformes** are six families of generally small, silvery fishes. The **atherinopsid** New World silversides are widespread freshwater and marine fishes that normally occur in schools in shallow water. Atherinopsids include the grunions (*Leuresthes* spp.) of southern and Baja California, which ride waves up beaches to spawn in wet sand every 2 weeks during the summer (see Chapter 23, Semilunar and lunar patterns). Sexual determination is under environmental control in some species, best studied in the Atlantic Silverside, *Menidia menidia* (see Chapters 10, 20). A radiation of 18 atherinopsid species, including apparent piscivorous species, has developed in lakes of the Mexican plateau (see Box 15.2). The **melanotaeniid** rainbowfishes of Australia and New Guinea are strongly sexually dimorphic freshwater fishes. Males have brighter colors and longer fins than females, traits that make them popular aquarium species. Such pronounced sexual dimorphism is rare in more primitive groups outside of the breeding season, except in some deepsea fishes. The small (<4 cm) **phallostethids** are peculiar Southeast Asian atheriniforms in which the pelvic girdle and other structures of the males are modified into a complex clasping and intromittent organ for holding onto females and fertilizing their eggs internally. Females lack a pelvic girdle; they are also unusual in that they lay fertilized eggs rather than having young develop internally, which is the more normal course for fishes with internal fertilization.

Beloniforms are predominantly silvery, marine fishes active at and sometimes above the surface of the water. The **adrianichthyids** include the medakas or ricefishes, *Oryzias*, that are used extensively in genetic, embryological, and physiological investigations. The suborder Belonoidei contains species with a number of anatomical features that show precursors and intermediate conditions during the evolution of rather specialized traits. The lower lobe of the caudal fin in primitive beloniforms has more principle rays than the upper lobe. A rounded or square tail in primitive groups has changed into a forked tail fin with a slightly elongate lower lobe in the **belonid** needlefishes, species which periodically leave the water in short, arcing leaps (Fig. 15.4A). The lower lobe is very pronounced in the exocoetid flyingfishes, which use it as a sculling organ to accelerate during take-offs and to extend their gliding flights that can last hundreds of meters (Davenport 1994; see Chapter 20, Evading pursuit). A tendency for elongation of the lower or both jaws occurs in all belonoid groups, expressed as a garlike prey capture structure in piscivorous needlefishes and as unequal jaw lengths in sauries and particularly in halfbeaks. During development, different families show different developmental rates for the two jaws before the adult condition is reached, suggesting that evolution within the group has involved alterations in developmental rate of the jaws (= "heterochrony") (Boughton et al. 1991; see Chapter 10, Evolution via adjustments in development: heterochrony, paedomorphosis, and neoteny). For example, the lower jaw of some juvenile needlefishes is at first longer than the upper jaw, which later catches up. In some flying fishes, the lower jaw is at first elongated but later in life both jaws are essentially equal in length and neither projects forward. Halfbeaks, despite their predatory appearance, use their elongate lower jaw to feed on floating pieces of seagrasses; some freshwater species take insects at the water surface. Their herbivory is even more notable given that hemiramphids lack a true stomach, grinding up plant material in a pharyngeal mill.

The **cyprinodontiforms** are a major group of freshwater fishes, many of which show a high tolerance for saline and

even hypersaline conditions (see Chapter 18, Deserts and other seasonally arid environments). They are largely surface swimmers, preying on insects that fall into the water, which they detect using lateral line pores on the upper surface of the head. Life history traits in different cyprinodontiform families take on extreme conditions. Some of the South American and African **aplocheilid** and **nothobranchiid** rivulines are annual fishes that live in temporary habitats, spawn during the rainy season and die, their genes preserved in eggs that lie in a resting state in bottom muds until the next rains; the eggs are sufficiently drought resistant to survive for over 1 year (see Chapter 18). *Kryptolebias* (formerly *Rivulus*) *marmoratus* of south Florida and the West Indies is the only fish species known to be self-fertilizing. Sexual dimorphism reaches extremes in the elongate, brightly colored median fins of male **rivulines** (e.g., lyretails, panchax), **poeciliids** (sailfin mollies, guppies, swordtails), and pupfishes. Some **goodeids** have a placentalike connection between the mother and the internally developing young (see Chapter 21, Parental care and Fig. 21.8).

The **cyprinodontid** pupfishes are environmentally tolerant fishes that can live in water of highly variable salinity and temperature, characteristics that have allowed them to invade fluctuating environments such as saltmarshes, springs, and desert ponds (see Chapter 18). The isolated nature of many such habitats fuels rapid speciation but also makes the inhabitants extremely vulnerable to environmental disturbance; many pupfishes and their relatives have been extinguished or currently have Critically Endangered status according to the International Union for the Conservation of Nature (IUCN 2004; see also www.desertfishes.org). Many species of *Orestias* have evolved in Andean lakes (see Box 15.2), including Lake Titicaca, which at 4570 m above sea level is the highest natural body of water populated by fishes. **Anablepid** four-eyed fishes, a phylogenetically intermediate family within the cyprinodontiforms, is extraordinary in its eye structure (Fig. 15.4C). Four-eyed fishes are surface dwellers that swim with their protruding eyes half out of water. The pupil of the eye itself is physically divided into dorsal and ventral halves, the upper half capable of forming focused images of objects in air and the lower half simultaneously forming images of objects underwater (an intertidal labrisomid, the Galápagos four-eyed blenny, *Dialommus fuscus*, has converged on a similar eye structure). Some of the live-bearing poeciliids are "species" that originated through hybridization and today do not include functional males; females instead use males of other species to activate embryogenesis, male genetic material being excluded from future generations (Meffe & Snelson 1989; Houde 1997; Uribe & Grier 2005; see Chapter 21, Gender roles in fishes). Poeciliids are an important ecological component of freshwater habitats on islands of the tropical western Atlantic and Caribbean, as well as coastal, tropical streams.

Series Percomorpha: basal orders

Series Percomorpha
- Order Stephanoberyciformes (75 species): Melamphaidae (bigscale fishes), Stephanoberycidae (pricklefishes), Hispidoberycidae (hispidoberycids), Gibberichthyidae (gibberfishes), Rondeletiidae (redmouth whalefishes), Barbourisiidae (Red Whalefish), Cetomimidae (flabby whalefishes), Mirapinnidae (tapertails), Megalomycteridae (largenose fishes)
- Order Beryciformes (144 species): Anoplogastridae (fangtooths), Diretmidae (spinyfins), Anomalopidae (flashlight fishes, lanterneye fishes), Monocentridae (pinecone fishes), Trachichthyidae (roughies, slimeheads), Berycidae (alfonsinos), Holocentridae (squirrelfishes)
- Order Zeiformes (32 species): Cyttidae (lookdown dories), Oreosomatidae (oreos), Parazenidae (smooth dories), Zeniontidae (armoreye dories), Grammicolepididae (tinselfishes), Zeidae (dories)
- Order Gasterosteiformes (278 species): Hypoptychidae (sand eel), Aulorhynchidae (tubesnouts), Gasterosteidae (sticklebacks), Indostomidae (armored sticklebacks), Pegasidae (seamoths), Solenostomidae (ghost pipefishes), Syngnathidae (pipefishes, seahorses), Aulostomidae (trumpetfishes), Fistulariidae (cornetfishes), Macroramphosidae (snipefishes), Centriscidae (shrimpfishes)
- Order Synbranchiformes (99 species): Synbranchidae (swamp eels), Chadhuriidae (earthworm eels), Mastacembelidae (spiny or tiretrack eels)
- Order Scorpaeniformes (1477 species): Dactylopteridae (flying gurnards), Scorpaenidae (scorpionfishes, rockfishes), Caracanthidae (orbicular velvetfishes), Aploactinidae (velvetfishes), Pataecidae (Australian prowfishes), Gnathanacanthidae (red velvetfishes), Congiopodidae (racehorses, pigfishes), Triglidae (sea robins, gurnards), Bembridae (deepwater flatheads), Platycephalidae (flatheads), Hoplichthyidae (ghost flatheads), Anoplopomatidae (sablefishes), Hexagrammidae (greenlings), Normanichthyidae (normanichthyids), Rhamphocottidae (grunt sculpins), Ereuniidae (deepwater sculpins), Cottidae (sculpins), Comephoridae (Baikal oilfishes), Abyssocottidae (deepwater Baikal sculpins), Hemitripteridae (searavens), Agonidae (poachers), Psychrolutidae (fathead sculpins), Bathylutichthyidae (Antarctic sculpins), Cyclopteridae (lumpfishes), Liparidae (snailfishes)

The most advanced euteleostean clade is the **Percomorpha**, a diverse and varied taxon that contains more than 13,000 species of largely marine families, although several successful freshwater groups also belong in this lineage. Percomorphs have in common an anteriorly placed pelvic girdle that is connected to the pectoral girdle directly or by a ligament; the pelvic fin also typically has an anterior spine and five soft rays, larger numbers of rays occurring in primitive percomorph taxa.

Figure 15.5
The Orange Roughy, *Hoplostethus atlanticus*, a trachichthyid beryciform. Photo by G. Helfman.

At the base of the percomorphs are two orders of either deepsea or nocturnal fishes, the stephanoberyciform pricklefish taxa and the beryciform squirrelfish taxa (but again see Box 15.1). These large-headed, round fishes have many percomorph characteristics, except the tail fin has a primitively large number of rays (18 or 19) as compared to the 17 caudal rays that typify most advanced percomorphs. The primitive **stephanoberyciforms** (gibberfishes, pricklefishes, cetomimoid whalefishes) are largely deepsea forms characterized by luminescent organs, weak or absent fin spines, and reduced squamation. **Beryciforms** often have the large eyes typical of nocturnal fishes and possess strong spines on the head or gill covers. Included among the beryciforms are such relatively shallow water luminescent forms as pinecone fishes and flashlight fishes, reef forms such as squirrelfishes, and the commercially important Orange Roughy, *Hoplostethus atlanticus* (Fig. 15.5). Beryciforms are well represented in the fossil record, dating back to the Late Cretaceous. **Zeiforms** are a confusing assortment of primitive marine percomorphs that have highly protrusible mouths and a unique caudal skeleton. Included in this order are such commercial species as the European John Dory, *Zeus faber*.

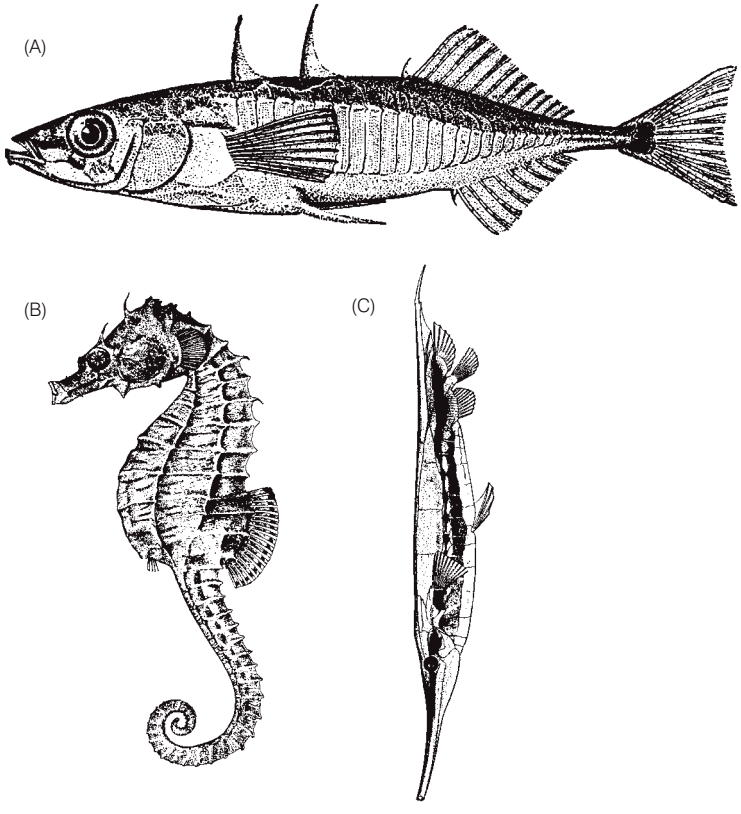


Figure 15.6
Gasterosteiforms. (A) A Three-spined Stickleback, *Gasterosteus aculeatus*. (B) A sea horse, *Hippocampus erectus*. (C) A 13 cm centriscid shrimpfish, *Aeoliscus strigatus*. Centriscids are extraordinary gasterosteiforms that often hover head-down among sea urchin spines, where they are particularly well camouflaged. The first dorsal spine forms the posterior end of the body while the second dorsal, caudal, and anal fins are directed downward. From Jordan (1905).

Acanthopterygians as a group are not as well represented in the deep sea as are more primitive taxa. After the stephanoberyciforms and primitive beryciforms, few deepsea fishes occur. The most advanced beryciforms, such as the squirrelfishes, are also the shallowest dwellers. It is possible that as more advanced clades arose within the Euteleostei, their specializations made them competitively superior to primitive groups and the younger taxa displaced the older out of productive shallow water habitats and into the less productive deepsea region. Alternatively, overriding trends within the Acanthopterygii include the development of stout spines and other hard structures (bony skull crests, spined scales, dermal ossifications), which may have been difficult to reverse. Since a common convergence among deepsea forms is the loss or reduction of hard body parts, acanthopterygians may have been phylogenetically constrained from developing the energy-saving traits necessary for existence in the deep sea. Which is not to say that deepsea acanthopterygians are marginally successful in deep waters; the cetomimid flabby whalefishes are second only to the oneirodid anglerfishes (a paracanthopterygian) in species diversity among bathypelagic forms, and may exceed anglerfishes in abudance in deeper waters. Interestingly, cetomimids have converged with anglerfishes in having dwarf males, although whalefishes are not known to be parasitic on the larger females.

Gasterosteiforms are generally small marine and freshwater fishes with dermal armor plates, small mouths, and unorthodox propulsion (Fig. 15.6). Sticklebacks are among the world's most intensively studied fishes behaviorally, physiologically, ecologically, and evolutionarily (Wootton 1984; Bell & Foster 1994). Although only seven stickleback species are recognized, separate populations often diverge in anatomical traits and may constitute distinct genomes. The extent of predator avoidance, spines, and dermal plates often vary in relation to the threat from predators experienced by a population, making them showcases of the evolutionary process, as is the repeated, independent appearance of species pairs in multiple lakes (e.g., Rundle et al. 2003; Boughman et al. 2005).

The suborder Syngnathoidei includes several unusually shaped fishes encased in bony rings, including pegasid seamoths and syngnathid pipefishes, sea dragons, and seahorses (Figs 15.6B, 15.7). In the primitive solenostomid ghost pipefishes, the female carries developing eggs in a brood pouch formed by pelvic fins fused to the ventral body surface. In more advanced groups, sexual role reversal is the norm, and syngnathid pipefishes and seahorses are the only vertebrates in which the male literally becomes pregnant. An evolutionary gradient of degrees of male parental care exist within the family and correspond to the recognized phylogeny of the group. Pipefish taxonomy is based in part on whether eggs are embedded or attached to the male's ventrum, whether the pouch is sealed or open, and whether plates or membranes protect the eggs. In primitive species, eggs are attached externally to the male's ventral surface where they develop and hatch. In more advanced species, the eggs are deposited within a pouch, fertilized, and the embryos develop within the pouch, where they obtain protection, oxygenation, osmoregulation, and nutrition from the male. Such role reversal in reproductive behavior includes females that actively court and compete for males (e.g., Rosenqvist 1990). Locomotion is accomplished by rapid undulation of the small dorsal fin; the caudal fin is lacking in seahorses, which have transformed the caudal peduncle region into a prehensile structure for holding onto structures. Because of their attractiveness and small size, seahorses are actively pursued for the aquarium trade but their feeding and water quality requirements are such that few survive for long in glass boxes. Of greater threat is unregulated and unsustainable harvest for tradi-

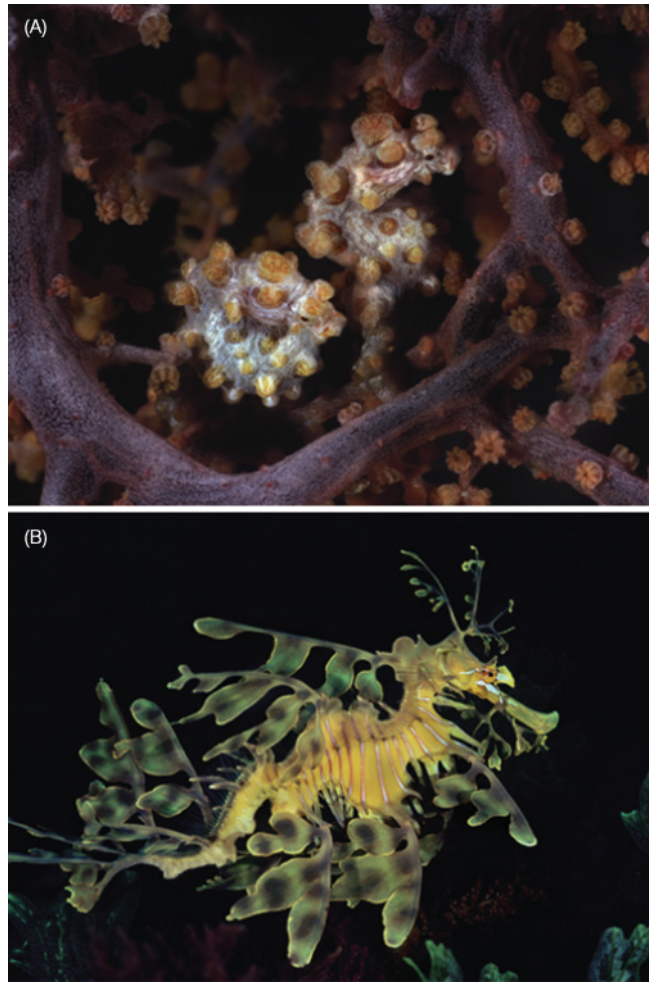


Figure 15.7
Protective resemblance in sea horses and their relatives. (A) The pygmy sea horse, *Hippocampus bargibanti*, resembles its sea fan habitat to a remarkable degree. (B) The protected leafy seadragon, *Phycodurus eques*, is a South Australian endemic that mimics the marine vegetation in which it lives. Go to www.dragonsearch.asn.au. Photos by David Hall, www.seaphotos.com.

tional Asian medicinal preparations (Vincent 1996). Because they mate for life and reproduce slowly, seahorses are particularly vulnerable to overcollecting. Fifty-one species have some international protection, with 39 listed in Appendix II of the Convention on International Trade in Endangered Species (CITES; www.cites.org) and 16 considered at risk by the IUCN (2004; see also http://seahorse.fisheries.ubc.ca).

Also exceptional within the gasterosteiforms are the aulostomoid trumpetfishes and cornetfishes, which are elongate, large (up to 1 m), lurking and stalking piscivores with very expandable mouths. The intriguing centriscid shrimpfishes of the Indo-Pacific are small, extremely compressed fishes with the shape and proportions of an edible peapod encased in thin bone (see Fig. 15.6C). Due to an almost right-angle flexure in the vertebral column, their second dorsal, caudal, and anal fins all point ventrally and they tend to swim with their dorsal edge leading while oriented head down. The fish typically hover head down among the spines of long-spined sea urchins where they are protected and difficult to see due to their thinness and a long black lateral stripe.

The **synbranchiforms** are a small order of primarily freshwater, eel-like fishes. The synbranchid swamp and rice eels are air-breathing fishes in Africa, Asia, and Central and South America. They have many unusual derivations, including loss of pectoral, pelvic, dorsal, anal, and, in some, caudal fins; most are protogynous (female first) hermaphrodites. Synbranchids also have a unique upper jaw arrangement in which the palatoquadrate attaches at two points to the skull, termed **amphystilic suspension** and not known in any other teleosts. Swamp and rice eels released by irresponsible aquarium keepers constitute a growing threat as an invasive species in south Florida, Georgia, and Hawaii (see www.invasivespeciesinfo.gov/aquatics/swampeel.shtml).

The **scorpaeniforms** are a large order of predominantly marine fishes (Fig. 15.8); their exact position within the percomorphs is a matter of considerable debate. Most have

(A)

(B)

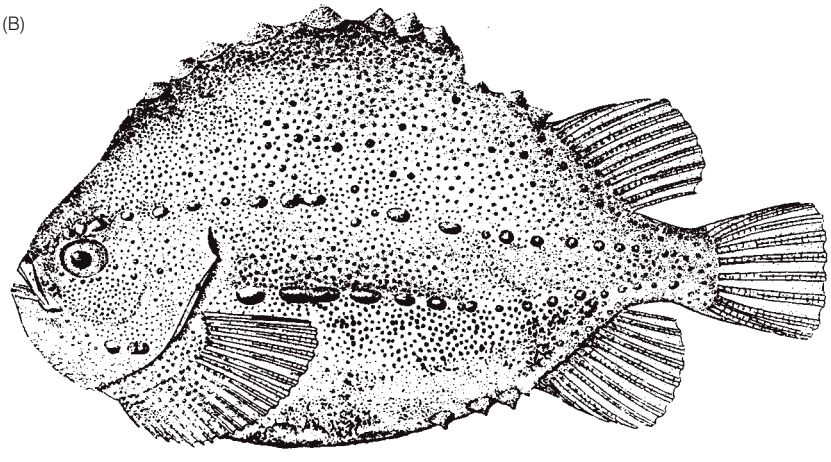


Figure 15.8

Scorpaeniforms. (A) A Canary Rockfish, *Sebastes pinniger*, one of the numerous sebastine rockfishes of the North Pacific. (B) The Lumpfish, *Cyclopterus lumpus*, of the North Atlantic. (A) photo by G. Helfman; (B) drawing by H. L. Todd, in Collette and Klein-MacPhee (2002).

spines projecting from different bones on the head, including a posteriorly directed spine derived from a bone below the eye, giving them the name "mail-cheeked fishes". Many scorpaeniforms lack scales, but this may be more part of a general suite of adaptations to benthic living than a phylogenetic trait. The dactylopterid flying gurnards have huge pectoral fins which they expand as they walk along the bottom on their elongate pelvic fins; it is unlikely that adult "flying" gurnards ever leap out of the water or for that matter ever swim far above the bottom. The scorpaenid scorpionfishes and rockfishes are a diverse group of benthic marine fishes with large mouths and venomous spines in their dorsal, anal, and pelvic fins. The sebastine rockfishes are a diverse (133 species), important commercial group of often live-bearing, long-lived (up to >140 years), overexploited species of the temperate North Pacific (e.g., Boehlert & Yamada 1991; Love et al. 2002). Other subfamilies within this group include the colorful and venomous lion or turkeyfishes (e.g., *Pterois*), as well as the camouflaged and highly venomous stonefishes (*Synanceia*) – the latter purported to possess the most deadly of fish venoms in their spines. The hexagrammid greenlings are littoral zone and kelp associated fishes endemic to the North Pacific. The family includes the highly edible, predatory, and significantly overfished Lingcod, *Ophiodon elongatus*.

The only freshwater scorpaeniforms are in the suborder Cottoidei, which includes the cottid sculpins of North American headwater streams and tidepools, as well as a species flock of comephorid oilfishes and other cottoid species in Lake Baikal in Asia (see Box 15.2). Many cottoids lack scales but have prickly skin. The Cabezon, *Scorpaenichthys marmoratus*, of the Pacific coast of North America is apparently unique among non-tetraodontiform teleosts in having toxic eggs. The most advanced scorpaeniforms are the cyclopteroid lumpfishes and snailfishes. The globose lumpfishes have bony tubercles arranged in rows around their body and a sucking disk made from modified pelvic fins, an unusual trait for fishes that do not frequent high-energy zones. The Lumpfish of the North Atlantic, *Cyclopterus lumpus*, is highly prized for its caviar and has been seriously depleted in parts of its range. Liparid snailfishes, which also have pelvic suction disks, occur broadly geographically and ecologically. They are found in most oceans from the Arctic to the Antarctic and can inhabit tidepools or benthic regions deeper than 7000 m.

Series Percomorpha, Order Perciformes: the perchlike fishes

The largest order in the Percomorpha, and for that matter of vertebrates, is the **Perciformes**, containing 160 families and over 10,000 species, more than a third of all fishes. Our discussion will focus on selected families within the 20 perciform suborders (family names appear in bold in the following accounts). As might be expected in such a diverse taxon, the classification of the perciforms is a subject of much debate (see Box 15.1). The success of perciforms is greatest but by no means limited to coral reef habitats, where six of the eight largest families abound (gobies, wrasses, seabasses, blennies, damselfishes, cardinalfishes). Two other large families, the cichlids and the croakers, reach their maximum diversity in tropical lakes and nearshore temperate marine habitats respectively. The fossil record for perciforms dates back to the Early Cenozoic, and recognizable members of most suborders had evolved by the Eocene, indicating very rapid evolution and diversification over a period of about 20 million years (Carroll 1988).

Suborder Percoidea

The largest perciform suborder is the Percoidei, containing 78 families and 3176 species (Fig. 15.9). Percoids, in contrast with lower teleosts such as ostariophysans and protacanthopterygians (and continuing trends in acanthopterygians and percomorphs), are characterized by: (i) the presence of spines in the dorsal, anal, and pelvic fins; (ii) two dorsal fins (never an adipose fin); (iii) ctenoid scales; (iv) pelvic fins in the abdominal position; (v) laterally placed and vertically oriented pectoral fins; (vi) maxilla excluded from the gape; (vii) physoclistous gas bladder; (viii) absence of orbitosphenoid, mesocoracoid, epipleural, and epicentral bones; (ix) acellular bone; and (x) never more than 17 principal caudal fin rays.

The basal families of percoids are what would generally be considered basslike fishes. **Centropomids** are primarily large, pisicivorous fishes of lakes, estuaries, and nearshore regions, including the snooks (*Centropomus*) of tropical America. Related **latids** include the Barramundi of Australia and Nile Perch of Africa (*Lates* spp.). Nile Perch and their relatives have been widely introduced in African lakes and have caused decimation of native endemic cichlids (see Chapter 26, Species introductions). The **moronid** temperate basses include lake-dwelling and anadromous predators in North America such as the White Bass and Striped Bass (*Morone* spp.). The closely related **polyprionid** wreckfishes include such commercially important species as the Atlantic Wreckfish (*Polyprion americanus*) and the Giant Sea Bass of California (*Stereolepis gigas*), the latter reaching lengths of 2 m and weighing up to 250 kg. The seabass family **Serranidae** contains 475 species and is one of the largest fish families (as many as 15 subfamilies have been variously recognized). It contains a tremendous diversity of sizes and shapes of fishes that have three spines on the opercle but may differ in many other characters. Serranids vary in size from 3 cm long planktivorous anthiines to the 3 m long, 400 kg Goliath

Suborder Percoidea (3176 species): Centropomidae (snooks), Ambassidae (Asiatic glassfishes), Latidae (lates), Moronidae (temperate basses), Percichthyidae (temperate perches), Perciliidae (southern basses), Acropomatidae (lanternbellies), Symphysanodontidae (slopefishes), Polyprionidae (wreckfishes), Serranidae (seabasses), Centrogeniidae (false scorpionfishes), Ostracoberycidae (ostracoberycids), Callanthiidae (groppos), Pseudochromidae (dottybacks), Grammatidae (basslets), Plesiopidae (roundheads), Notograptidae (bearded eelblennies), Opistognathidae (jawfishes), Dinopercidae (cavebasses), Banjosidae (banjofishes), Centrarchidae (sunfishes, black basses), Percidae (darters, perches), Priacanthidae (bigeyes), Apogonidae (cardinalfishes), Epigonidae (deepwater cardinalfishes), Sillaginidae (sillagos), Malacanthidae (tilefishes), Lactariidae (false trevallies), Dinolestidae (long-finned pikes), Scombropidae (gnomefishes), Pomatomidae (Bluefish), Nematistiidae (Roosterfish), Coryphaenidae (dolphinfishes), Rachycentridae (Cobia), Echeneidae (remoras), Carangidae (jacks, pompanos), Menidae (Moonfish), Leiognathidae (ponyfishes, slimeys, slipmouths), Bramidae (pomfrets), Caristiidae (manefishes), Emmelichthyidae (rovers), Lutjanidae (snappers), Caesionidae (fusiliers), Lobotidae (tripletails), Gerreidae (mojarras), Haemulidae (grunts), Inermiidae (bonnetmouths), Nemipteridae (threadfin breams), Lethrinidae (emperors), Sparidae (porgies), Centracanthidae (picarel porgies), Polynemidae (threadfins), Sciaenidae (croakers, drums), Mullidae (goatfishes), Pempheridae (sweepers), Glaucosomatidae (pearl perches), Leptobramidae (beachsalmon), Bathyclupeidae (bathyclupeids), Monodactylidae (moonfishes, fingerfishes), Toxotidae (archerfishes), Arripidae (Australasian salmon), Dichistiidae (galjoen fishes), Kyphosidae (sea chubs), Drepaneidae (sicklefishes), Chaetodontidae (butterflyfishes), Pomacanthidae (angelfishes), Enoplosidae (oldwives), Pentacerotidae (armorheads), Nandidae (Asian leaffishes), Polycentridae (Afro-American leaffishes), Terapontidae (grunters, tigerperches), Kuhliidae (flagtails, aholeholes), Oplegnathidae (knifejaws), Cirrhitidae (hawkfishes), Chironemidae (kelpfishes), Aplodactylidae (marblefishes), Cheilodactylidae (morwongs), Latridae (trumpeters), Cepolidae (bandfishes), Sphyraenidae (barracudas)

Grouper, *Epinephelus itajara*, which eats lobsters and small turtles as well as fishes. Three subfamilies are currently recognized, the first two (Serraninae and Anthiinae) consisting of mostly small forms such as hamlets, sand perches, and the colorful *Anthias*. The subfamily Epinephelinae is defined by long, stout or filamentous dorsal and/or pelvic fin spines in the larvae (see Chapter 9, Larval morphology and taxonomy). It contains most commercially important species such as groupers, hinds, coneys, gag, and scamp but also includes diminutive and striking basslets and the chemically protected soapfishes (e.g., *Rypticus*, *Grammistes*) which exude a soaplike toxin from their skin when disturbed. Many serranids are hermaphroditic, usually starting as female and then later becoming male (protogyny), although some hamlets and members of the genus *Serranus* function simultaneously as either sex. Sex change and easily located, traditional spawning aggregations have led to massive overfishing of many large serranids (e.g., Nassau Grouper, *Epinephelus striatus*), prompting the need for highly regulated fisheries (Beets & Friedlander 1999). To confuse the taxonomic issue, most species known as basslets belong to the related family **Grammatidae**, which also includes the neon-colored Royal Gramma that lives under ledges in the Caribbean and is popular among divers and aquarists.

Two important percomorph families in North American fresh waters are the centrarchids and the percids. The **Centrarchidae** contain 31 species, including the numerous sunfishes, crappies, and rockbasses (*Lepomis*, *Pomoxis*, *Ambloplites*) as well as the seven black basses in the genus *Micropterus* (e.g., Largemouth, Smallmouth, etc., plus undescribed species in the southeastern USA). Centrarchids are the dominant carnivores in most lakes in the USA and southern Canada and are also known for their nesting behavior, the males digging and defending circular nests on the bottom through much of the summer. Centrarchids are native to the region east of the Rocky Mountains with the exception of the Sacramento Perch, *Archoplites interruptus*, a California endemic with a shrinking native range (Moyle 2002). Centrarchids have been widely introduced elsewhere, so widely and successfully that their importation is now outlawed or severely regulated in several countries (Cowx 1997; Helfman 2007).

The family **Percidae** is one of the most successful non-ostariophysan freshwater families in the world. At least 201 species of percids exist, 187 of which occur in North America. The dominant lake forms are larger species such as the Yellow Perch (*Perca flavescens*) and Walleye (*Sander vitreus*) (Colby 1977; Craig 1987). Yellow Perch have their

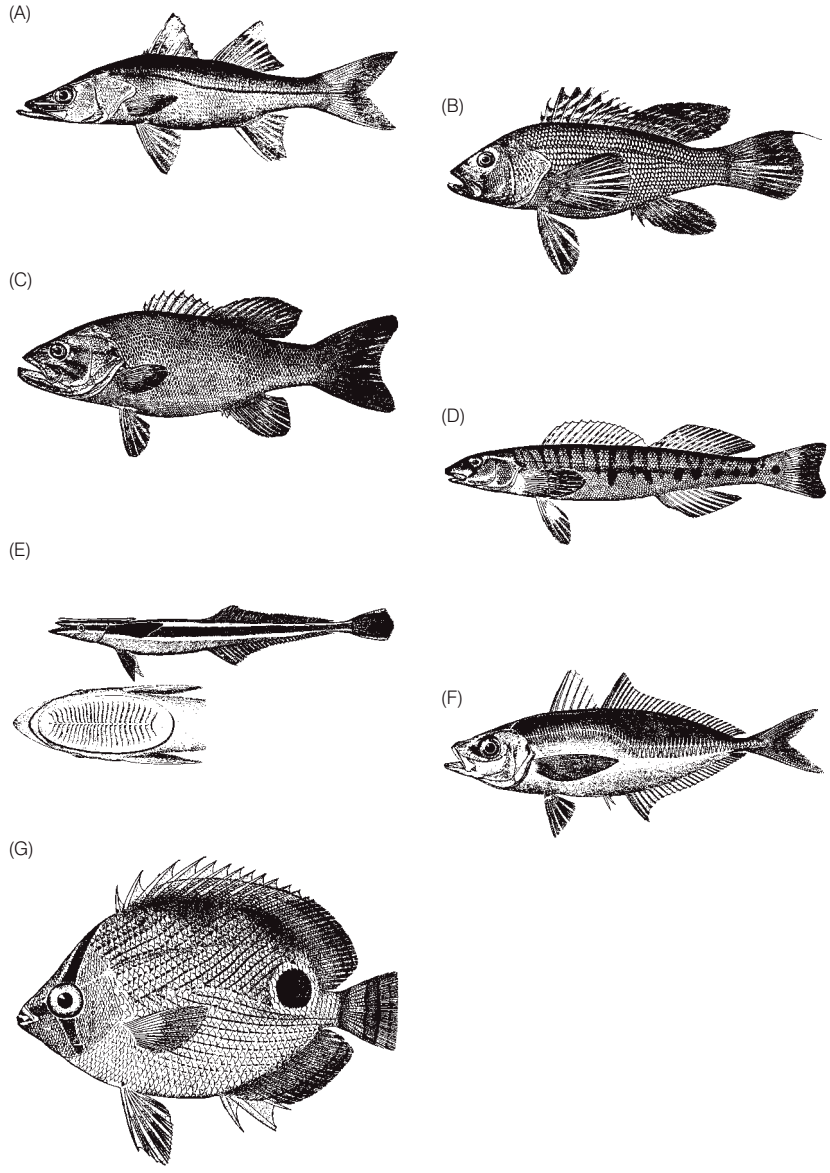


Figure 15.9

Representative percoid fishes. (A) A centropomid Snook, *Centropomus undecimalis*. (B) A serranid Black Sea Bass, *Centropristis striata*. (C) A centrarchid Smallmouth Black Bass, *Micropterus dolomieu*. (D) A percid darter, the Log Perch, *Percina caprodes*. (E) An echeneid Sharksucker, *Echeneis naucrates*, with a top view of the first dorsal fin that forms a suction disk. (F) A carangid Rough Scad, *Trachurus lathami*. (G) A chaetodontid Foureye Butterflyfish, *Chaetodon striatus*. (A, C, D, G) from Jordan 1905; (B, E, F) drawing by H. L. Todd, in Collette and Klein-MacPhee (2002).

counterpart in the Eurasian Perch, *P. fluviatilis*; three species of *Sander* pikeperches also occur in Europe (Collette & Banarescu 1977). North American streams contain at least 184 species of darters, mostly in the genera *Percina* and *Etheostoma* (Fig. 15.10). The greatest diversity is in the southeastern USA; Tennessee alone houses 90 darter species. These small, benthic fishes feed primarily on aquatic insect larvae and other invertebrates in fast flowing, clean water where males defend nesting rocks and court females. During the breeding season the males take on color patterns that rival the brightest poster colors of tropical fishes (e.g., Page 1983; Etnier & Starnes 1993; see www.cnr.vt.edu/efish/families/percidae.html). Darters are disproportionately imperiled because siltation and other forms of pollution

Figure 15.10

The tangerine darter, *Percina aurantiaca*, the second largest of the nearly 200 species of darters endemic to North America (*c.* 18 cm). Photo by J. DeVivo. For a kaleidoscope of darter photos, see www.cnr.vt.edu/efish/families/percidae.html.

and habitat modification interact with their small sizes, small geographic ranges, headwater habitats, and, especially, benthic breeding and feeding habits. Somewhere between one-half and two-thirds of all darter species are considered to be at risk of extinction, and the Maryland Darter, *Etheostoma sellare*, is thought to be extinct (Warren et al. 2000; Jelks et al. 2008).

The **apogonid** cardinalfishes are a speciose (*c*. 273 species) family of small (<10 cm), nocturnal coral reef fishes. Their large eyes, large mouths, distinctly separated dorsal fins (the second with a single spine), deep bodies, and relatively pointed heads distinguish them from most other reef fishes that hover motionlessly just above or in structure. Some cardinalfishes mouth-brood their eggs, the male or female being responsible in different species. Many cardinalfishes live in close association with invertebrates and use them as refuges (see Chapter 22, Interspecific relations: symbioses). A few Indo-Pacific species enter estuaries, and several New Guinea species are restricted to fresh water. The dramatically colored and narrowly distributed Banggai Cardinalfish, *Pterapogon kauderni*, was once thought to be extinct in the wild – a very rare occurrence among marine fishes (Fig. 15.11). It has apparently recovered as a result of captive breeding and perhaps inadvertent releases from aquarium holding facilities (Vagelli & Erdmann 2002). The **malacanthid** tilefishes are a marine group that inhabits burrows. Sand tilefishes (e.g., *Malacanthus*) are tropical species that live over shallow, sandy areas and dig complex burrows which they reinforce with shell and coral fragments, pieces of which are piled in a mound at the burrow's entrance. Their engineering activities create hard bottom patches that are used by small fishes and invertebrates that would otherwise not colonize sandy regions (see Chapter 25, Fishes as producers and transporters of sand, coral, and rocks). The larger temperate latiline tilefishes (e.g., *Caulolatilus*) are commercially sought species that inhabit large burrows in deeper soft bottom regions, although it is unknown whether they construct the holes themselves.

Figure 15.11

Banggai Cardinalfish, endemic to the Banggai Islands of Indonesia, were depleted due to collecting for the aquarium trade. However, captive animals in a holding facility escaped and multiplied and have even increased the originally limited natural range. See Helfman (2007) for details. Photo by G. Helfman.

The next dozen or so percomorph families (lactariids through caristiids) are generally active, marine, water column dwellers with relatively compressed, often silvery bodies. The larger species are piscivores and the smaller ones are zooplanktivores. **Lactariid** false trevallies and **dinolestid** long-finned pikes have converged on the body shapes and habits of predatory jacks and barracudas, respectively. The cosmopolitan **pomatomid** Bluefish, *Pomatomus saltatrix*, which occurs in most major ocean basins except the eastern Pacific, has a well-deserved reputation for voraciousness (see Hersey 1988). This aggregating predator will enter a school of prey fish and slash and dismember far more individuals than are actually eaten; attacks on humans unfortunate or foolish enough to be in the water during such feeding frenzies are well documented. The family **Nematistiidae** is sometimes combined with the next four families (dolphinfishes, cobia, remoras, and jacks) to form a clade known as carangoids. The colorful Roosterfish, *Nematistius pectoralis*, is a monotypic piscivore of warm, eastern Pacific, inshore areas. It looks like an amberjack with a cockscomb of seven elongate dorsal spines. It is actively sought as a gamefish and attains lengths of 1.5 m and can weigh 50 kg. The **coryphaenid** dolphinfishes or mahimahis include two species of open water, surface-oriented predators that are often found in association with floating structure or seen chasing flyingfishes. Male Dolphinfish (bulls) have a square head profile involving expansion of the bony portion of the supraoccipital region (forehead) (Fig. 15.12), whereas in females the forehead slopes more gradually; such obvious skeletal sexual dimorphism is rare in acanthopterygians. The golden coloration of corphyphaenids has earned them the Spanish name *dorado* and their color-changing habits when brought on board a boat are legendary; Yann Martel in *Life of Pi* likens subduing a mahimahi with a club as "beating a rainbow to death" (Martel 2003, p. 185).

The monotypic Cobia, *Rachycentron canadum* (**Rachycentridae**), looks and swims like a large (up to 1.5 m) remora without a suction disk. Sportfishers frequently locate cobia by fishing near manta rays, but the nature of the association is unexplored. The **echeneid** remoras or sharksuckers are a highly specialized group of eight percomorphs in which the first dorsal fin has been modified into a sucking organ for attachment to sharks, billfishes, whales,

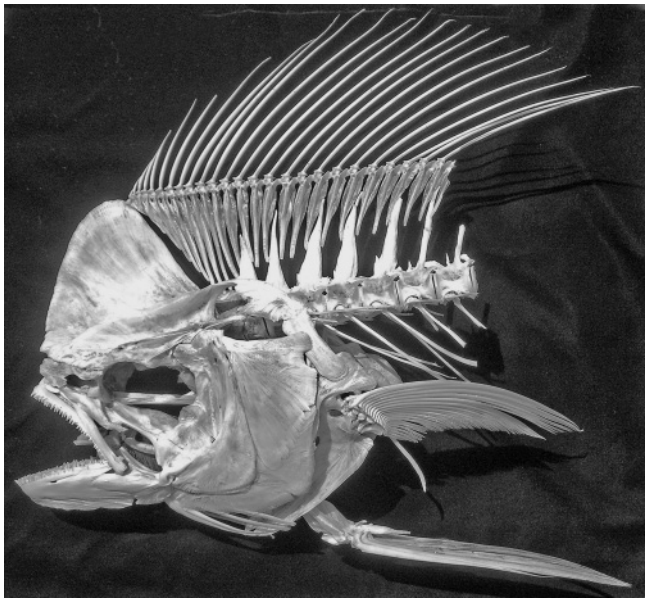


Figure 15.12

Dolphinfish, dorado, or mahimahi, *Coryphaena hippurus*, exhibit extreme sexual dimorphism. The male shown here has a greatly enlarged supraoccipital bone in its forehead, which gives it the characteristic square-headed appearance. Females have a much narrower and streamlined profile. Skeletal preparation by Grant Stoecklin, www.helterskeletons.com.

Figure 15.13

A Mutton Snapper, *Lutjanus analis*, resting behind a gorgonian coral in St. Croix. Snappers are twilight and nocturnal predators on reef fishes throughout the tropics. Photo by G. Helfman.

turtles, and an occasional diver. The adhesive suction disk is a lamellar structure supported and controlled by a complex series of muscles and skeletal elements that function to erect and depress the laminae and create suction pressures. A force in excess of 17 newtons was required to dislodge a remora from shark skin; earlier studies indicated that a 67 mm long common sharksucker could support a pail of water that weighed 11 kg (see Fulcher & Motta 2006). Some remoras such as the large (1 m) *Echeneis naucrates* are frequently seen free-swimming, whereas smaller species are almost always attached to hosts and may clean their gills as well as feed on scraps from the predatory host's meals.

The closely related **carangid** jacks and pompanos are a large (140 species) family of tropical nearshore and pelagic predators and zooplanktivores that range in size from the small scads (*Decapterus*, *Selar*, *Trachurus*) to the large amberjacks and pompanos (*Seriola*, *Caranx*). Carangids tend to be slightly to very compressed, the extreme occurring in the Lookdown, *Selene vomer*, which literally disappears when it faces an observer head-on. Carangids of all sizes are often found in shoals and evidence of cooperative hunting exists in a few large species (e.g., *Caranx melampygus*; see Chapter 19, Attack and capture). Carangids engage in a form of highly efficient and powerful locomotion, termed **carangiform swimming**, involving side-to-side movement of primarily the tail; thrust is transferred from the body musculature to the tail via tendons that cross the caudal peduncle region (Chapter 8, Locomotion: movement and shape).

A subsequent group of families (lutjanids through nemipterids) consists of generally heavy-bodied, tropical fishes that swim near the bottom and feed on large invertebrates and fishes (with some notable exceptions). The **lutjanids** are a large family (105 species) of ecologically diverse but generally carnivorous marine fishes inhabiting shallow to moderate depths in tropical and warm temperate seas and estuaries (e.g., Polovina & Ralston 1987). The typical snapper is a fairly large (up to 1 m), heavy-bodied, suprabenthic, nocturnal or crepuscular predator with large canine teeth, such as the Gray, Red, Mangrove, or Mutton snappers (*Lutjanus* spp., *Pristopomoides* spp.) (Fig. 15.13). However, many snappers live in the water column and are more streamlined, including the Vermilion and Yellowtail snappers (*Rhomboplites*, *Ocyurus*). A closely related family, the **caesionid** fusiliers, are small, streamlined, and brilliantly colored planktivores with forked tails and protrusible mouths that school near drop-offs and reef edges on coral reefs of the Indo-West Pacific. **Lobotid** tripletails get their name from the unusual arrangement of soft dorsal, soft anal, and caudal fins of nearly equal size and rounded shape, the dorsal and anal fins placed posteriorly on the body overlapping the tail fin. Tripletails are heavy-bodied, basslike fishes of estuarine and fresh waters worldwide in temperate and tropical waters. Adults can reach a meter in length and are uncommon; juveniles are more frequently encountered floating leaflike on their sides in mangrove regions. The silvery mojarras (**Gerreidae**) are common inhabitants of sandy or silty regions near coral reefs and

other shallow, warm water habitats worldwide; some species enter fresh water. Their body shape and feeding habits are somewhat incongruous. They have a forked tail and mouth that protrudes slightly downwards, which might suggest zooplanktivory, but they are typically observed foraging head-down with their extremely protractile mouths extended into the bottom sediments. When they emerge they typically expel clouds of sediment out their gill openings, having retained benthic invertebrates with their gill rakers.

Grunts (**Haemulidae**) are moderate-sized coral reef fishes that are unusual in that they are more diverse in the New rather than the Old World tropics. Most grunts form shoals as juveniles and some such as the porkfish, *Anisotremus*, which is common in the Florida Keys, continue to shoal as adults. They are typically nocturnal feeders on benthic or grassbed associated invertebrates, undertaking distinctive migrations between daytime resting and nighttime feeding regions (see Box 22.2). The **inermiid** bonnetmouths are haemulid derivatives adapted for zooplanktivorous feeding. They have the slender bodies, forked tails, and protractile mouths typical of many zooplanktivorous fishes. Porgies (**Sparidae**) are gruntlike in appearance but are more diversified in their feeding than the haemulids. The western Atlantic Sheepshead, *Archosargus probatocephalus*, has massive pharyngeal dentition used for crushing hard-bodied prey such as mollusks. Several sparids, such as the Pinfish, *Lagodon rhomboides*, feed extensively on plants, making this one of the few percoid families to include strongly herbivorous species (herbivory becomes more common in more advanced groups). Together with the **centracanthids**, **lethrinids**, and **nemipterids**, the porgies form a superfamily of related families known as sparoids; the sparids are the only family in the group in the western Atlantic region.

The next three families contain fishes that are frequently seen swimming just above and probing into the bottom with modified appendages. **Polynemid** threadfins are tropical marine fishes with highly specialized pectoral fins that are divided into two parts. The upper webbed portion is located laterally and shaped like a normal pectoral fin, whereas the ventral portion consists of three to seven long, unconnected rays that extend down from the throat region and are used to feel for prey on the bottom. The mouth is subterminal, as befits a bottom feeder. Some **sciaenid** croakers and drums also have a subterminal mouth. Many species have one or several small chin barbels. Sciaenids are a widespread tropical and temperate family and are particularly diverse in the southeastern USA. This large family (270 species) includes such important commercial and sportfishes as the Red Drum (spot tail bass), Black Drum, croakers, weakfish, sea trouts, kingfishes, White Seabass, corbinas, and the endangered Mexican Totoaba and Chinese Bahaba (the last two species can exceed 100 kg in mass). The common names for the family come from sound production habits that involve the vibration of muscles attached to the gas bladder. As is frequently the case with sound-producing fishes, sciaenid otoliths are exceptionally large. The role of acoustic stimuli in the biology of sciaenids is also reflected in their very extensive lateral line, which extends posteriorly onto the tail and anteriorly as numerous pits and canals on the head. Although a predominantly marine family, freshwater species are common in South America, and one species, the Freshwater Drum, *Aplodinotus grunniens*, may have the largest natural latitudinal range of any freshwater fish, occurring throughout the Mississippi River and adjacent drainages of North America and into Central America, from southern Saskatchewan and Quebec to Guatemala. The third bottom-oriented family consists of the **mullid** goatfishes. This tropical family of medium-sized, nearshore marine predators has two highly prehensile chin barbels that the fishes use to probe bottom sediments for prey. Their foraging activities frequently flush invertebrates from the sand and it is not unusual to see wrasses and carangids following goatfishes and capturing escapees.

Monodactylid fingerfishes and **toxotid** archerfishes are brackish water families of chiefly Indo-Pacific distribution. The monodactylids, or monos, are popular aquarium fishes. Their silvery-white, laterally compressed bodies are exaggerated by extremely tall dorsal and anal fins, making some species twice as deep as they are long. Adult *Monodactylus* lack a pelvic fin, although juveniles possess one. They are convergent in shape and ontogenetic pelvic loss with the very compressed carangid Germanfish, *Parastromateus niger*. The archerfishes are a well-known and unique group of small, surface-dwelling estuarine and freshwater fishes that feed actively on terrestrial prey. Insects are shot out of overhanging vegetation with bullets of water produced by compressing the gillcovers and shooting water drops along a groove created by the tongue and palate. This behavior is all the more fascinating because the fish corrects for the curving trajectory of its propelled droplets and target movement as well as for light refraction at the water's surface, its eyes being submerged during hunting (Dill 1977a; Schuster et al. 2006). **Kyphosid** sea chubs (also called rudderfishes) are an herbivorous family of 42 reef species that swim actively in shoals relatively high above the reef compared to most other herbivores. Kyphosids are unique among fishes in that at least two western Australian species contain symbiotic bacteria in their guts that break down algae via fermentation (Rimmer & Wiebe 1987). Although a predominantly tropical family, two temperate derivative species, the Opaleye, *Girella nigricans*, and the Halfmoon, *Medialuna californica*, extend into California waters.

Some authors feel that the kyphosids, monodactylids, and toxotids form, with the next five or so families, an unranked group known as the Squammipinnes, a name that refers to the rows of scales that cover the base of the dorsal and anal fins. The best known families in this group are the butterflyfishes and angelfishes. The **chaetodontid** butterfly-

fishes include 122 tropical shallow water species. Their center of diversity is in the Indo-Pacific region where about 100 of the species occur. The tropical Atlantic contains 13 species and the eastern Pacific has only four species. In many people's minds, butterflyfishes are synonymous with coral reefs (Burgess 1978; Motta 1989), and their presence and abundance is proposed as a measure of the health of coral reef habitats (Ohman et al. 1998). Butterflyfishes are colorful and swim conspicuously about the reef during the daytime, often in pairs or small shoals, residing for long periods on the same reefs and with the same partners. Trophically they fall into several categories of microconsumers, feeding either on coral polyps, small invertebrates hidden in crevices in the reef, tube worms, or on zooplankton. Anatomically they are deep-bodied, highly compressed forms, their body shape being exaggerated by stout dorsal, pelvic, and anal spines and a slightly to greatly elongated snout region. Closely related to and often mistaken for butterflyfishes are the similarly or larger sized angelfishes (**Pomacanthidae**). A major distinguishing feature between the two is the existence of a stout, posteriorly projecting spine at the angle of the preopercular bone and the absence of a pelvic axillary process in angelfishes. Many angelfishes undergo dramatic ontogenetic color changes, several species having confusingly similar but striking patterns as juveniles that change to species specific and still-striking adult patterns. Larger species such as the Caribbean French and Gray angelfishes frequently form pairs. Trophically, angelfishes differ from butterflyfishes in consuming sessile, benthic invertebrates such as sponges, tunicates, and anthozoans. Some species are known to follow sea turtles and feed on their feces, which may explain their disconcerting habit of hovering near designated latrines associated with undersea habitats such as Tektite and Hydrolab, before such submarine structures had internal plumbing. Again, about three-quarters of angelfish species occur in the Indo-Pacific. Angelfishes are among the few marine species in which hybrids are frequently discovered (e.g., Pyle & Randall 1994).

Most of the remaining families in the suborder Percoidea are relatively small. Among the more speciose groups are the **nandid** and closely related **polycentrid** leaffishes of South American, African and southern Asian fresh waters, which are best known for their striking morphological resemblance to floating leaves, a deception they enhance behaviorally by drifting slowly through the water toward unsuspecting prey, which they engulf with a remarkably expandable mouth. **Terapontid** grunters are a marine and freshwater family containing 48 species that have a unique means of producing sounds. Paired muscles run from the back of the skull to the dorsal surface of the gas bladder; in other sound-producing fishes that utilize muscles to vibrate the gas bladder, such as gadoids, triglids, and sciaenids, the muscles are derived from trunk musculature and originate in the body wall. **Kuhliid** flagtails are predominantly marine and estuarine inhabitants but some species have evolved to fill ecological niches in freshwater habitats on oceanic islands.

Five subsequent families are placed in the superfamily Cirrhitoidea, united by elongated and unbranched lower five to eight rays in their pectoral fins. The colorful **cirrhitid** hawkfishes are small to medium reef predators that are best known for sitting absolutely still on tops of corals in seemingly conspicuous locales, waiting for potential prey fishes to either not notice them or to habituate to their presence (a Hawaiian hawkfish is the only predator known to have eaten a Cleaner Wrasse). Hawkfishes look like a cross between a small seabass and a scorpionfish, but they are readily identified by the presence of filamentous tufts or cirri at the top of each spine in the first dorsal fin and by the elongated pectoral rays characteristic of the superfamily. One fairly deepwater reef species, the Longsnout Hawkfish, *Oxycirrhites typus*, occurs almost exclusively in black coral trees. Its deepwater habits may more closely reflect depletion of its preferred perch, which has been removed from accessible shallow locations due to the jewelry trade. The next to last family of percoids are the **cepolid** bandfishes, which vary in their morphology from elongate, eel-like forms to fairy bassletlike, deep water forms.

The barracudas (Sphyraenidae) appear to be percoids, although some morphological data suggest that they are primitive, basal members of the Scombroidei, the suborder that contains the tunas (Orrell et al. 2006). Twenty-one species of barracuda inhabit tropical and subtropical regions of the Atlantic, Pacific, and Indian oceans. Most barracudas are schooling predators, an important exception being the usually solitary Great Barracuda, *Sphyraena barracuda* (Paterson 1998). Great barracuda approach 2 m in length (a topic of considerable controversy), have fanglike, flattened teeth capable of slicing cleanly through most prey, and have the unnerving habit of following divers around the reef, motivated by either curiosity or territoriality (Fig. 15.14; see also Fig. 19.1).

Suborder Elassomatoidei

Suborder Elassomatoidei (six species): Elassomatidae (pygmy sunfishes)

The **elassomatid** pygmy sunfishes are interesting because of their strong convergence with the true sunfishes (Centrarchidae) and their miniaturization (maximum length 45 mm, but several species are smaller than 20 mm). The six elassomatid species are primarily dwellers of swampy habitats in southeastern USA (e.g., Everglades Pygmy Sunfish, Okefenokee Pygmy Sunfish). Many males take on iridescent

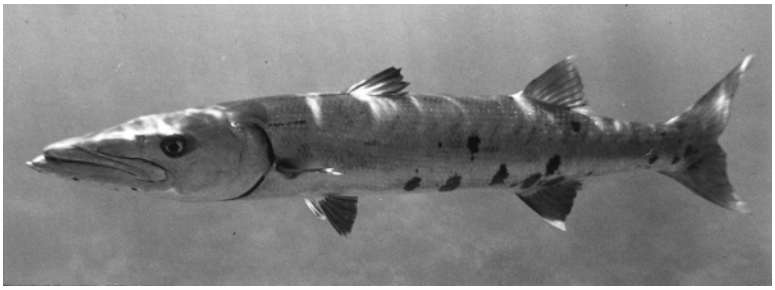


Figure 15.14
A sphyraenid, the Great Barracuda, *Sphyraena barracuda*. Photo by G. Helfman.

blue coloration during the breeding season. The actual taxonomic position of this enigmatic group is a matter of some debate, with different authors placing them outside the perciform order and more closely aligned with more primitive mugilomorphs, atherinomorphs, gasterosteiforms, or synbranchiforms.

Suborder Labroidei

Suborder Labroidei (2274 species): Cichlidae (cichlids), Embiotocidae (surfperches), Pomacentridae (damselfishes), Labridae (wrasses), Odacidae (cales), Scaridae (parrotfishes)

Although some of the 16 remaining perciform suborders contain very speciose families (e.g., blennies, gobies), by far the numerically most successful suborder is the Labroidei. Labroids are predominantly tropical, marine fishes (e.g., damselfishes, wrasses, parrotfishes), with a few species in the first two families inhabiting warm temperate waters. Two additional families, the surfperches and odacids, are temperate and marine. The most successful family in the suborder is the tropical freshwater cichlids, although no single biological generality applies to all members of this fantastically speciose and varied family of fishes. The six families are united primarily on the basis of pharyngeal jaw morphology, involving features of both the upper and lower jaws. Pharyngeal adaptations for handling a diversity of prey types have contributed substantially to the success of several labroid families.

Cichlids (initial "ci" sounded as in "pops*i*cle") are viewed as the basal group of the suborder. Among the more than 1350 cichlid species are many aquarium fishes that have achieved popularity because of their small size, colorfulness, and willingness to behave and breed within the confines of an aquarium. Familiar South American species include freshwater angelfishes (*Pterophyllum*), discus (*Symphysodon*), oscars (*Astronotus*), convict cichlids (*Archocentrus*), Peacock Bass (*Cichla*), and gravel-eaters (*Geophagus*). One species, the Rio Grande Cichlid, *Cichlasoma cyanoguttatum*, gets as far north as Texas and is known to have invaded Lake Pontchartrain, Louisiana. Numerous cichlids, particularly African tilapias, have been deliberately or accidentally introduced in Florida, California, and Hawaii, chiefly for aquaculture purposes. Although diverse in the New World (*c*. 400 species), the great majority of cichlids occur in Africa, where they have radiated explosively into numerous species flocks (Box 15.2). Old World cichlids include fishes in the genera *Haplochromis*, *Lamprologus*, *Oreochromis*, *Pseudotropheus*, *Sarotherodon*, and *Tilapia* (and many others). Most cichlids build nests and many African forms brood the eggs and young in the mouth of either the male or more usually the female. A few species occur in Israel and Iran and also in India and Sri Lanka, where they commonly inhabit estuaries (e.g., *Etroplus*). Cichlids are convergent in behavior, morphology, and ecology with centrarchid sunfishes. The two families can be distinguished by two nostrils on each side of the head and a continuous lateral line in sunfishes, whereas cichlids have only one nostril on each side and an interrupted lateral line (Fryer & Iles 1972; Keenleyside 1991; Lévêque 1997; Barlow 2000; Kullander 2003; and many others; see www.cichlidpress.com for spectacular photos and additional references).

The **embiotocid** surfperches look very much like some of the larger, deep-bodied cichlids. However, they are an entirely (with one exception) marine family of small to medium, inshore fishes that occur most commonly around kelp beds, rocky reefs, surf zones, and tidepools. Twenty of the 23 species occur along the Pacific coast of North America, the other three living in Korea and Japan. They are the only labroids that are live-bearers, the female giving birth to fully developed, large young. In a few species, males are even born reproductively mature (see Chapter 9, Fertilization). Trophically, some are specialized as zooplanktivores, whereas most pick invertebrates from the bottom or off plants. The **pomacentrid** damselfishes are generally smaller, more colorful, tropical marine

Box 15.2

BOX 15.2

Explosive speciation and species flocks

When a volcano erupts, an earthquake causes uplifting, a landslide blocks a river or divides a lake, or drought and flood cycles accompany longer term climatic changes, freshwater habitats can become **isolated**, separating small numbers of fishes from their conspecifics, predators, and competitors. The reproductive future of such an isolated individual or individuals is usually rather bleak, as potential mates and resources may also be in short supply in the newly created habitat. But such events occasionally lead to an evolutionary bonanza, as evidenced by several so-called species flocks or species swarms. A **species flock** is a group of closely related species that share a common ancestral species and that are endemic to an isolated region such as a single lake or island (Greenwood 1984). Flocks evolve when a newly created habitat with essentially open niches is colonized and the colonizing species experiences a relaxation of the many selection pressures that normally kept its population in check. Descendants of the founders disperse, differentiate, and fill the open niches. The end product is **rapid speciation** – a literal explosion of speciation events – and the production of several descendant species in the area.

Some of the most spectacular assemblages of fishes and other animals worldwide represent the end products of explosive speciation. Non-fish examples include such showcases of evolution as the fruit flies, land snails, and honeycreepers of the Hawaiian Islands, Darwin's finches in the Galápagos Islands, and the amphipods of Lake Baikal in Asia. Fish examples are numerous, instructive, and involve many different teleostean as well as some non-teleostean taxa. In addition, the fossil record shows us that the process of explosive speciation has operated dramatically in the distant as well as recent past.

The best known fish flocks occur among the cichlid fishes of the three Great Lakes of Africa: Malawi, Tanganyika, and Victoria (Fig. 15.15). The first two lakes are

Figure 15.15
This aquarium at the Georgia Aquarium is not unrepresentative of a scene over a rocky area of Lake Malawi where there has been an explosive speciation among cichlids. To view some of the spectacular body shape and color variation among African cichlids, go to www.cichlidworld.com/photo.html. Photo by G. Helfman.

long, deep, rift valley lakes, situated along a split in the earth's crust that is nearly 3000 km long. Lake Victoria, the largest lake in Africa, is more round and shallow, having been created as rivers were blocked by slow uplifting of the basin. These lakes vary in size between 28,000 and 69,000 km^2, putting them within the size range of the Laurentian Great Lakes of North America (19,000–82,000 km^2). Although of similar sizes, the species diversities of the lakes are totally dissimilar. The five Laurentian Great Lakes together contain about 235 fish species, whereas their African counterparts contain more than five times that number. The African Great Lakes each contain more fish species than any other lakes in the world (Fryer & Iles 1972; Greenwood 1981, 1991; Ribbink 1991; Goldschmidt 1996; Kornfield & Smith 2000; Snoeks 2000; Lamboj 2004).

The exact number of species in each African lake is difficult to determine because the region is remote from academic institutions that specialize in fish taxonomy, which means that many species remain to be collected or described, although concerted efforts continue. In addition, anatomical differences among some species are subtle (identification of species requires cytogenetic and biochemical analysis), and there is good evidence that environmental degradation and introduced species have recently wiped out many species (see Chapter 26, Introduced predators). Approximations for the three lakes indicate the following distributions (L. R. Kaufman, pers. comm.):

	Lake Malawi	*Lake Tanganyika*	*Lake Victoria*
Cichlids	700–1000	180–250	400–500
Endemic cichlids	695–995	178–248	395–495
Non-cichlids	53	113	65

Conservatively, there are perhaps 75 genera and 1300–1750 species of cichlids in the three lakes (estimates vary widely), as well as smaller flocks in smaller lakes and the rivers of Central Africa (e.g., Greenwood 1991; Stiassny et al. 1992), and flocks of non-cichlids such as catfishes in Lake Malawi, and of mastacembelid eels, claroteid and mochokid catfishes, and latid perch in Lake Tanganyika (Agnese & Teugels 2001; Lévêque et al. 2008).

The relevant points here are that most of the fishes in each lake are cichlids, most or all of the cichlids are endemic, and in each lake it is likely that most or all of the endemic cichlids share a common ancestor (Meyer et al. 1990; Meyer 1993), although some assemblages undoubtedly resulted from multiple invasions involving multiple ancestors (e.g., Kaufman 2003). The morphological and ecological divergence from such an ancestor is astounding, given that Tanganyika and Malawi are only 2–10 million years old. The largest and smallest cichlids in Lake Tanganyika are *Boulengerochromis microlepis*, a predator, which attains a length of 80 cm, whereas small planktivores of the genus *Lamprologus* may be only 4 cm long as adults. The difference in mass between adults of the two genera is about 8000-fold. Morphological diversity includes African cichlids that artificially resemble many different families of teleosts and occupy habitats and niches that parallel those of the other teleosts (Fig. 15.16). More spectacular still, sedimentation, radiocarbon dating, and mitochondrial DNA data all indicate that Lake Victoria may have been completely dry as recently as 12,500 years ago, which means that 300 endemic species there evolved in a very short period (Johnson et al. 1996). Age analysis of lakes, as with most aspects of African cichlid biology, is an active field with ever-changing conclusions (e.g., Seehausen 2002).

Trophically, African cichlids do it all. Trophic groups include species that specialize in eating phytoplankton, sponges, sediments, periphyton, leaves, mollusks, benthic arthropods, zooplankton, fish scales and fins, fish eyes, eggs and embryos, and other fishes. Major anatomical adaptations associated with different trophic habitats are found in the lips, marginal dentition, gill rakers, and particularly the pharyngeal jaws of the different trophic groups. Two flocks-within-flocks occur in Lake Malawi, where each subflock has differentiated into a particular feeding type. Approximately 27 (but perhaps as many as 200) species of closely related *mbuna* cichlids live over rocky areas and feed on the algae and associated microfauna of the algae, a food type known as *aufwuchs*. An additional flock of approximately 17 *utaka* cichlids live together and feed on zooplankton (Fryer & Iles 1972; Ribbink 1991; Lévêque 1997).

Whereas the African cichlids form the largest species flocks among fishes, other examples are often as dramatic (Lévêque et al. 2008). The following is a partial list of well-known flocks and some of their interesting characteristics:

1. The oldest extant species flock of fishes occurs in Lake Baikal, Russia, the oldest and deepest lake in the world. Here, sculpinlike cottoid fishes have differentiated into perhaps three families and approximately 33 species in 12 genera, including four recently described species (N. Bogutskaya, pers. comm.). Highly derived members of this group include two species of live-bearing, pelagic, comephorid Baikal oilfishes, a marked difference from the ancestral benthic, egg-laying sculpins (see also Berra 2001). Lake Baikal has also produced a flock of amphipods and has an endemic, freshwater species of monk seal. Habitat degradation in the lake has unfortunately pushed several Baikal endemics onto endangered species lists.
2. As many as three genera and 18 species of cyprinids form a flock in Lake Lanao of the Philippines, which sits above an uplifted waterfall 18 m high. This dramatic and controversial flock includes fishes with "**supralimital jaw specializations**", indicating that

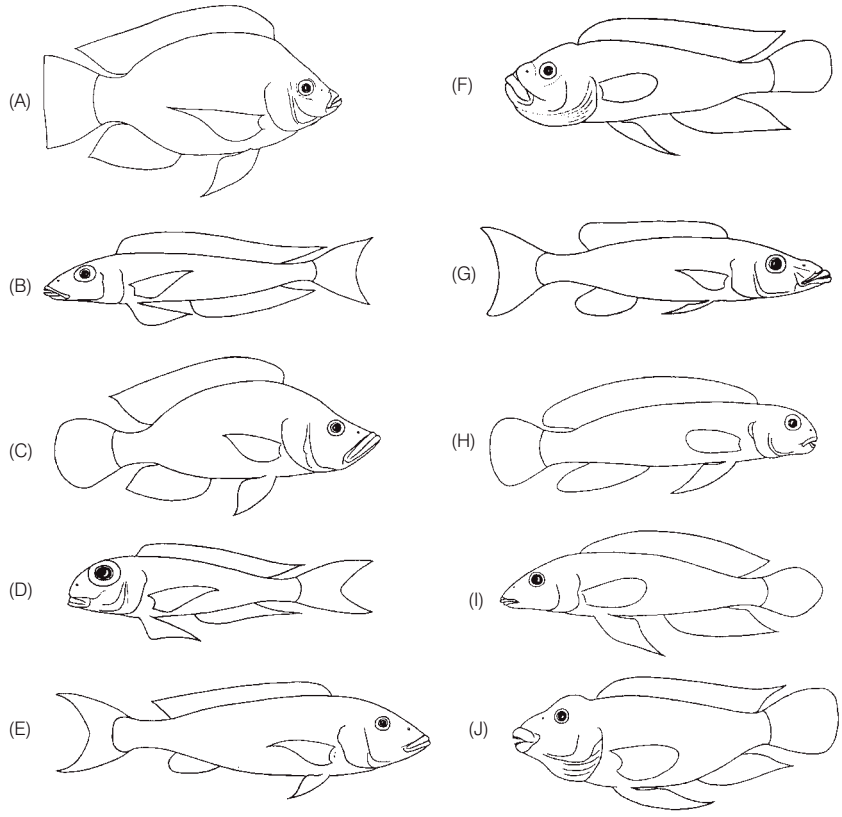


Figure 15.16

Diversity in body shape among African cichlids. These fishes belong to several different genera of cichlids, yet are roughly similar in body form to several other teleostean families. Cichlid genera and suggested convergences are: (A) Tilapia versus a centrarchid sunfish; (B) *Xenotilapia* versus a malacanthid tilefish; (C) *Serranochromis* versus a serranid seabass; (D) *Xenotilapia* versus a gobiid goby; (E) *Boulengerochromis* versus a lutjanid red snapper; (F) *Telmatochromis* versus a batrachoidid toadfish; (G) *Rhamphochromis* versus a centropomid snook; (H) *Telmatochromis* versus an opistognathid jawfish; (I) *Julidochromis* versus a labrid wrasse; and (J) *Spathodus* versus a scarid parrotfish. From Fryer and Iles (1972), used with permission.

derived species have jaw characteristics outside the normal variation found within the rest of the family. The flock is also unique in that the presumed ancestor, *Puntius binotatus*, still occurs in lowland streams below the waterfall. The validity of the flock and its traits are obscured by the destruction of holotypes during World War II and subsequent, multiple introductions of game and forage species that have displaced the native fishes; only three of the original cyprinids still occur in the lake (Kornfield & Carpenter 1984).

3 Eighteen species of atherinopsid silversides occur in a few lakes of the Mesa Central of Mexico. Diversification in this group includes a wide range in adult sizes and feeding types, from relatively typical, small (6 cm) zooplanktivores to piscivorous giants 30 cm long with specific names like *lucius* and *sphyraena* ("pike" and "barracuda") (Barbour 1973; Echelle & Echelle 1984).

4 A complex of flocks occurs among killifishes in Lake Titicaca and the surrounding lakes of the Peruvian and Bolivian Andes. Most of these species belong to one widespread genus, *Orestias*. Because several lineages are involved, the killifish assemblage is actually made up of several flocks rather than a single flock, the largest being about 15 species. The species have diversified into deep water, midwater, planktivorous, piscivorous, miniaturized, and broad-headed forms, a departure from the surface-dwelling, insect-feeding killifish norm (Parenti 1984).

5 Eight species of coregonid ciscoes evolved from a common ancestor in the Laurentian Great Lakes of

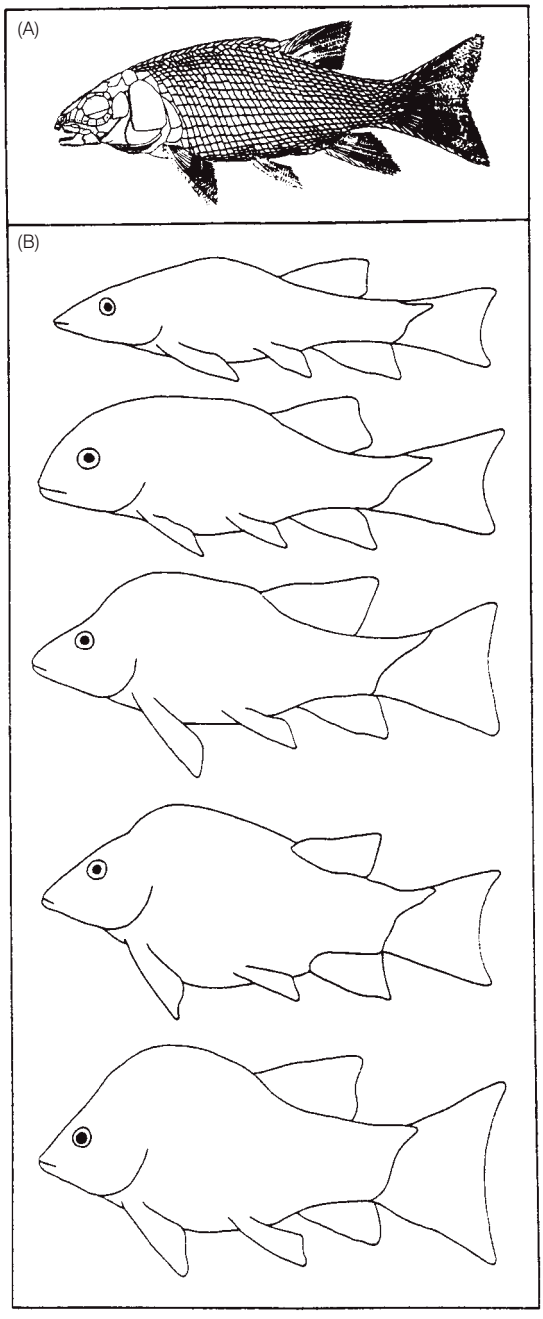


Figure 15.17
Variation in morphology of an ancient species flock. (A) A completely reconstructed individual of the Jurassic neopterygian *Semionotus*. (B) Variation in body form of species related to *Semionotus* that probably co-occurred in a single lake. From McCune (1990), used with permission.

North America. It is also likely that smaller flocks of coregonids have arisen in lakes of the western USA, Canada, and northern Europe, totaling perhaps 45 species, with repeated convergent modifications in eye size, body size and shape, gill raker number and morphology, snout shape, migration patterns, and spawning behavior (Smith & Todd 1984; Kottelat 1997).

6 Approximately 15 species of cyprinid fishes in the genus *Labeobarbus* cooccur in Lake Tana of Ethiopia. They are in part unusual in that eight species are piscivores, which is an unorthodox feeding pattern for minnows (Nagelkerke et al. 1994; Palstra et al. 2004).

7 Historical continuity is evident in flocks of semionotid fishes that occupied the rift valley lakes of what is now the northeastern coastline of North America between North Carolina and Nova Scotia (McCune et al. 1984; McCune 1990). Semionotids were very successful Jurassic neopterygians that may have been ancestral to modern gars (Lepisosteidae) (see Chapter 11, Subclass Neopterygii). Semionotid flocks of up to 17 species formed and were extinguished repeatedly as lakes filled and evaporated on a 21,000-year cycle over a period of 33 million years. Within the genus *Semionotus*, body shape varied substantially, including elongate pikelike forms, rounded sunfishlike forms, and intermediate shapes (Fig. 15.17). The setting and speciation patterns directly parallel flock formation in the modern African rift valley lakes. Other "fossil flocks" include a radiation of eight sculpin species during the Pliocene in Lake Idaho in the western USA (Smith & Todd 1984).

The diversity of species that exist, their ecological relationships and innovations, and the repeatability of the process are remarkable examples of speciation and adaptation, even occurring in taxa that we do not normally think of as highly variable, speciose, or particularly rapidly evolving. How can such speciation occur, particularly in lakes that may only be a few thousand years old? A small lake near the edge of Lake Victoria may provide a clue. Lake Nabugabo sits 3 km away and 15 m above Lake Victoria, draining into the larger lake through a swamp. Six species of *Haplochromis* cichlids occur in Nabugabo, five of which are endemic and have close relatives in Victoria. Charcoal dates from former strandlines indicate that Nabugabo is only 4000 years old and that Victoria has repeatedly risen and overflowed into Nabugabo and other surrounding lakes, providing colonists for the smaller lakes. As waters receded, these colonists were isolated from competitors and predators and would have been able to occupy the niches of the newly created small lakes, speciating in as little as 4000 years. As the larger lake rose again, the new

species could now swim into the larger, ancestral lake, increasing its diversity if they were unable to interbreed with their former conspecifics. As this scenario was repeated in numerous small, satellite lakes around Victoria, the generation of many species that would eventually occupy the larger lake is imaginable. It is through such **allopatric** processes of isolation and differentiation that species flocks in most lakes are likely to have developed.

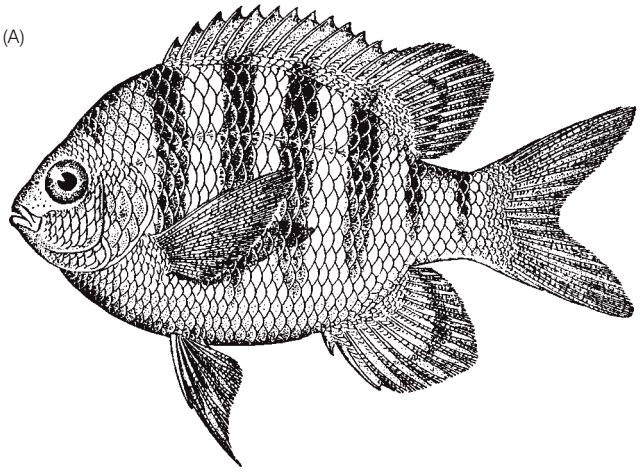
For Lake Victoria in particular, where rock-dwelling species are abundant, the "satellite lake hypothesis" is not entirely satisfactory because few of the satellite lakes have rocky habitats. Other processes, involving within-lake (**sympatric**) development of species with minimal dispersal, have been proposed (e.g., Greenwood 1991; Galis & Metz 1998). Sexual selection of females for different colored males, reinforced by morphological and behavioral plasticity that leads to feeding specializations, is likely to have contributed (see Chapter 17, The cichlid radiation of Lake Malawi; Chapter 21, Sexual selection, dimorphism, and mate choice; Chapter 26, Watershed perturbation). Regardless of mechanism or mechanisms, African cichlids represent "the most explosive speciation and adaptive radiation in vertebrate evolution yet described" (Galis & Metz 1998, p. 2).

equivalents of the surfperches (Fig. 15.18A). Many damselfishes are herbivorous (e.g., *Stegastes* spp.), whereas others are zooplanktivorous and show the usual adaptations associated with life in the water column above structure, namely a fusiform body, forked tail, and highly protrusible mouth (e.g., *Chromis* spp.). Herbivorous damselfishes are typically territorial, guarding a small patch of reef substrate in which they feed, hide, and in the case of males, court females and guard developing eggs. No post-hatching care of young is shown except in one Indo-Pacific species, *Acanthochromis polyacanthus*. Some species are intimately associated with invertebrates, such as the anemonefishes (*Amphiprion*, *Premnas*) (see Chapter 22, Interspecific relations: symbioses). This is a tropical family containing 315 species that reaches its highest diversity in the Indo-Pacific region, with a few species in each ocean basin occurring in warm temperate waters (e.g., in California, the Blacksmith, *Chromis punctipinnis*, and the state marine fish, the Garibaldi, *Hypsypops rubicundus*) (Emery & Thresher 1980; Allen 1991; see also papers in Allen et al. 2006) (Fig.15.19).

The next three families are closely related. The largest family is the wrasses, **Labridae**, a remarkably diverse and widespread marine taxon of at least 450 species that occurs in all tropical seas. Many temperate and even cool temperate members occur in both the Pacific and Atlantic oceans, such as the eastern Pacific California Sheephead (Fig. 15.18B) and Senorita (*Semicossyphus*, *Oxyjulis*), the western Atlantic Tautog and Cunner (*Tautoga*, *Tautogolabrus*), and several eastern Atlantic wrasses (*Labrus* spp.). Wrasses range in size from 5 cm (many species) to the Giant Humphead (or Maori or Napoleon) Wrasse of the Indo-Pacific, *Cheilinus undulatus*, which can be 2.3 m long, weigh 200 kg, and has the unlikely diet of cowries and crown-of-thorns starfish (Fig. 15.18D). It is depleted almost everwhere it is found and many Pacific island nations now outlaw its export and even capture (Sadovy et al. 2003). Pharyngeal jaws are especially diversified among labrids, several species able to handle well-protected prey such as crabs, mollusks, and echinoderms. Labrids typically bounce along in the water column using labriform locomotion, a paddling motion of their pectoral fins, stopping momentarily above the bottom to capture prey with protractile jaws and stout teeth, picking zooplankters out of the water column, or removing external parasites from other fishes (see Chapter 8, Locomotory types). The razorfishes (*Hemipteronotus*, *Xyrichtys*) are very compressed and escape disturbances by diving rapidly into bottom sediments. Wrasses as a group are strongly diurnal and enter sandy bottoms or reef crevices at night to sleep. Many wrasses change sex, most starting off life as females and later changing to very differently colored and shaped males (see Chapter 21, Gender roles in fishes).

The **odacids** are a small family of 12 species limited to the temperate waters of New Zealand and southern Australia. They are intermediate in appearance between wrasses and parrotfishes, having the elongate wrasse body form but the non-protractile jaws and fused teeth of parrotfishes. The **scarid** parrotfishes include 88 species of tropical marine fishes best known for their fused teeth that form a parrot-like beak (Fig. 15.18C). The beak is used for biting off algal fronds or pieces of dead coral or scraping the surface of live coral, which is then passed to massive pharyngeal mills for grinding and extracting algal cells from the coral matrix. As with wrasses, parrotfishes generally change color and sex, from initial phase females to terminal phase males. Parrotfishes are generally larger than wrasses, with some species such as the blue and rainbow parrotfishes of the Atlantic (*Scarus* spp.) and the bumphead parrotfish of the Pacific (*Bulbometopon*) attaining a meter in length. These spectacular, large species are becoming rare due to overfishing and are seldom seen outside of protected areas (Dulvy & Polunin 2004).

(A)



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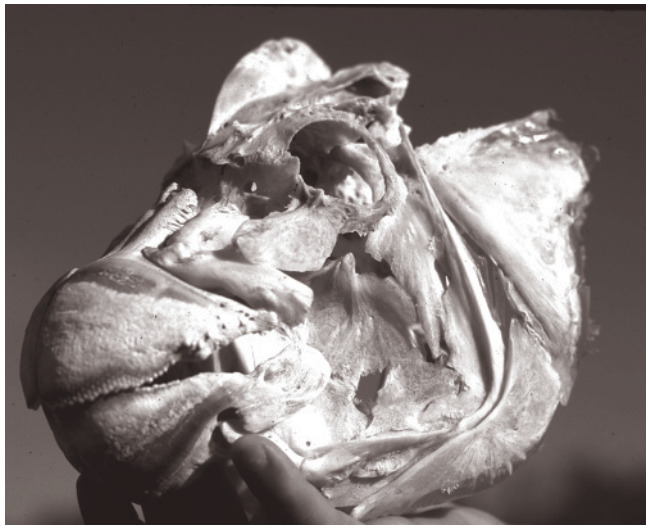

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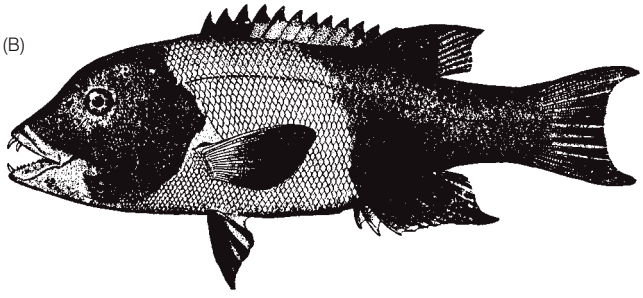

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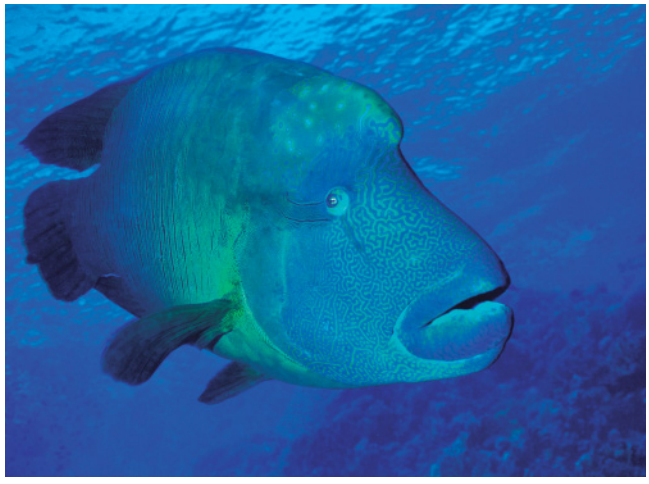


Figure 15.18

Representative labroids. (A) A pomacentrid damselfish, the Sergeant Major, *Abudefduf saxatilis*. (B) A labrid, the California Sheephead, *Semicossyphus pulcher*. (C) Head of a Rainbow Parrotfish, *Scarus guacamaia*, showing the fused, parrotlike beak. (D) The Napoleon or Humphead Wrasse (*Cheilinus undulatus*), the largest member of the speciose wrasse family. (A, B) from Jordan (1905); (C) photo by G. Helfman; (D) photo by D. Hall, www.seaphotos.com.

Figure 15.19

The Garibaldi, *Hypsypops rubicundus*, a temperate pomacentrid damselfish common in kelp beds of southern California, It really is that orange. Photo by G. Helfman.

Suborder Zoarcoidei

Suborder Zoarcoidei (340 species): Bathymasteridae (ronquils), Zoarcidae (eel pouts), Stichaeidae (pricklebacks), Cryptacanthodidae (wrymouths), Pholidae (gunnels), Anarhichadidae (wolffishes), Ptilichthyidae (quillfishes), Zaproridae (prowfish), Scytalinidae (graveldivers)

The zoarcoids as a group are generally elongate fishes of the North Pacific that occupy benthic habitats ranging from tidepools to abyssal depths. The **zoarcid** eel-pouts are eel-like fishes with round heads, long dorsal and anal fins, and pointed tails. Some eel pouts give birth to live young after eggs develop internally, a condition referred to as ovoviviparity (see Chapter 9, Embryology). Zoarcids inhabit soft bottoms at moderate to great depths (20–3000 m). Most species occur in the North Pacific, some in the North Atlantic, in deep tropical regions of both oceans, and about 10% of the 230 species occur in the southern oceans near Antarctica. In contrast, the **stichaeid** pricklebacks and **pholid** gunnels are most common in intertidal and shallow, nearshore habitats, primarily in North Pacific waters. Members of both families are primarily microcarnivores, although two pricklebacks, *Cebidicthys violaceus* and *Xiphister mucosus*, are herbivorous year-round, an uncommon trait at high latitudes for any fishes (Horn 1989). The **anarhicadid** wolffishes or wolf-eels are the anatomical and ecological equivalents of moray eels at high latitudes (Fig. 15.20). Attaining lengths of 2.5 m and weighing 45 kg, these large benthic predators of the North Pacific and Atlantic often live under rocks and have large anterior conical canines and massive lateral and palatine molars for catching and crushing crustaceans, clams, sea urchins, and fishes.

Suborder Notothenioidei

Suborder Notothenioidei (125 species): Bovichtidae (temperate icefishes), Pseudaphritidae (catadromous icefishes), Eliginopidae (Patagonian blennies), Nototheniidae (cod icefishes), Harpagiferidae (spiny plunderfishes), Artedidraconidae (barbeled plunderfishes), Bathydraconidae (Antarctic dragonfishes), Channichthyidae (crocodile icefishes)

The notothenioids are commonly referred to as the icefishes (Fukuchi et al. 2006; see Fig. 18.9). The suborder is restricted primarily to high latitudes of the southern hemisphere, with greatest diversity in benthic habitats of Antarctica. These cold water fishes show numerous physiological and behavioral adaptations to prevent their tissues from freezing, including the production of a variety of glycoprotein antifreezes (see Chapter 7, Coping with temperature extremes). Many of the fascinating characteristics of the biology of this group are detailed in Chapter 18 (Antarctic fishes) and will not be repeated here. The **bovichtids** of

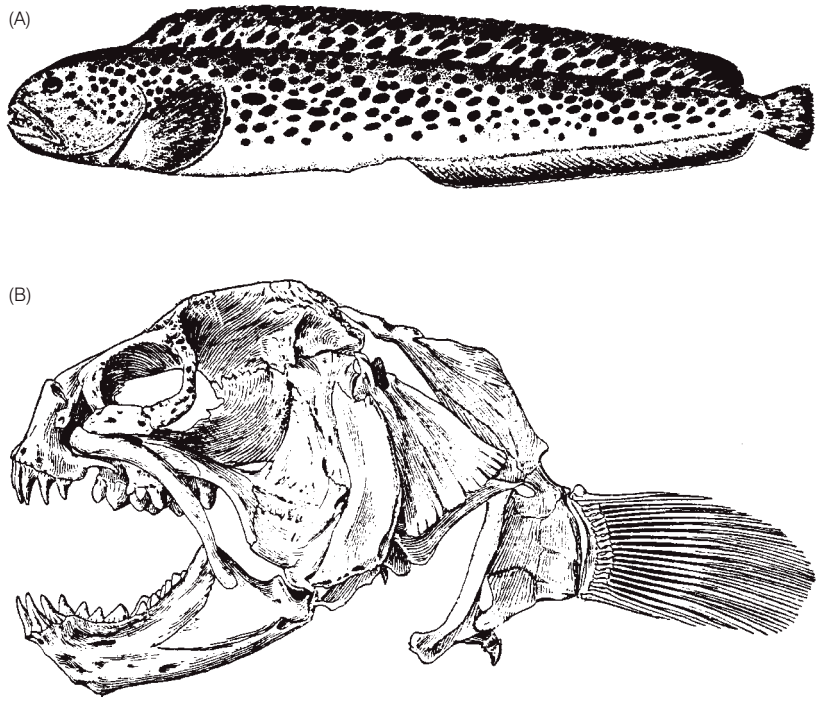


Figure 15.20

Zoarchoids. (A) A zoarcoid Atlantic wolffish, *Anarhichas lupus*. (B) A skull of the related Pacific Wolf-eel, *Anarrhichthys ocellatus*, showing the massive, diversified dentition of these predators (see also Fig.8.8). From Jordan (1905).

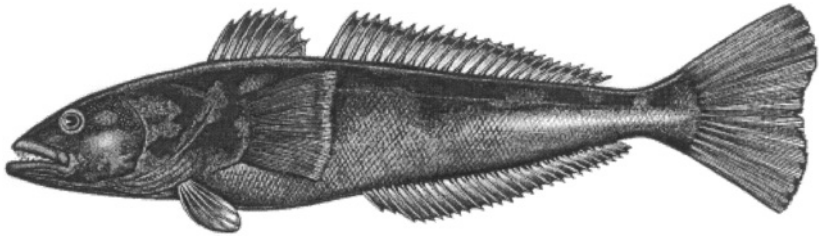


Figure 15.21
The Patagonian Toothfish, *Dissostichus eleginoides*, a large, long-lived nototheniid of southern oceans subjected to considerable illegal, unreported, and unregulated (IUU) fishing. Take a pass on Patagonian Toothfish. Drawn by Bruce Mahalski, from Lack and Sant (2001), used with permission of www.traffic.org.

Australia, New Zealand, and southern South America are considered the stem group for the rest of the suborder. **Nototheniid** cod icefishes are predominantly benthic, with some secondarily pelagic species that achieve neutral buoyancy by depositing lipids in their muscles and by reduction of skeletal material, two adaptations to water column existence that occur convergently in other families derived from benthic ancestors (e.g., cottoid Baikal oilfishes, and many deepsea forms). The best known nototheniid is the Patagonian Toothfish (or Chilean seabass), *Dissostichus eleginoides*, a large (to 2.4 m, 130 kg), long-lived (to 50 years), slow reproducing, and grossly overfished benthopelagic predator (Fig. 15.21). The **channichthyid** crocodile icefishes are well studied because they lack red blood cells, hemoglobin, and myoglobin, making their blood and flesh colorless. These traits probably reflect the high amount of dissolved oxygen in cold Antarctic waters.

Suborder Trachinoidei

Suborder Trachinoidei (212 species): Chiasmodontidae (swallowers), Champsodontidae (gapers), Trichodontidae (sandfishes), Pinguipedidae (sand perches), Cheimarrhichthyidae (New Zealand Torrentfish), Trichonotidae (sanddivers), Creediidae (sand burrowers), Percophidae (duckbills), Leptoscopidae (southern sandfishes), Ammodytidae (sand lances), Trachinidae (weeverfishes), Uranoscopidae (stargazers), Pholidichthyidae (convict blennies)

Trachinoids are mostly benthic, questionably related marine fishes, several of which sit buried in the sand throughout the day or seek refuge in the sand when not feeding. **Chiasmodontid** swallowers depart from the suborder norm in being one of the few acanthopterygians to occupy mesopelagic and bathypelagic depths. They show convergent traits with other deepsea fishes, including a large mouth, long teeth, slender jaw bone elements, distensible mouth and stomach, black coloration, and photophores. The **Cheimarrichthyidae** consist of a single New Zealand species, *Cheimarrichthys fosteri*. It is known as the Torrent fish, reflecting its daytime habitat in turbulent streams. Its body form, inferior mouth, large horizontally placed pelvics, and broad flattened head converge with other swift water fishes such as Longnose Dace, balitorine hillstream loaches, African kneriids, amphiliid loach catfishes, clingfishes, and rhyacichthyid loach gobies (see Chapter 18, Strong currents and turbulent waters). **Trichonotid** sanddivers share a peculiarity with some elasmobranch rays by having protuberant eyes and a dorsal eyelid of sorts made up of an iris flap with strands that extend over the lens. Both groups rest on or bury in the sand in shallow water with only their eyes visible.

Ammodytid sand lances are small, elongate, shoaling fishes that feed on zooplankton in the water column by day and spend nighttime buried in the sand. The **trachinid** weeverfishes are well-known eastern Atlantic and Mediterranean benthic fishes with highly venomous opercular and dorsal spines. The **uranoscopid** stargazers are another venomous family, with two grooved spines and an accompanying gland sitting just behind the gill cover and above the pectoral fins. Stargazers also lie on the bottom or bury in the sand, with their dorsally located eyes exposed. Their incurrent nostrils are directly connected to the mouth, which may allow them to breathe while buried. A fleshy filament extends upward from the floor of the mouth and is used to lure prey. Stargazers include some of the only marine teleosts that are electrogenic, strong pulses of electricity (up to 50 volts) being produced by highly modified extrinsic eye muscles. They discharge when captured and may also use electricity to stun prey. Stargazers are convergent in body form and habits with paracanthopterygian toadfishes and blennioid dactyloscopid sand stargazers.

Suborder Blennioidei

Suborder Blennioidei (818 species): Tripterygiidae (triplefin blennies), Dactyloscopidae (sand stargazers), Blenniidae (combtooth blennies), Clinidae (kelp blennies), Labrisomidae (labrisomid blennies), Chaenopsidae (tube blennies)

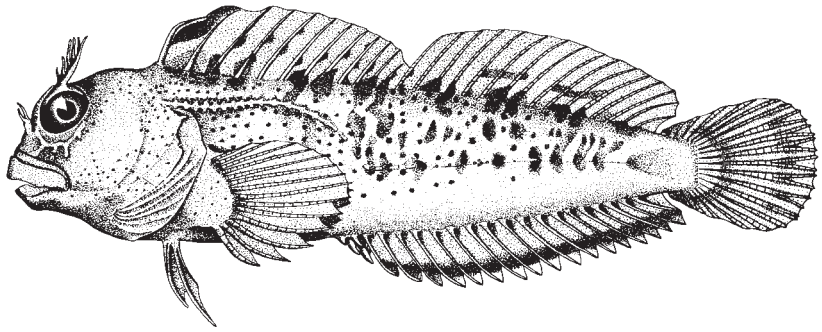


Figure 15.22
A bleniid blenny, *Blennius yatabei*, from Japan. From Briggs (1974), used with permission of McGraw-Hill, Inc.

Blennioids are small, benthic, marine fishes of tropical and subtropical regions (Fig. 15.22). They generally possess long dorsal and anal fins and fleshy flaps termed cirri on some part of the head. Triplefin blennies (**Tripterygiidae**) derive their name from having a soft dorsal fin plus a spiny dorsal fin divided into two parts (hakes and cods are the only other fishes with three distinctive dorsal fins). **Dactyloscopid** sand stargazers look like miniaturized (to 15 cm) uranoscopid stargazers with their oblique mouths and stalked eyes. They similarly have a specialized breathing mechanism probably related to their burying habits. In most fishes, water is brought into the mouth and out the gills by the combined actions of buccal and opercular pumps (see Chapter 5, Respiration and ventilation). Sand stargazers move water via a branchiostegal rather than an opercular pump. Fingerlike projections inside the mouth may keep sand out of the gills. Some dactyloscopid males care for eggs by carrying them under the axil of each pectoral fin.

The combtooth blennies of the family **Blenniidae** are very diverse, accounting for 360 species of mostly small, benthic fishes in tropical and subtropical waters worldwide. The comblike teeth are used to crop algae in many species. Many of the advanced nemophine sabre-toothed blenniids (*Aspidontus*, *Meiacanthus*) swim freely in the water column and are also involved in mimetic relationships with other fishes. The best known example is the cleanerfish mimic, *Aspidontus taeniatus*. This sabre-toothed blenny strongly mimics the blue and black coloration and bobbing solicitation dance of labrid cleanerfishes, particularly of the Cleaner Wrasse, *Labroides dimidiatus*. When allowed to approach a posing host fish, rather than cleaning the host, *Aspidontus* bites off a piece of fin (juvenile *L. dimidiatus* are also mimicked by juvenile fang blennies, *Plagiotremus rhinorhynchos*). Other sabre-toothed blennies attack passing fish and remove scales or pieces of fin (they attack prey as large as skindivers and generally attack once the diver has passed overhead, which is always a surprising, painful, and distinctly unsettling experience). Some of the sabre-toothed species are referred to as poison-fanged blennies because of their hollow lower canines that can inject a toxin. Poison fang blennies (*Meiacanthus*) may be mimicked by similarly colored blennies (e.g., *Ecsenius*, *Plagiotremus*, *Runula*) and thus gain protection from predators (Losey 1972; Springer & Smith-Vaniz 1972; Moland & Jones 2004).

Clinids, also known as kelpfishes and fringeheads (including the intriguingly named Sarcastic Fringehead), vary in size from 5 cm up to the predatory Giant Kelpfish, *Heterostichus rostratus*, which reaches 60 cm. Clinids are shallow water, benthic forms associated closely with structure in both temperate southern and northern hemispheres. Some clinids give birth to live young. **Chaenopsid** pike blennies and tube blennies are small, tropical, New World fishes that are most often found living in or with corals. Many tube blennies are essentially infaunal. Shortly after settling from the plankton, a tube blenny will take up residence in an available polychaete worm tube and is likely to remain there for the rest of its life.

Suborders Icosteoidei, Gobiesocoidei, and Callionymoidei

The monotypic suborder Icosteoidei and family **Icosteidae** contains the very peculiar North Pacific Ragfish, *Icosteus aenigmaticus*. Elliptical in shape and highly compressed, spineless, scaleless, without pelvic fins as an adult, and with a largely uncalcified cartilaginous skeleton, these 2 m long pelagic predators look like a free-swimming flatfish with a limp body. They are a reported favorite prey of sperm whales.

The suborder Gobiesocoidei contains 140 species, all in the clingfish family **Gobiesocidae**. Gobiesocids are a shallow water to amphibious family of small marine fishes often found in high-energy wave zones. The pelvic fins are modified into a sucking disk, the body is depressed, the head is rounded and flattened, and the skin is smooth and scaleless (Fig. 15.23). They have a unique pectoral girdle and vertebral rib arrangement. A relative giant in the family, the 30 cm Chilean *Sicyases sanguineus* feeds on snails, barnacles, chitons, and other high intertidal prey as well as many kinds of algae, often preferring the wave-splashed supratidal region to more regularly inundated depths (or heights) (Paine & Palmer 1978). Its flesh is reputed to have aphrodisiac qualities.

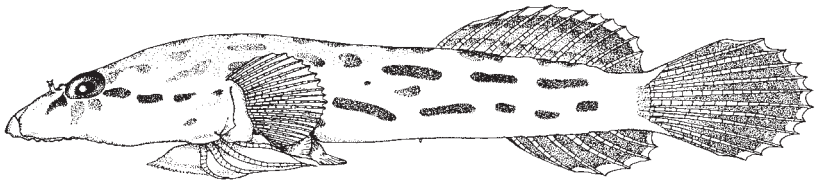


Figure 15.23
A gobiesocid clingfish, *Gobiesox lucayanus*, from the West Indies. From Briggs (1974), used with permission of McGraw-Hill, Inc.

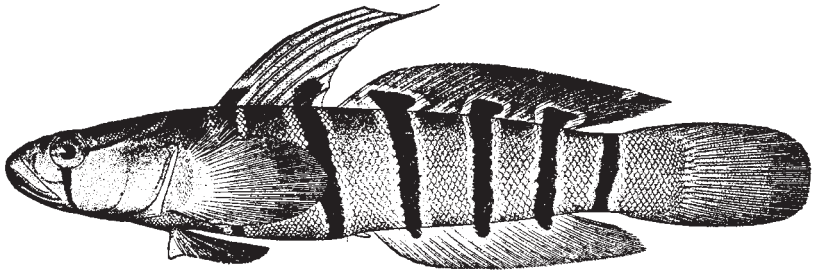


Figure 15.24
A Japanese goby, *Pterogobius daimio*. From Jordan (1905).

Two families make up the suborder Callionymoidei, the **callionymid** dragonets (182 species) and the poorly studied, deeper water **draconettid** slope dragonets (12 species). Dragonets are a chiefly marine family of small, shallow water fishes in the Indo-West Pacific. Some species are pale white and live over sand, whereas others associated with hard bottoms are quite colorful. The family includes a popular aquarium species, the green and orange mandarinfish or Splendid Dragonet, *Synchiropus splendidus* (see Fig. V, p. 423).

Suborder Gobioidei

Suborder Gobioidei (2211 species): Rhyacichthyidae (loach gobies), Odontobutidae (freshwater sleepers), Eleotridae (sleepers), Xenisthmidae (xenisthmids), Kraemeriidae (sand gobies), Gobiidae (gobies), Microdesmidae (wormfishes), Ptereleotrids (dartfishes), Schindleriidae (infantfishes)

Gobioids are usually small, benthic or sand-burrowing fishes, mostly marine but about 10% inhabit fresh water. Gobioids, as is common among benthic fishes, lack a gas bladder. Different families show differing degrees of fusion of the pelvic fin. Two families, the sleepers and gobies, account for 95% of the species in the suborder, the latter family being by far the largest. In the stream-dwelling **rhyacichthyid** loach gobies of Indo-Australia, the flattened anterior third of the body in combination with the pelvic fins form a sucking disk for holding position in fast-flowing water. The **eleotrid** sleepers are small to medium (to 60 cm), widely distributed estuarine and stream fishes of tropical and subtropical regions. They are often the major predators of stream systems on oceanic islands such as Hawaii and New Zealand and have a complex life history that includes a marine planktonic larva, reflecting a probable marine ancestry for the family. Pelvic fins are usually separated. Elongate **kraemeriid** sand gobies often rest in sand with just the head exposed, frequently in wave-tossed areas.

The **gobiid** gobies (Fig. 15.24) constitute the largest family of marine fishes in the world, with more than 1950 species (the distinction of largest fish family overall is contested among gobies, cyprinids, and cichlids, all with around 2000 species). Gobies usually have their pelvic fins united, some species using them as a suction disk for clinging to hard substrates. Many species live on mud or sand or in association with invertebrates such as sponges, sea urchins, hard and soft corals, and shrimps (see Chapter 22, Interspecific relations: symbioses). The Neon Goby, *Gobiosoma oceanops*, is an important cleanerfish in the Caribbean and is convergent in coloration with labrid cleanerfishes of the tropical Pacific. Other derivative species include the essentially amphibious mudskippers (*Periophthalmus*, *Boleophthalmus*); these are so successful out of water that they are sometimes referred to as land gobies. Gobies are generally small (< 10 cm) and some are among the world's smallest fishes. Diminutive species include an Indian Ocean species, *Trimmatom nanus*, which matures at 8–10 mm, and several species in the genera *Eviota*, *Mistichthys*, and *Pandaka* that mature at about 10 mm. The largest goby is a western Atlantic/Caribbean form, the Violet Goby, *Gobioides broussenetti*, a purplish eel-like fish about 50 cm long with elongate dorsal and anal fins. Although predominantly marine, some of the freshwater species are important members of island stream assemblages, including species capable of ascending waterfalls and occupying headwater regions far

from the ocean (e.g., Hawaiian *Lentipes*). Goby systematists include among their ranks the Emperor of Japan (e.g., Akihito 1986).

The remaining gobioids are mostly small, eel-like, tropical marine fishes that live on or in sand. The **microdesmid** wormfishes are similar to kraemeriids, burrowing in sand and mud. The related, spectacularly colored **ptereleotrids** are also known as hover gobies, dartfishes, or firefishes, names which describe their coloration and their habit of hovering above the bottom and diving rapidly into a burrow when disturbed. The **schindleriid** infantfishes are an enigmatic family of three species of small (2 cm) pelagic fishes that are neotenic or paedomorphic, which means that they are essentially adults that retain larval traits or larvae that have developed functional gonads. Retained larval characteristics in schindleriids include a larval-type kidney (pronephros), lack of pigmentation, and unossified skeleton. The extremely small size of many gobioids may represent convergent neotenic pathways (Johnson & Brothers 1993). Many fish families contain species that have evolved through heterochronic alterations in developmental sequences (see beloniforms above and Chapter 10); an example analogous to schindleriids involves nettastomatid duckbill eels, in which the leptocephalus larvae possess developed ovaries (Castle 1978).

Suborder Kurtoidei

Suborder Kurtoidei (two species): Kurtidae (nurseryfishes)

The **kurtids** of the Indo-Malay and northern Australia regions are interesting because of the peculiar manner in which males care for the eggs. Males have a hooklike growth of the supraoccipital crest on the top of their heads to which the eggs are attached and where they are carried until hatching (see Fig. 21.9). The means of attachment and time at which fertilization occurs are apparently unknown (Berra & Humprey 2002).

Suborder Acanthuroidei

Suborder Acanthuroidei (129 species): Ephippidae (spadefishes), Scatophagidae (scats), Siganidae (rabbitfishes), Luvaridae (louvar), Zanclidae (moorish idol), Acanthuridae (surgeonfishes)

This suborder contains, with one exception, a group of medium-sized, compressed fishes with small mouths that usually form shoals over coral reefs or in nearby habitats. The **ephippid** spadefishes (e.g., *Chaetodipterus*, western Atlantic) and batfishes (e.g., *Platax*, Indo-Pacific) are conspicuous inhabitants of drop-offs and passes around reefs, although young spadefishes also frequent sandy beaches along the Atlantic coast of the USA. Juveniles of both genera look and act remarkably like floating leaves, and juvenile batfishes are popular in the aquarium trade. Their growth to large size however makes them less desirable pets, prompting aquarists to release Indo-Pacific batfishes into south Florida (Semmens et al. 2004). The **scatophagid** scats bear a slight resemblance to serrasalmine piranhas, but as their name implies, their feeding habits tend more toward feces and detritus than to live prey. They are inhabitants of estuaries and the lower portions of rivers in the Indo-Pacific, where they are reputed to hang out near sewage outfalls. Rabbitfishes (**Siganidae**) are reef, grassbed, and estuarine herbivores with a unique pelvic formula of I, 3, I, reflecting the hard spine at either edge of the fin. Rabbitfishes are in fact very spiny fishes, their first dorsal spine projecting forward rather than upward, and many of the spines possessing a painful toxin (the forward projecting spine frequently impales the uninitiated fisher). Although most rabbitfishes are countershaded species that shoal in seagrass and mangrove areas, reef-dwelling species such as the Fox-face, *Lo vulpinus*, converge in coloration and habitat with butterflyfishes and even form apparently monogamous pairs, as happens in several butterflyfishes. The monotypic louvar, *Luvarus imperialis* (**Luvaridae**), is a pelagic derivative of the suborder (see Fig. 2.1). It is a large (to 1.8 m, 140 kg), non-shoaling fish with extremely high fecundity, a large female containing nearly 50 million eggs. Louvars converge with the pelagic scombroids (see below) in having a lunate tail and a lateral keel on the caudal peduncle, and the posteriorly set dorsal and anal fins resemble the finlets of the tunas and mackerels. The head shape looks more like a dolphinfish, another pelagic species. Louvars feed on jellyfishes, salps, and ctenophores.

The Moorish Idol, *Zanclus canescens* (**Zanclidae**) is another monotypic species related to the surgeonfishes. It is a strikingly shaped and colored Indo-Pacific and eastern Pacific reef fish that is remarkably convergent with butterflyfishes in body form, coloration, and behavior, including elongate dorsal spines and projectile horns above the eyes, as in the butterflyfish genus *Heniochus*. The 80 species of **acanthurid** surgeonfishes, unicornfishes, and tangs are most easily distinguished by the knifeblade present on the caudal peduncle. This blade is a modified scale and can exist as fixed, laterally projecting plates in *Prionurus* and the unicornfish genus *Naso*, or as single, forward-projecting knives that are exposed as the fish flexes its body. The blade is

often covered with a toxic slime, the strength of the toxin apparently directly related to the length of the blade. The peduncular blade makes surgeonfishes among the few fishes that should not be grasped by the tail. Unicornfishes derive their name from a long bony protuberance on the head of some species that serves an unknown function. Surgeonfishes are often beautifully colored fishes, the color changing with age. As a group they are herbivorous (except for planktivorous unicornfishes); species differ in dentition, jaw mechanics, and the body angles at which they remove algae from the reef.

Suborder Xiphioidei

Suborder Xiphioidei (10 species): Xiphiidae (swordfish), Istiophoridae (billfishes)

Chief predators on even relatively large tunas are the temperate and warm temperate **xiphiid** Swordfish, *Xiphias gladius*, and the more tropical **istiophorid** sailfishes, spearfishes, and marlins (*Istiophorus*, *Tetrapturus*, *Kejikig*, and *Makaira*). The suborder includes some of the fastest and largest predators in the sea. The bill in both groups consists of an expanded premaxillary bone that is depressed and smooth in the swordfish and more rounded and prickly in marlins and their relatives. Other differences include no pelvic fins, a single caudal keel, and relatively stiff, sharklike pectoral, dorsal, and anal fins in the swordfish. The istiophorids in contrast have long pelvic filaments, flexible pectorals, double keels, and a long, depressible spiny dorsal that reaches its extreme expression in the sail of the sailfish, a structure of debated function. Controversy has also raged over how and whether billfishes utilize their bill for feeding, but recent observations indicate it can serve as a spear or as a cutlass or billy (see Box 19.1). Billfishes have independently evolved cranial endothermy (see Chapter 7, Heterothermic fishes; Chapter 18, The open sea). Swordfish attain sizes of 530 kg, whereas both Blue and Black marlin grow to 900 kg.

Suborder Scombroidei

Suborder Scombroidei (114 species): Scombrolabracidae (longfin escolar), Gempylidae (snake mackerels), Trichiuridae (cutlassfishes or hairtails), Scombridae (mackerels, Spanish mackerels, tunas)

Scombroids (Orrell et al. 2006) include some of the largest and most economically valuable predators in the sea, namely the tunas. The suborder is characterized by a nonprotractile mouth in more advanced groups, a secondary modification given the general trend in teleosts towards increasing protrusibility. Several families have independently evolved some form of endothermy and heat conservation (see Chapter 7, Heterothermic fishes; Chapter 18, The open sea).

The monotypic *Scombrolabrax heterolepis* (**Scombrolabracidae**) is a peculiar 30 cm long deep water oceanic fish with a protractile jaw and a unique gas bladder arrangement that includes numerous bubblelike projections that fit into depressions of expanded vertebral accessories. The **gempylid** snake mackerels include 24 species of pelagic and deep water predators characterized by an elongate body, large mouth with long teeth, a long spiny dorsal fin, and a series of dorsal and ventral finlets just ahead of the tail. The family includes the cosmopolitan Oilfish, *Ruvettus pretiosus*, a large (1.8 m, 45 kg) predator of moderate depths. It is sometimes referred to as the castor-oil fish because of the purgative quality of its meat. An active fishery for Oilfish in the Comoro Islands off eastern Africa captures endangered Coelacanths as bycatch (see Chapter 13, The living Coelacanths, at least for now). The **trichiurid** cutlassfishes look like very compressed, silvery snake mackerels that have lost their pelvic fins, most of their anal fin, finlets, and most of the tail. The fanglike teeth belie a diet of large zooplankton, at least in smaller individuals. Trichiurids can be remarkably abundant and constitute major fisheries. The Largehead Hairtail, *Trichiurus lepturus*, consistently ranks in the top 10 in global fishery landings, averaging 1.5 million metric tons annually (FAO 2004).

The **scombrid** mackerels and tunas are highly adapted for a mobile, open sea existence in terms of anatomy, physiology, and behavior (Fig. 15.25; see Chapter 18, The open sea). Primitive members of the group, such as the mackerels and Spanish mackerels and relatives (*Scomber*, *Scomberomorus*, and the wahoo, *Acanthocybium*) tend to live closer to shore, whereas advanced members are highly pelagic and nomadic. Although chiefly a tropical and subtropical family, several species move into cold waters for feeding. Sizes range from relatively small, 50 cm mackerels (*Scomber*, *Auxis*) to the giant Bluefin Tuna, *Thunnus thynnus*, at >3 m and 650 kg. Most are schooling fishes of tremendous commercial importance (e.g., Sharp & Dizon 1978). Several tuna species are overfished, especially the three bluefin species (Bluefin, *T. thynnus*; Pacific Bluefin, *T. orientalis*, and Southern Bluefin, *T. maccoyii*), which have been depleted throughout their ranges because of their extreme economic value (Collette 1999; Maggio 2000; Safina 2001b). In 2001, a single 200 kg Bluefin Tuna caught off northern Japan sold at the Tsukiji Central Fish Market in Tokyo for US$173,600 (= $860/kg or $390/lb) (Associated Press 2001).

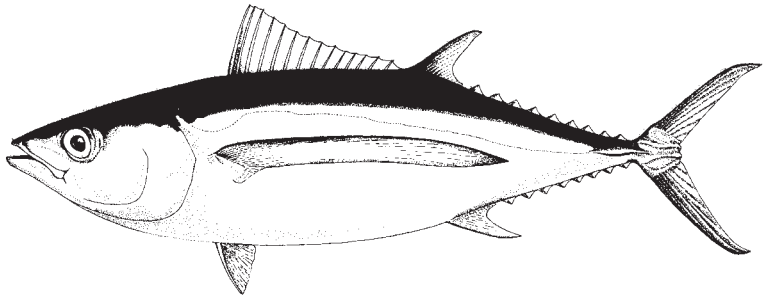


Figure 15.25
A scombrid, the Albacore, *Thunnus alalunga*. From Briggs (1974), used with permission of McGraw-Hill, Inc.

Suborder Stromateoidei

Suborder Stromateoidei (70 species): Amarsipidae (amarsipas), Centrolophidae (medusafishes), Nomeidae (driftfishes), Ariommatidae (ariommatids), Tetragonuridae (squaretails), Stromateidae (butterfishes)

Stromateoids are generally tropical and warm temperate fishes of the open sea that often associate as juveniles with floating or swimming objects, particularly with siphonophores and jellyfishes. A characteristic of the suborder is a thick-walled sac in the pharyngeal region that contains "teeth" made from hardened papillae. **Centrolophid** medusafishes bear a superficial resemblance to the icosteid ragfish. **Nomeid** driftfishes, as the name implies, hover around and under floating logs, siphonophores, jellyfishes, and seaweed as juveniles and occur in deeper water as adults. Juveniles of the Man-of-war Fish, *Nomeus gronovii*, live with impunity amongst and even feed on the stinging tentacles of the Portuguese man-of-war. **Ariommatids** are superficially similar to the carangid scads (i.e., *Decapterus*). The **tetragonurid** squaretails are round fishes encircled by ridged scales and with a long caudal peduncle that has a single keel on either side formed from scale ridges. They feed on pelagic cnidarians and ctenophores which they bite with specialized knifelike teeth. **Stromateid** butterfishes and harvestfishes are round or elliptical in profile with a forked tail and are similar in shape to some carangids; they are sometimes referred to as pompanos, a name more correctly applied to several carangids. As with many open sea groups, butterfishes lack pelvic fins as adults (for unknown reasons).

Suborder Anabantoidei

Suborder Anabantoidei (120 species): Anabantidae (climbing gouramies), Helostomatidae (kissing guoramies), Osphronemidae (gouramies)

Anabantoids are also called labyrinth fishes because of a complexly folded, auxiliary breathing structure derived from the epibranchial of the first gill arch located above the gills in the gill chamber (see Chapter 5, Air-breathing fishes). Functionally, the "suprabranchial organ" is the primary breathing structure for many species, and fish in well-aerated aquaria will die if not allowed to gulp air at the surface. In most anabantoids, the male exhales a nest of mucous-covered bubbles among which eggs are laid and which he guards. **Anabantid** climbing gouramis or climbing perches are African and Asian freshwater fishes that derive their name from their ability to move across wet ground (and supposedly even up wet tree trunks), jerking along by thrusts from the tail while the pectoral fins and gill covers act as props. The Kissing Gourami, *Helostoma temmincki*, is the sole member of the family **Helostomatidae**. The peculiar kissing behavior of this species is derived from its feeding habits that involve scraping algae from surfaces using horny teeth on distinctive lips. The function of kissing, in which two individuals repeatedly press their open mouths against each other, is poorly understood.

The family **Osphronemidae** is divided into four subfamilies and 86 species. The osphronemine Giant Gouramy, *Osphronemus goramy*, reaches 80 cm in length and is a popular food fish that is cultured throughout Southeast Asia. Its air-breathing abilities make keeping it alive in fish markets easy. The Macropodinae includes the Siamese fighting fishes and paradisefishes. Bettas (Siamese Fighting Fish, *Betta*) are used extensively in behavioral and genetic studies. Males are exceedingly pugnacious towards each other. They are bred and fought like fighting cocks, making them one of the few fishes cultured for reasons other than food, appearance, or research. Fights to the death in the confines of an aquarium do not reflect real-life situations where a subordinate fish can flee from a dominant. Luciocephalines in the genus *Colisa* shoot water droplets at terrestrial insects, in a manner analogous to that of the toxotid archerfishes (Dill 1977a). The luciocephaline Pikehead, *Luciocephalus pulcher*, is an elongate stalking predator on small fishes with a body form characteristic of other such piscivores (elongate jaws, slender body, dorsal and anal fins set far back on body, rounded tail; see Chapter 8, Locomotion: movement and shape; Chapter 19, Attack and capture).

As befits an advanced percomorph, Pikeheads have the most protrusible mouth of any teleost. When feeding, the mouth is shot forward rapidly, surrounding the prey. Pikeheads have an interesting bone in the gular region of their throats that is analogous to the gular plate(s) of the primitive coelacanth, Bowfin, bichirs, and some elopomorphs; whether this reinvented gular bone functions in oral incubation of eggs or in mouth protrusion is unclear (Liem 1967).

Suborder Channoidei

Suborder Channoidei (29 species): Channidae (snakeheads)

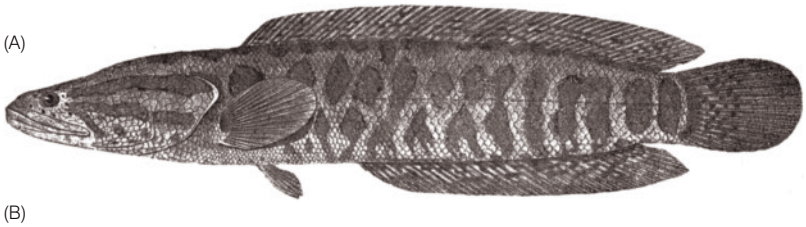
Snakeheads (**Channidae**) are highly predatory freshwater fishes of tropical Asia and Africa. They have a suprabranchial breathing organ reminiscent of that of the anabantoids and are primarily swamp dwellers. The robust, elongate bodies, long dorsal and anal fins, and ringed eyespot on the caudal peduncle give some channids a superficial resemblance to a Bowfin (Fig. 15.26). Some snakeheads reach over 1.8 m in length and 20 kg in mass and are prized food fishes. Small species and young individuals of larger species are sold in the pet trade, and live individuals are sold as food fish. Because they grow large and are predatory, or because people want to establish desirable food species outside their native range despite the ecological consequences, snakeheads have been released into the wild in numerous Asian and North American locales and are reproducing at least in Florida, Hawaii, and Maryland (Fuller et al. 1999; Courtenay & Williams 2002). Courtenay and Williams (2002) analyzed the potential negative impact snakeheads could have in regions where they are or were likely to become established and concluded the potential for significant ecological harm was high. Snakehead importation and transfer across state lines is now illegal in the USA.

Suborder Caproidei

Suborder Caproidei (11 species): Caproidae (boarfishes)

Our treatment of perciforms ends appropriately with an enigmatic group whose exact placement remains something of a puzzle. In many earlier treatments, the **caproid** boarfishes were thought to be pre-perciforms, most closely allied with the zeiform dories, which they resemble. Some recent analyses retain that analysis (e.g., Tyler et al. 2003) whereas others consider them an advanced perciform, a decision Nelson (2006) follows but with uncertainty. These are medium-sized (to 30 cm), reddish, deep-bodied, rhomboid, schooling fishes of moderate depths (50–600 m).

(A)



(B)

Fig. 15.26

Snakeheads. (A) The Northern Snakehead, *Channa argus*. This Southeast Asian native was established in a pond in Maryland in 2002. (B) The Giant Snakehead, *Channa micropeltes*, a large (up to 1 m and 20 kg) freshwater predator of Southeast Asian still waters. (A) from Courtenay and Williams (2002); (B) photo by Jean-Francois Healias, Fishing Adventures Thailand, www.anglingthailand.com.

Series Percomorpha: advanced percomorph orders – flatfishes and twisted jaws

Order Pleuronectiformes

Order Pleuronectiformes (678 species): Psettodidae (spiny turbots), Citharidae (largescale flounders), Scophthalmidae (turbots), Paralichthyidae (sand flounders), Pleuronectidae (righteye flounders), Bothidae (lefteye flounders), Paralichthodidae (measles flounders), Poecilopsettidae (bigeye flounders), Rhombosoleidae (rhombosoleids), Achiropsettidae (southern flounders), Samaridae (crested flounders), Achiridae (American soles), Soleidae (soles), Cynoglossidae (tonguefishes)

Flatfishes are distinctive, compressed acanthopterygians that all share certain features, most noticeably a marked asymmetry that includes having both eyes on the same side of the head in juveniles and adults (Fig. 15.27). Flatfishes begin life as bilaterally symmetrical, pelagic fishes but during the larval period or shortly thereafter, one eye migrates to the other side and the fish settles to the bottom, lying on its blind, more flattened side (see Chapter 10, Complex transitions: smoltification in salmon, metamorphosis in flatfish). Eye movement is made more complicated by the position of the anterior portion of the dorsal fin, which often originates above or ahead of the eyes. Teeth, scales, paired fins, and pigmentation also typically differ between sides. Families are generally either right-eyed or left-eyed defined by which eye stays put. Flatfishes are benthic, carnivorous, marine fishes (with perhaps 10 freshwater derivative species) that lack a gas bladder; most live in shallow to moderate depths in Arctic, temperate, and tropical locales. Some species are able to change the coloration of the eyed side to match the shading pattern of the background upon which they rest. Flatfishes constitute important fisheries for forms known as dab, flounders, halibuts, plaice, sole, tonguefishes, turbots, and whiffs. Approximately 500 of the 678 species are in five large families. Ancestral, intermediate, and closely related forms to flatfishes are not known and the fossil record is limited.

The primitive **psettotid** spiny turbots show the least movement of the eye during metamorphosis. The **Paralichthyidae** include the Summer Flounder (*Paralichthys dentatus*) and California Halibut (*P. californicus*), the latter species reaching a size of 1.5 m and 30 kg. The **pleuronectid** righteye flounders include the larger halibuts such as the Atlantic and Pacific halibuts. Females of the Pacific species, *Hippoglossus stenolepis*, may live 40 years and reach barndoor proportions of 3 m long and 200 kg mass, but may not mature until they are 16 years old. The fishery for Pacific Halibut, unlike that of the depleted Atlantic species, is one of the better managed fisheries in the world. Several other commercially important flatfish species are pleuronectids, including the Arrowtooth Flounder, Petrale Sole, Rex Sole, Winter Flounder, Yellowtail Flounder, and English Sole. Among the **bothid** lefteye flounders is the Peacock Flounder (*Bothus lunatus*) of the Caribbean. An **achirid** American sole, the Hogchoker, *Trinectes maculates*, commonly invades rivers of Florida and the Atlantic coast of the USA. The true soles however are in the family **Soleidae**, which are usually right-eyed. Among the soleids is the Red Sea Moses Sole, *Pardachirus marmoratus*, which exudes a toxin, pardaxin, reported to be a natural shark repellant. The Common Sole, *Solea solea*, of European waters is reported to raise its black-tipped pectoral fin when disturbed in an action that mimics the raising of the dorsal fin of venomous trachinid weeverfishes. The **cynoglossid** tonguefishes are the most elongate of the flatfishes and also show considerable variation in habitat, including shallow water and burrowing forms (e.g., Blackcheek Tonguefish,

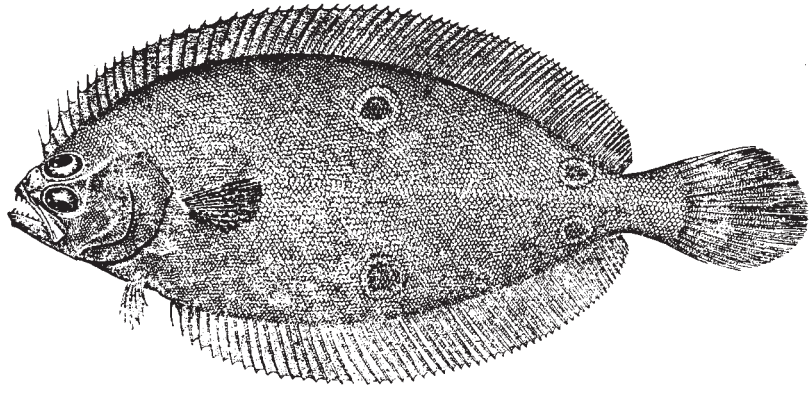


Figure 15.27
A pleuronectiform, the bothid Fourspot Flounder, *Paralichthys oblongus*. Drawn by H. L. Todd in Collette and Klein-MacPhee (2002).

Symphurus plagiusa), several species that occur as deep as 1900 m, as well as purely freshwater forms (three species from Indonesia).

Order Tetraodontiformes

Order Tetraodontiformes (357 species): Triacanthodidae (spikefishes), Triacanthidae (triplespines), Balistidae (triggerfishes), Monacanthidae (filefishes), Ostraciidae (boxfishes, trunkfishes, cowfishes), Triodontidae (three-toothed puffer), Tetraodontidae (puffers), Diodontidae (porcupinefishes, burrfishes), Molidae (molas, ocean sunfishes)

The pinnacle of teleostean evolution is reached among the highly derived fishes of the order Tetraodontiformes. The name refers to the common pattern of four teeth in the outer jaws of puffers (an alternative name, Plectognathi, means twisted jaw). Tetraodontiforms are characterized by a high degree of fusion or loss of numerous bones in both the head and body. In the head region, such bones as the parietals, nasal, infraorbital, and posttemporal are commonly missing, both hyomandibular and palatine bones may be firmly attached to the skull, and the maxilla is fused to the premaxilla. The pelvic fins and lower vertebral ribs are often missing and the vertebral number is reduced from the common acanthopterygian condition of 26 to as little as 16. The skin has a thick, leathery feel and is covered by scales that are modified into spines, bony plates, or ossicles, some of rather spectacular proportions. Tetraodontiforms tend to eat animals that are generally unavailable to most other reef fishes, such as sponges, sea urchins, hard corals, and jellyfishes. Some are predators on sessile benthic invertebrates (triggerfishes, puffers), others are water column swimmers above the reef that feed on zooplankton (Black Durgon Triggerfish), and some are large, offshore planktivorous species (Gray Triggerfish; Fig. 15.28A) or jellyfish feeders (Ocean Sunfish). All but 20 species are marine. Even though tetraodontiforms are recognized as the most

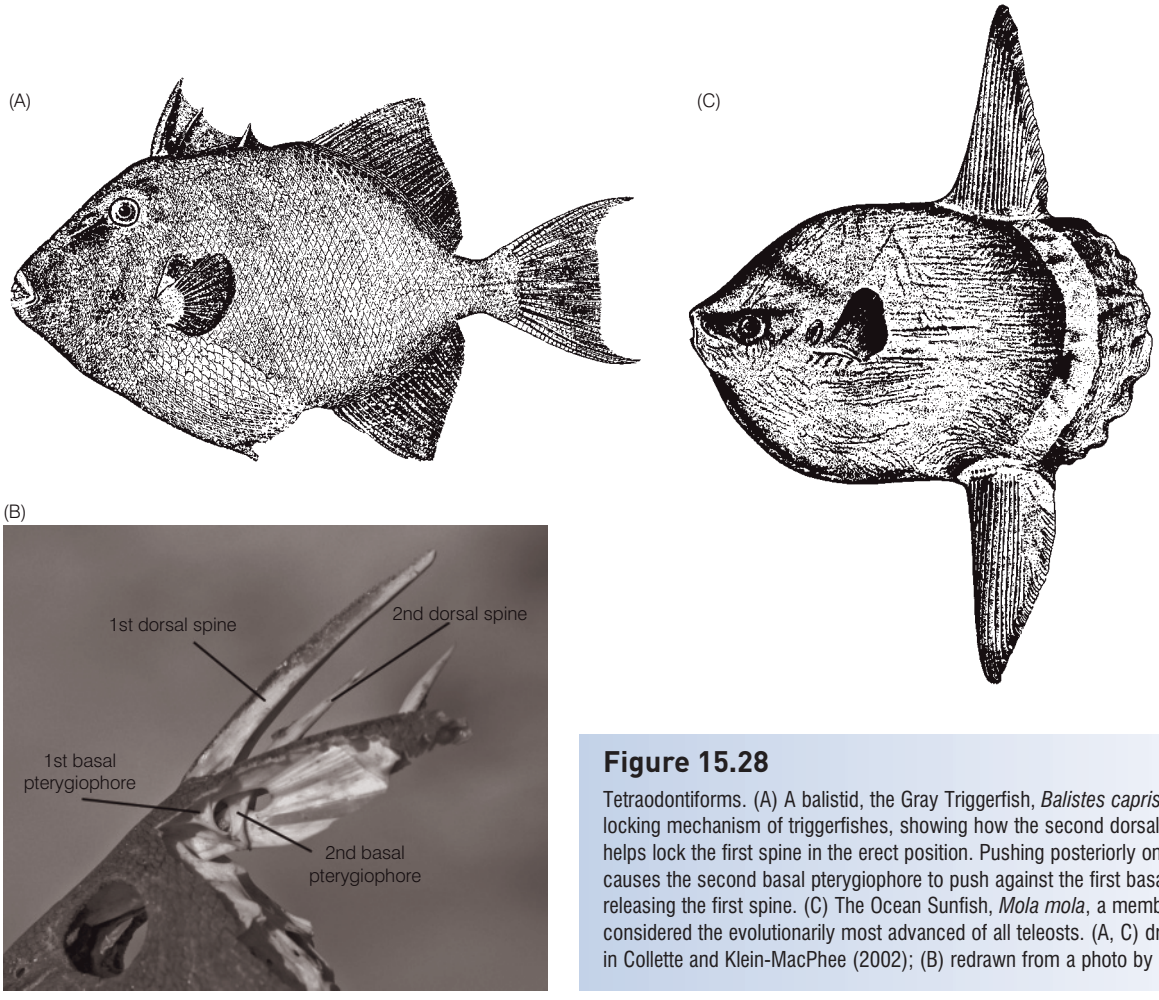


Figure 15.28

Tetraodontiforms. (A) A balistid, the Gray Triggerfish, *Balistes capriscus*. (B) The spine-locking mechanism of triggerfishes, showing how the second dorsal spine fits into and helps lock the first spine in the erect position. Pushing posteriorly on the second spine causes the second basal pterygiophore to push against the first basal pterygiophore, releasing the first spine. (C) The Ocean Sunfish, *Mola mola*, a member of the family considered the evolutionarily most advanced of all teleosts. (A, C) drawn by H. L. Todd in Collette and Klein-MacPhee (2002); (B) redrawn from a photo by G. Helfman.

advanced of the teleosts, the fossil record for the group goes back at least to the Early Eocene and quite likely the Late Cretaceous, once again pointing out that modern bony fishes have a long evolutionary history.

The superfamily of leatherjackets (Balistoidea) contains the triggerfishes (**Balistidae**) and the filefishes (**Monacanthidae**). In many species, the first dorsal spine is particularly long and stout and can be locked in the erect position via an interaction with the second spine (Fig. 15.28B). The base of the smaller second spine protrudes forward and fits into a groove on the posterior edge of the first spine, locking the first spine into position. Depressing the second spine releases the lock, hence the name triggerfish. Sound production in this group is common, produced by grinding of the teeth or vibration of the gas bladder via the pectoral spine; the legendary Hawaiian name for the triggerfishes *Rhinecanthus aculeatus* and *R. rectangulus* is *humuhumu nukunuku apua'a*, which means "the fish that sews with a needle and grunts like a pig". These fishes can also rotate their two eyes independently. In the **ostraciid** boxfishes, the entire body except the fins and caudal peduncle are encased in a bony box, which is triangular or rectangular in cross-section. Stout spines sometimes protrude anteriorly just above the eyes and posteriorly just ahead of the anal fin. Swimming is accomplished via undulations of median fins (see Chapter 8, Locomotory types).

The suborder Tetraodontoidei contains the puffers and ocean sunfishes. Ironically, and despite family names focused on dentition, these fishes lack true teeth. Instead the jaw bone itself has a cutting edge that differentiates into separated teeth or is fused as a parrotlike beak. Puffers are able to inflate their body by filling the stomach with water (see Box 20.1). Three families of puffers are generally recognized based on the number of toothlike structures in each jaw: a single three-toothed species (**Triodontidae**), the smooth and sharpnose puffers with four teeth (**Tetraodontidae**), and the spiny puffers, burrfishes, and porcupinefishes with two fused teeth (**Diodontidae**). Tetraodontids have prickly skin. Because of bone loss and fusion, tetraodontids produce tasty, boneless fillets, but many species concentrate a powerful toxin, tetraodotoxin, in their viscera which can cause death in humans. Specially licensed and supervised *Fugu* restaurants in Japan serve the meat of puffers of the genus *Takifugu*, which contains small amounts of the toxin and provides a narcotic high. Despite such chemical protection, pufferfishes are commonly eaten by sea snakes. The few freshwater members in the order are tetraodontids. Diodontids have spines of varying length that are erected when the fish inflates, creating a large, round, and essentially inedible pincushion.

The most advanced tetraodontiforms and teleosts are the four species of very unfishlike appearing, temperate and tropical molas (**Molidae**). The body is essentially rectangular in side view with very tall, thin dorsal and anal fins that propel the fish (Fig. 15.28C). They lack a true tail but instead have a "pseudocaudal" tail fin made up primarily of dorsal and anal fin rays. The Ocean Sunfish, *Mola mola*, gets to be 3 m long, 4.2 m high, and may weighs as much as 2300 kg (www.oceansunfish.org). Fecundities of 300 million eggs have been reported, an apparent record among fishes. Although usually pelagic feeders on jellyfishes, Ocean Sunfishes periodically move inshore to kelp beds off central California, apparently to have external parasites removed by cleanerfishes in the nearshore region.

Interestingly, molas have a large number of cartilaginous elements or cartilage-lined bones in their skull and in their fin supports (Tyler 1980). It is somewhat ironic that such a highly derived group returns anatomically to a starting point in fish evolution, as represented by primitive hagfishes, lampreys, sharks, and chondrosteans with their cartilaginous skeletons. Molas can therefore serve to remind us of several important aspects of the evolutionary process and our attempts to understand it. The task of determining primitive versus advanced traits can be complicated by secondarily derived characteristics, such as a very advanced species with a gular bone (e.g., the luciocephalid pikehead) or with a cartilaginous skeleton (see also the account above for the icosteid ragfish). And also important is that phylogenetically primitive fishes are not necessarily poorly adapted or somehow inferior to more advanced groups; the mola's rediscovery of the utility of cartilage underscores the observation that all living fishes are the successful result of the trial and error processes of mutation and natural selection.

Summary

SUMMARY

1. Most fishes (14,800 species in 267 families) belong to the superorder Acanthopterygii and have highly protrusible jaws, a complex pharyngeal apparatus, two dorsal fins, and spines in the first dorsal, anal, and pelvic fins. Three series are recognized, the Mugilomorpha, Atherinomorpha, and Percomorpha. Mugilomorph mullets are marine and freshwater fishes with unconnected pectoral and pelvic girdles. Atherinomorphs (silversides, needlefishes, flyingfishes, halfbeaks, killifishes, and livebearers) are shallow water, marine or freshwater fishes that live near the surface and have a unique jaw protrusion mechanism.
2. The remaining nine orders are percomorphs. Stephanoberyciforms (whalefishes) and beryciforms (flashlight fishes, roughies, squirrelfishes) live in the moderate to deep sea, except for the reef-dwelling squirrelfishes; most are nocturnal.
3. Gasterosteiforms are small fishes with dermal armor plates, small mouths, and unorthodox propulsion. Pipefish and seahorse males become pregnant, carrying developing embryos in a ventral pouch. Scorpaeniforms are mostly marine, benthic fishes, except for freshwater cottid sculpins; many have head spines and venomous fin spines (e.g., turkeyfishes, stonefishes, scorpionfishes).
4. The largest percomorph order is the Perciformes, with 160 families and 10,000 species, including most marine and freshwater fishes of littoral zones. Perciforms have abdominal pelvic fins, lateral pectoral fins, and fewer than 18 caudal rays. Basal families are in the suborder Percoidei (78 families, 3176 species) including snooks, temperate basses, and the diverse seabasses. Centrarchid sunfishes and percids (darters, perches, pikeperches) are important freshwater percoids of North America. Other percoids include predatory carangoids, such as carangid jacks and pompanos, Cobia, dolphinfishes, and the shark-sucking remoras. Heavy-bodied, tropical, benthic, predatory families (snappers, sparoids) as well as fishes with barbels or feelers (croakers, threadfins, goatfishes) are placed here. Other percoid families include archerfishes that shoot insects out of overhanging vegetation and the colorful coral reef butterflyfishes and angelfishes.
5. The suborder Labroidei has several speciose families. Cichlids are primarily freshwater fishes that have undergone explosive speciation, forming species flocks in Central African lakes. Other labroid families are the primarily tropical damselfishes, wrasses, and parrotfishes, and the temperate surfperches and odacids. Zoarchoids are tidepool and deep ocean, benthic fishes (eel pouts, gunnels, wolf-eels). Notothenioid icefishes dominate the Antarctic and have many adaptations to very cold water. Blennioids (clinids, blennies) and gobioids (sleepers, gobies) are large suborders of generally small, benthic, marine species.
6. The suborder Acanthuroidei includes the spadefishes, rabbitfishes, and surgeonfishes, the latter two being important families of coral reef herbivores. Xiphioids and scombroids (billfishes, mackerels, tunas) are the fastest and largest predatory bony fishes in the sea. Tunas and billfishes have independently evolved endothermy and heat conservation. Stromateoids are also largely pelagic marine fishes that associate with floating objects. The most advanced perciform suborders are the Anabantoidei (gouramies) and Channoidei (snakeheads), which are African and Asian freshwater fishes, many with specialized gill structures for breathing atmospheric oxygen.
7. Pleuronectiform flatfishes begin life as pelagic, symmetrical larvae but metamorphose into adults that lie on the bottom on one side and displace many body organs, most noticeably the eyes. Tetraodontiforms are primarily tropical reef dwellers, including triggerfishes, boxfishes, puffers, and porcupinefishes. They often have beaklike jaws, many fused skull and axial bones, and spiny, leathery skin. The most advanced tetraodontiforms are the Giant Ocean Sunfishes, which have a surprising amount of cartilage in their skeletons.
8. Although potentially frustrating to students and non-systematists, relationships among acanthopterygians are a matter of active research and equally active debate. Many groups are only provisionally placed in the acanthopterygian phylogeny, and much remains to be learned about this, the most successful and speciose group of modern vertebrates.

Supplementary reading

SUPPLEMENTARY READING

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Figure IV *(opposite)*

A recently discovered 10 cm long Indonesian antennariid, nicknamed the Psychedelic Frogfish (Lophiiformes: Antennariidae) (Chapters 14, 18). Among its atypical traits are its shallow water habitat, lack of an illicial lure, jet propulsion and bouncing method of movement, and practice of hiding in holes, not to mention the spectacular head and body coloration. See Pietsch et al. (2009). Photo by D. Hall, www.seaphotos.com.

PART IV

Zoogeography, genetics, and adaptations

Chapter 16

Zoogeography

Chapter contents

CHAPTER CONTENTS

Fishes live almost everywhere water occurs, but even a casual glance at species lists from different localities demonstrates that few places have the same kinds of fishes. The challenge then becomes one of discerning patterns in the present distribution of different species, genera, families, and higher taxa, and then trying to understand how these patterns are related to the evolution of the different groups. Basically, we are asking how and why fish faunas differ and how different fishes got where they are today. These questions form the basis of the science of zoogeography.

Historically, the study of fish distribution in the major zoogeographic regions has been divided into marine and freshwater components. Marine fishes comprise about 58% of the approximately 28,000 species of fishes, whereas freshwater fishes make up about 41% (Fig. 16.1).

Marine fishes

Although terrestrial humans refer to our planet as earth, it is really Planet Ocean. Not only is 71% of the planet's surface covered with water, but because water supports life from the surface down to the oceans' greatest depths of 11,000 m, the total oceanic living volume is 300 times greater than the terrestrial. Anyone first observing our planet from outer space would be struck by this and surely would name the planet for its blue water cover, unique in the solar system.

Much recent attention has been directed at biodiversity (the numbers of species present) in tropical rainforests. The huge biodiversity in tropical areas is accounted for largely by radiation of one group, the insects. If we turn to the sea, we may not find as many total species, in part because insects have not diversified there. However, at the level of **phyletic diversity** (numbers of different phyla present), the seas support a greater animal biodiversity than does land. Of 33 animal phyla, 32 occur in the sea, and 15 of these are exclusively marine (Norse 1993).

Major ecological divisions

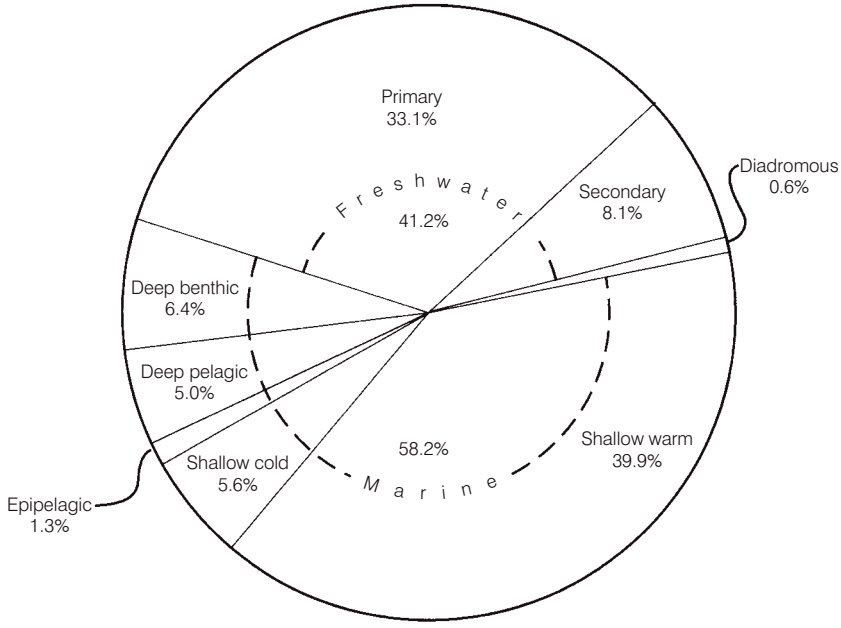
Four main ecological divisions are recognized among the 16,000+ species of marine fishes:

1. **Epipelagic** fishes, which dwell from the surface down to 200 m, make up 1.3% of the total, or about 360 species.
2. **Deep pelagic** fishes include about 1400 species, or about 5% of the total. These water column dwelling fishes can be further subdivided into **mesopelagic** fishes, which live between 200 and 1000 m, and deeper dwelling **bathypelagic** fishes.
3. **Deep benthic** fishes comprise about 1800 species, or 6.4% of the total.
4. **Littoral or continental shelf** species are shallow-dwelling fishes that inhabit the shore and shelf above 200 m. They are the largest group, constituting 45% of the total, or about 12,600 species.

Epipelagic fishes

The diversity and adaptations of surface-dwelling fishes are treated in Chapter 18 (The open sea), so attention here will focus on their zoogeography. Many epipelagic species are worldwide in distribution. However, many inshore epipelagic species have more restricted distributions. One member of a family may be confined to one side of an ocean and be represented by another, allopatric species (a closely

Figure 16.1
Percentages of Recent fish species living in various habitats. From Cohen (1970).



related species not occurring in the same area), living on the other side of the ocean.

As examples, consider the distribution patterns of some tunas (Scombridae), halfbeaks (Hemiramphidae), and needlefishes (Belonidae). Most species of tunas of the genus *Thunnus* are widespread offshore. Several species, including Albacore (*T. alalunga*), Yellowfin (*T. albacares*), and Bigeye (*T. obesus*) have continuous distributions, indicating that genetic interchange occurs among populations in the Atlantic, Indian, and Pacific oceans. Little tunas of the genus *Euthynnus* have a different distribution pattern, more closely associated with the shore. One species occurs in the Atlantic (*E. alletteratus*), one in the Indo-West Pacific (*E. affinis*), and one in the eastern Pacific (*E. lineatus*). Among Spanish mackerels, *Scomberomorus*, distributions of species are even more shore associated, with allopatric species in the Atlantic, Indo-West Pacific, and eastern Pacific (Collette & Russo 1985b).

Turning to halfbeaks (Hemiramphidae), species of the genus *Hemiramphus* are more widespread than species of the more inshore genus *Hyporhamphus*. For example, two species of *Hemiramphus* are found on both sides of the Atlantic, and one species (*He. far*) is widespread throughout the Indo-West Pacific (and has even invaded the eastern Mediterranean Sea through the Suez Canal). In contrast, all species of *Hyporhamphus* in the western Atlantic differ from those in the eastern Atlantic, Indo-West Pacific, and eastern Pacific.

Similarly, needlefishes (Belonidae) of the genera *Ablennes* and *Tylosurus* are much more widespread than species of the genus *Strongylura* (Cressey & Collette 1970). *Ablennes* is worldwide, and two species of *Tylosurus* (*T. acus* and *T. crocodilus*) are nearly worldwide, with different subspecies recognized in parts of their ranges. Species of *Strongylura* are more numerous and have more restricted distributions, like species of *Hyporhamphus*.

Distributions of epipelagic inshore fishes may be limited by temperature, either directly or indirectly. For example, for needlefishes (Fig. 16.2), a clear relationship exists between temperature and the northernmost and southernmost distribution records of species of *Strongylura*.

Deepwater fishes

Many species of deep water fishes (see Chapter 18, The deep sea) are also widespread. In looking at their distributions, we cannot rely on surface maps, because ocean basins may have underwater **sills**, ridges that act as barriers to the distribution of deep water fishes. Sills act as barriers because they physically inhibit the movement of fishes and they also restrict the mixing of waters. For example, the Mediterranean Sea is continuous with the Atlantic Ocean at the surface via the 12.9 km wide Straits of Gibraltar. However, at 1200 m, the Mediterranean Sea is 14°C, whereas the adjacent Atlantic Ocean is 2.5°C at the same depth and these depths are interrupted by a 286 m deep sill. Another sill at 350 m separates the western from the eastern Mediterranean at the Strait of Sicily (Patarnello et al. 2007). Similarly, the Red Sea is 23°C at 125 m, whereas the Indian Ocean is 2.5°C at the same depth, but the two areas are separated by a shallow sill. Deep water fishes adapted to the cool temperatures of the Atlantic and Indian oceans may not be able to penetrate the Mediterranean and Red seas because they cannot tolerate the warm temperatures at the sill that separates the ocean from the adjacent sea.

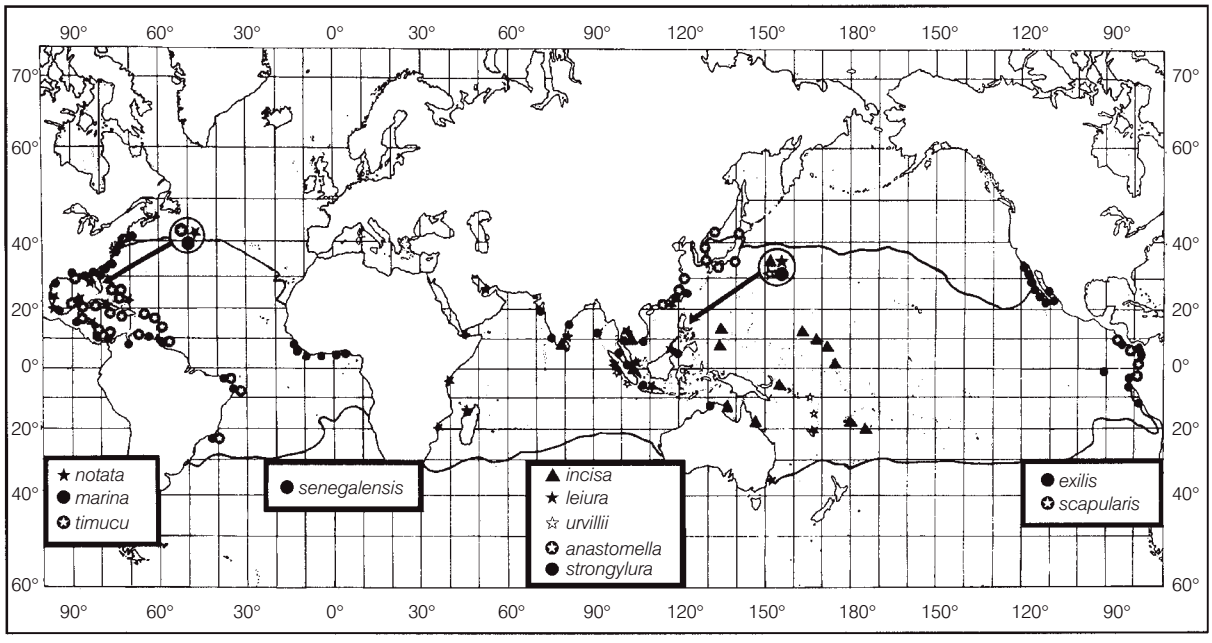


Figure 16.2

Distribution of marine populations of 11 species of needlefishes of the genus *Strongylura* in relation to the 23.9° isothere. Adapted from Cressey and Collette (1970).

Littoral fishes

Temperature is also a major limiting factor for the distribution of shallow water fishes. The greatest diversity of marine fish species is in tropical waters. Part of this great biodiversity is associated with the coral reefs that provide habitat for the fishes and their prey. Reef-building corals are restricted to depths above 100 m in clear waters warmer than 18°C; corals reach their maximum extent at 23–25°C. Common groups of coral reef fishes include moray eels (Muraenidae); squirrelfishes (Holocentridae); several families of percoids such as seabasses (Serranidae), grunts (Pomadasyidae and Haemulidae), snappers (Lutjanidae), cardinalfishes (Apogonidae), and butterflyfishes (Chaetodontidae); and some more advanced families such as damselfishes (Pomacentridae), wrasses (Labridae), parrotfishes (Scaridae), gobies (Gobioidei), blennies (Blennioidei), surgeonfishes (Acanthuridae), triggerfishes (Balistidae), and boxfishes (Ostraciidae).

Marine zoogeographic regions

Global biogeographic patterns in the marine environment were outlined by Ekman (1953, but first published in German in 1935) and Briggs (1974, 1995). Briggs' patterns focused on a system of coastal and shelf provinces partly defined by their degree of endemism. A system of 64 large marine ecosystems (LMEs) was developed over recent years by Kenneth Sherman and others. LMEs are relatively large areas of 200,000 km^2 or greater characterized by distinct bathymetry, hydrography, productivity, and trophically dependent populations (Sherman et al. 2005). About 90% of the world's annual yield of marine fisheries is produced within the boundaries of the 64 LMEs. A new global system for coastal and shelf areas, Marine Ecosystems of the World (MEOW), is a hierarchical nested system of 12 realms containing 62 provinces and 232 ecoregions (Spalding et al. 2007).

The simplest division of the distributions of inshore marine fishes is into four major marine regions, in order of decreasing biodiversity: (i) Indo-West Pacific, (ii) western Atlantic, (iii) eastern Pacific, and (iv) eastern Atlantic. These regions are separated from each other either by continents or by large expanses of open ocean, and each has been subdivided into different units by different authors.

Indo-West Pacific region

The Indo-West Pacific region – from South Africa and the Red Sea east through Indonesia and Australia to Hawaii and the South Pacific Islands, all the way to Easter Island – contains about one-third of the species of shallow marine fishes, about 3000 species, compared to no more than 1200 in any other region. Multiple datasets show global maxima of marine biodiversity to be in the Indo-Malay-Philippines Archipelago. Analysis of distribution data for 2983 marine species of fishes, other vertebrates, and invertebrates reveals a pattern of richness on a finer scale and identifies a peak of marine biodiversity in the central Philippine Islands and a secondary peak between peninsular Malaya and Sumatra

(Carpenter & Springer 2005). Biodiversity is also high in many other marine taxa in this region (Briggs 1974). There are approximately 70 genera and about 500 species of hermatypic (reef-building) corals in this region, which is 10 times the number of species present in the western Atlantic (Rosen 1988). Among other groups, the Indo-West Pacific contains about 1000 species of bivalve mollusks (including all the giant clams, Tridacnidae), twice that in the western Atlantic; and 49 of the 50 species of sea snakes (Hydrophiidae), compared to one species in the eastern Pacific. Some families of fishes such as the whitings (Sillaginidae) and rabbitfishes (Siganidae) are endemic to the Indo-West Pacific.

The Pacific Plate (Fig. 16.3) forms a major biogeographic unit of the Indo-West Pacific. The Pacific Plate is the largest of the earth's lithospheric plates (Box 16.1) and occupies most of the area that has been referred to as the Pacific Basin (Springer 1982). The number of taxa decreases sharply as one proceeds eastward across the western margin of the plate. In addition, there is a high degree of endemism on the plate.

An instructive example of the kinds of distributions one finds associated with specific regions and plates occurs with Spanish mackerels of the genus *Scomberomorus* (Collette & Russo 1985b). Of the 18 species in the genus, 10 occur in the Indo-West Pacific, but they are noticeably absent from the Pacific Plate (Springer 1982, fig. 40). One species, *Scomberomorus commerson*, is widespread throughout much of the Indo-West Pacific. This distributional pattern cannot tell us much because, as with plesiomorphic characters (see Chapter 2), widespread species are not as informative about the causes of the distribution patterns as those with more restricted distributions.

In contrast, the ranges of three species, *S. guttatus*, *S. koreanus*, and *S. lineolatus* (Fig. 16.4), stop at the continental margin, at what is known as Wallace's Line (see below under Oriental region). Australia and southern New Guinea, east of Wallace's Line, have a Spanish mackerel fauna that consists of four different species: *S. multiradiatus*, *S. semifasciatus*, *S. queenslandicus*, and *S. munroi*. These four species do not extend into the East Indies or even to the north coast of New Guinea, although they easily could swim that far. This distribution pattern is obviously not simply a result of present ecological factors but instead must be historical, related to the earlier evolution and dispersal of the genus. The present island of New Guinea resulted from the collision of two plates that may have contained two different fish faunas.

Western Atlantic region

The western Atlantic region includes the temperate shores of North America, the Gulf of Mexico, the tropical shores of the Caribbean Sea, and the tropical and temperate shores of South America. Genetic data indicate that two islands, Ascension and St. Helena, once thought to be part of the eastern Atlantic actually show more similarities to Brazil in the western Atlantic. The radiation of tropical shore fishes

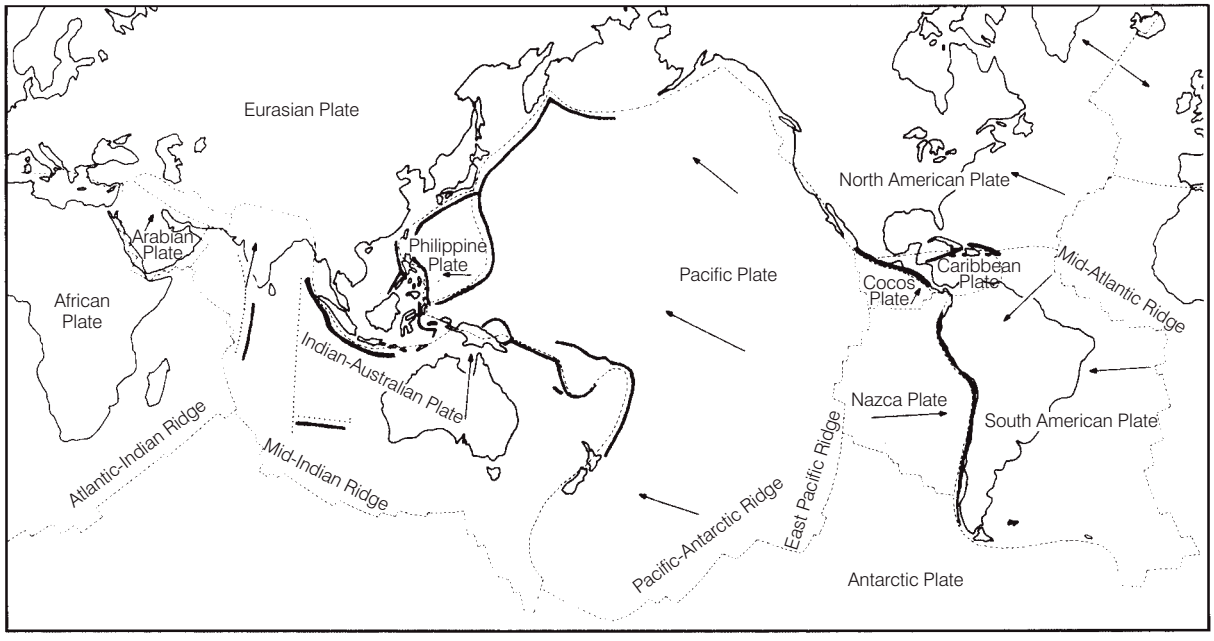


Figure 16.3

The earth's important tectonic features. Dashed lines denote margins of major lithospheric plates; arrows indicate direction of plate movements. Adapted from Springer (1982).

Box 16.1

Continental drift, tectonic plates, and fish distributions

Continents and ocean basins have changed dramatically in location and size during the earth's history. Continents are blocks of largely granitic and sedimentary rocks. Continents "drift" because they literally float on top of the earth's denser basaltic crust. New crust develops at midoceanic ridges as basalt upwells from the earth's mantle. This basalt flows outward, causing spreading of the basaltic seafloor plates and widening of ocean basins. The moving plates carry the overlying continents with them. Crust finally is subducted (dives under) at oceanic trenches and plate margins. The notion of **continental drift** was first formally proposed by Alfred Wegener in 1915 to explain the fit that the west coast of Africa makes with the east coast of South America (Wegener 1966). Wegener's concept was ridiculed by most scientists for many years but has gained acceptance as geophysical and paleontological evidence accumulated.

Understanding the present distributions of fishes and many other taxa requires understanding that the present arrangement of the continents is very different from past arrangements. The present continents were at one time all part of a single landmass, **Pangaea**, which had coalesced by the Silurian (430 million years ago). About 180 million years ago, during the Mesozoic, Pangaea split into a northern portion, **Laurasia** (Eurasia and North America), and a southern portion, **Gondwana**). Gondwana later split into South America, Africa, Australia, and Antarctica about 90 million years ago. Present widespread distributions of several fish taxa, such as lungfishes, osteoglossomorphs, and ostariophysans (see below), may well have been formed when the southern continents were still connected, before the breakup of Gondwana.

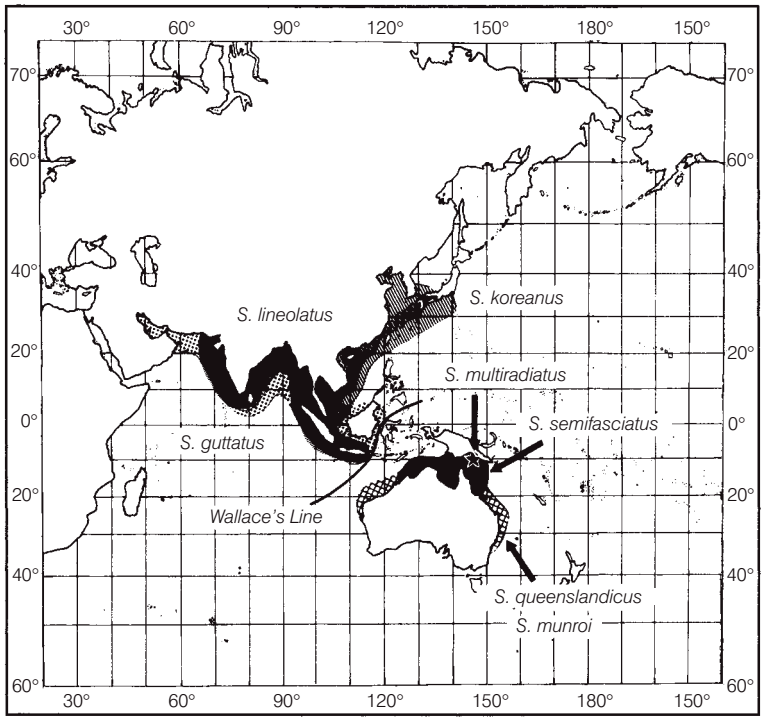


Figure 16.4

The ranges of seven Indo-West Pacific species of Spanish mackerels (*Scomberomorus*), three continental and four Australian, with reference to Wallace's Line delimiting the continental margin. Adapted from Collette and Russo (1985b).

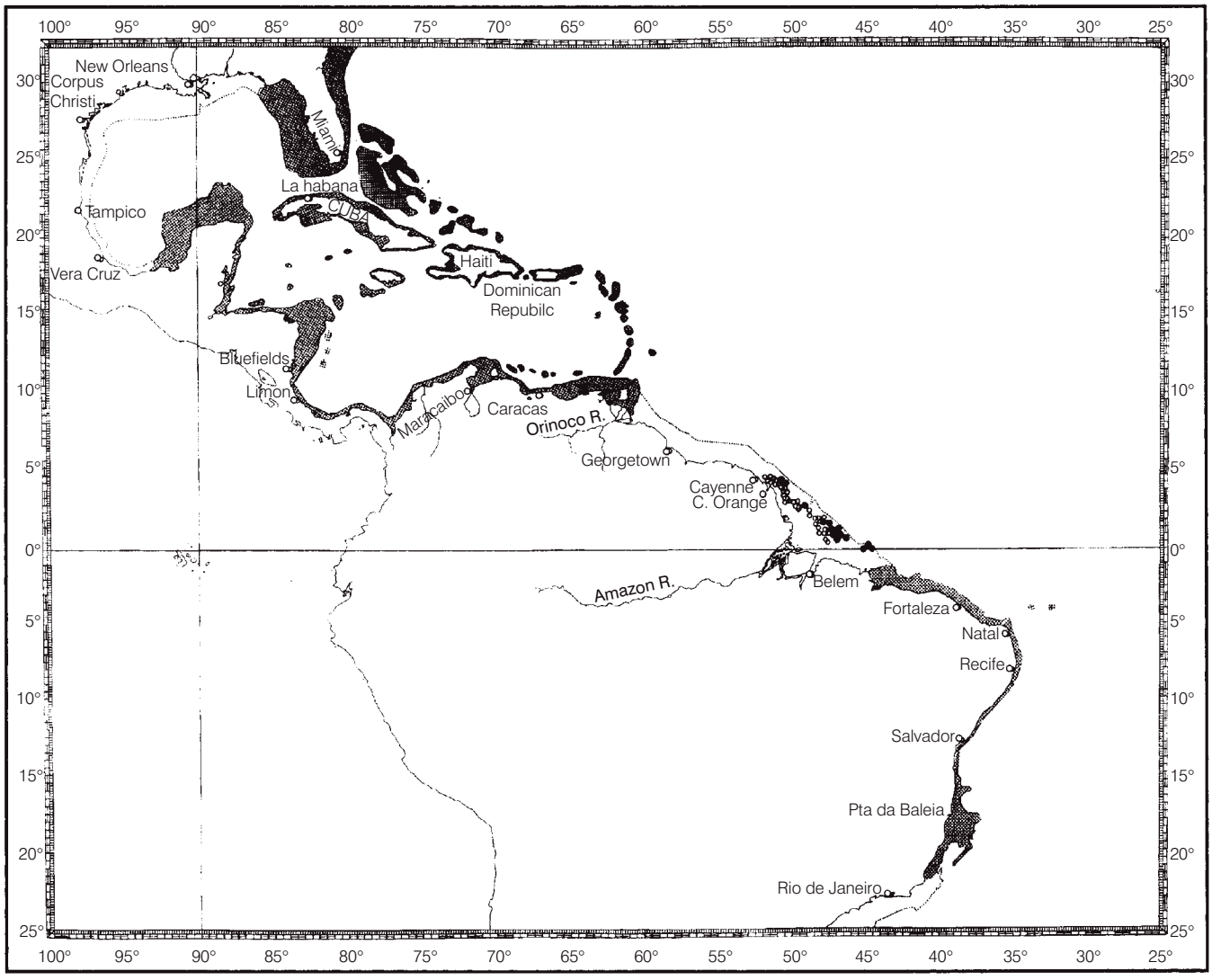


Figure 16.5

Distribution of coral reef fishes (shaded areas) in the tropical western Atlantic. Black dots indicate 14 stations where coral reef fishes were caught in association with sponges. Adapted from Collette and Rützler (1977).

in the western Atlantic is associated with the presence of the habitat created by West Indian coral reefs; 16–24 genera of zooxanthellate (containing symbiotic algae) corals occur there (Rosen 1988). The fish fauna of the western Atlantic region comprises about 1200 species. This coral reef fish fauna is partially divided into northern and southern parts by the freshwater outflow of the Amazon River. Bottom trawling below the freshwater outflow of the Amazon River in 1975 closed part of the supposed "gap" in fish distributions (Collette & Rützler 1977). At 14 benthic stations off the mouth of the Amazon under the superficial freshwater layer, a typical reef fish fauna of 45 species was found, but these "coral reef" species were associated with 35 species of sponges in water too turbid for coral growth (Fig. 16.5).

Sponges provide the necessary structural habitat for "coral reef" species, which allows genetic continuity between the two supposedly separated populations. However, shallower water species are separated by the fresh waters of the Amazon outflow (Floeter et al. 2008). Rocha et al. (2002) showed the variable effects of the Amazon outflow on three species of the surgeonfish genus *Acanthurus*. The Amazon outflow is a strong barrier to dispersal of *A. bahianus*, a modest barrier for *A. coeruleus*, and has no discernable effect on *A. chirurgus*, which has been collected on deep soft bottoms with sponge habitats under the Amazon outflow. Both *A. bahianus* and *A. coeruleus* live in shallower waters and are not as tolerant of silt as *A. chirurgus*.

Although many groups show their maximum diversity in the Indo-West Pacific, a few show maximum diversity in

the Americas. Two-thirds of the species of toadfishes, Batrachoididae, occur in New World waters (Collette & Russo 1981). The most generalized subfamily, the Batrachoidinae, is worldwide. However, the two most specialized subfamilies, the luminous midshipmen (Porichthyinae) and the venomous toadfishes (Thalassophryninae), are restricted to the western Atlantic and eastern Pacific (plus a few freshwater species derived from Atlantic or Pacific marine species).

Eastern Pacific region

The eastern Pacific region contains another radiation related to and only recently separated from the western Atlantic. The region contains only four to eight genera of zooxanthellate corals (Rosen 1988) and fewer species of fishes than are present in the western Atlantic. Some widespread taxa, such as the Bluefish (*Pomatomus saltatrix*) and Cobia (*Rachycentron canadum*), are absent. The **eastern Pacific barrier**, the huge expanse of open water between the central and south Pacific islands and the American mainland, acts as a distance barrier limiting the movement of 86% of shore species from the central Pacific (Briggs 1974).

Elevation of the Panamanian Isthmus approximately 3 million years ago separated the continuous distribution of species into eastern Pacific and western Atlantic populations. David Starr Jordan, pioneer American ichthyologist (see Chapter 1), referred to such pairs of species as **geminate species**, related species divided by the isthmus, such as the Spanish mackerels, *Scomberomorus sierra*, in the eastern Pacific, and *S. brasiliensis*, in the Caribbean Sea. Some geminate species have clearly differentiated into what can be called good species from a morphological and sometimes from a genetic point of view as well, such as Spanish mackerels and toadfishes of the genus *Batrachoides*. Others, such as the halfbeaks of the genus *Hyporhamphus* are less well differentiated morphologically, making molecular methods useful to reach decisions on the status of the populations on either side of the isthmus (see Chapter 17, The Panama barrier).

The completeness of the eastern Pacific barrier is, however, not quite as distinct as Briggs (1974) implied (Lessios & Robertson 2006). Several Indo-West Pacific shore fishes actually cross the eastern Pacific barrier and are found at offshore islands such as the Revilligedos off the coast of Mexico, and Clipperton and Cocos off the coast of Costa Rica. Distributions of a species of mackerel (*Scomber australasicus*) and a needlefish (*Tylosurus acus melanotus*) extend from the western Pacific through the Hawaiian Islands to these islands, but these species are replaced by related forms (*S. japonicus* and *T. pacificus*, respectively) along the eastern Pacific coast of Middle America. These exceptions to the completeness of the eastern Pacific barrier may be related to habitat differences between the offshore islands and the mainland.

The Panama Canal connects the eastern Pacific with the western Atlantic. However, unlike the Suez Canal, the Panama Canal is not at sea level. It contains a freshwater lake, Lake Gatun, in its middle, and fresh water is used to raise the water level in a series of locks to lift ships up to the lake and then down to the ocean on the other side. This freshwater barrier prevents marine species from moving between the two oceans, with the exception of a few species that tolerate a wide range of salinities (McCosker & Dawson 1975). A proposed sea-level canal would allow mixing of the two different faunas and might have grave effects on the fishes and marine invertebrates on both sides of the isthmus. Diseases, parasites, and aggressive Indo-West Pacific species that pose little current danger in the eastern Pacific, such as the crown-of-thorns starfish and a sea snake, might do severe damage to coral reefs and the fish fauna of the western Atlantic (Briggs 1974).

Eastern Atlantic region

In the eastern Atlantic Ocean, tropical shore fishes are restricted to the Gulf of Guinea, a relatively small area that extends from Dakar, Senegal, to Angola, and includes offshore islands such as the Cape Verde Islands, Annobón, and Fernando Po. Coral cover is sparse in the tropical part of the eastern Atlantic, partly due to the large amount of freshwater runoff and accompanying sediment that flows out of such rivers as the Congo, Niger, and Volta. Only a few eastern Atlantic localities have as many as four to eight genera of zooxanthellate corals, other localities having only one to three genera (Rosen 1988). The eastern Atlantic is depauperate in many fish and invertebrate groups and contains only about 500 species of shore fishes. A few families, such as the porgies (Sparidae), have radiated in the eastern Atlantic.

Comparisons among genera of shore fishes of the western Atlantic, eastern Pacific, and eastern Atlantic demonstrate the relative depauperate nature of many eastern Atlantic groups. For example, four genera that contain two to four species each in the western Atlantic and eastern Pacific have only a single species in the eastern Atlantic (Table 16.1). Such comparison of patterns of diversity among different families can tell us much about not only the zoogeography of a group but also its probable phylogenetic history, particularly if we apply modern approaches to both zoogeography and phylogeny (Box 16.2).

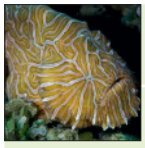
Mediterranean Sea

The Mediterranean Sea is a somewhat depauperate part of the eastern Atlantic Ocean, with about 540 species of fishes. Drying out during the Messinian Salinity Crisis millions of years ago eliminated most fishes from the Mediterranean, and cooler temperatures in the Straits of Gibraltar prevented warm water fishes found in the Gulf of Guinea from moving into the warm waters of the eastern Mediterranean

Table 16.1

Numbers of species in selected genera of inshore fishes from the western Atlantic, estern Pacific, and Gulf of Guinea (numbers in parentheses indicate freshwater species of marine origin).

Family	Genus	Western Atlantic	Eastern Pacific	Eastern Atlantic
Scombridae	*Scomberomorus*	4	2	1
Belonidae	*Strongylura*	3 (+1)	2 (+1)	1
Hemiramphidae	*Hyporhamphus*	3 (+2)	4	1
Batrachoididae	*Batrachoides*	3 (+1)	3	1
Totals		13 (+4)	11 (+1)	4



Box 16.2

BOX 16.2

Vicariance biogeography and Spanish mackerels of the *Scomberomorus regalis* species group

Historically, the first step in biogeography, the study of the distribution of all the organisms on our planet, has been to map the distributions of plants and animals (Ekman 1953; Darlington 1957; Briggs 1974, 1995). The next step was to ask, "why are these species distributed in this manner?" Until recently, the answers were usually couched in terms of "areas of endemism", which refers to regions to which certain species are restricted. Sometimes such areas were equated with "centers of origin" where species evolved and from which species dispersed to wherever they are found today. There is little doubt that such dispersal occurs, but we are still left with the question, "is this the primary explanation for the present distribution of most species?"

A potentially more complete answer can be given by a concept known as **vicariance biogeography** (Nelson & Platnick 1981; Nelson & Rosen 1981; Humphries & Parenti 1999). This method requires good phylogenetic information on the relationships of the species that comprise a group, as well as their distributions. Present distributions can then be compared with phylogenetic relationships to assess relative movements of biota or pieces of real estate containing the biota. This comparison is accomplished by replacing the terminal taxa in a cladogram with their geographic distributions to form an **area cladogram**. The search is for repeated distribution patterns that may be explained by **vicariant events**, such as movements of continents, collisions of islands on different tectonic plates, outcroppings of mountains or peninsulas to divide populations, or capture of a stream by headwater erosion of another drainage.

The process by which cladistics and zoogeography complement each other and inform us about a group's phylogeny can be demonstrated with the *Scomberomorus regalis* species group of Spanish mackerels. This group is defined as monophyletic based on the unique presence of nasal denticles, toothlike structures within the nasal cavity (Collette & Russo 1985a, 1985b). There are six Atlantic and eastern Pacific species relevant to this discussion: *tritor*, *maculatus*, *concolor*, *sierra*, *brasiliensis*, and *regalis* (Fig. 16.6). The five most advanced species (all except *S. tritor*) have a branch arising from the fourth left epibranchial artery (Fig. 16.7). The four most advanced species (all except *tritor* and *maculatus*) have developed a long posterior process on the pelvic girdle. The three most advanced species (*sierra*, *brasiliensis*, and *regalis*) have a coeliaco-mesenteric shunt connecting the fourth right epibranchial artery with the coeliaco-mesenteric artery. The two most advanced species (*brasiliensis* and *regalis*) have lost the pterotic spine from the back of the skull.

Comparing the distribution of the six species (Fig. 16.6) with the phylogeny (Fig. 16.7) indicates that the eastern Atlantic species (*tritor*) is the plesiomorphic sister species of the rest of the species group. Next comes the western Atlantic *maculatus* and then the two eastern Pacific species,

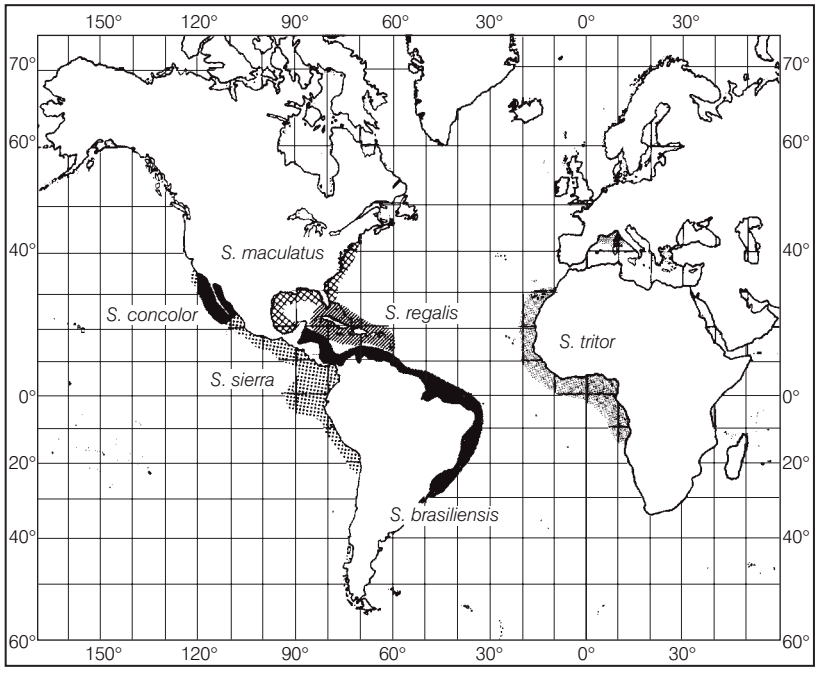


Figure 16.6
Ranges of the regalis group of Spanish mackerels (*Scomberomorus*). Adapted from Collette and Russo (1985a).

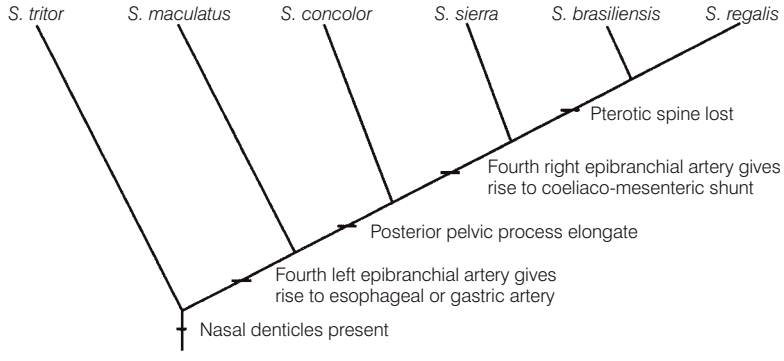


Figure 16.7
Cladogram of the *Scomberomorus regalis* group of Spanish mackerels. Adapted from Collette and Russo (1985a).

concolor and *sierra*, suggesting speciation following elevation of the Isthmus of Panama, as discussed earlier for geminate species. The two most advanced species, *brasiliensis* and *regalis*, are both found in the western Atlantic, with *regalis* occupying an unusual habitat for Spanish mackerels, namely, coral reefs.

These patterns among Spanish mackerels can then be compared with patterns of other species in Table 16.1 to see if there are commonalities among distributions. Are the single eastern Atlantic species of the halfbeak *Hyporhamphus*, of the needlefish *Strongylura*, and of the toadfish *Batrachoides* the plesiomorphic sister species of the western Atlantic and eastern Pacific species in these genera? Did these patterns arise from the widening of the Atlantic Ocean as the plates containing the Americas and the Old World (see Fig. 16.3) moved farther apart? Molecular genetic studies are needed to provide additional information on the relationships of such taxa and estimates of the timing of evolution of the species involved. Such data are available for some of the groups and support this pattern for Spanish mackerels (Banford et al. 1999) but not for the needlefishes (Banford et al. 2004).

when the Atlantic and Mediterranean were reconnected at the end of the Messinian Salinity Crisis about 5.3 million years ago (Patarnello et al. 2007). In 1869, a sea-level route, the Suez Canal, was opened, connecting the warm but depauperate eastern Mediterranean with the Red Sea, the latter being part of the rich Indo-West Pacific region. For some time after construction, faunal transfers between the Red Sea and the Mediterranean were inhibited by the saline waters of the Bitter Lakes in the middle of the canal. In the first edition of *A history of fishes* in 1931, Norman reported that 16 species of Red Sea marine fishes had moved through the Suez Canal and established themselves in the eastern Mediterranean Sea. In the ensuing decades, Adam Ben-Tuvia, Daniel Golani, and others raised the number to 24, 27, 31, 46, and most recently to 68 (Golani 2006). All but one of the species (a seabass, *Dicentrarchus*) are what are termed **Lessepsian migrants** (named after Ferdinand Lesseps who was in charge of constructing the canal), having moved in one direction, from the Red Sea into the eastern Mediterranean. At least 24 species of Red Sea origin have reached as far west as the southeastern Aegean Sea. As an example of how successful a migrant can be, the Brushtooth Lizardfish (*Saurida undosquamis*) was first taken in the Mediterranean in 1952. By 1955, 266 tons of this lizardfish were landed by local trawlers, constituting close to 20% of the trawler catch in Israeli waters (Golani 1993).

Why have these movements been virtually one-directional? First, the diversity of inshore fishes is greater in the Red Sea, part of the Indo-West Pacific fish fauna, than in the Mediterranean, suggesting that niches are more completely filled in the Red Sea, which means fewer ecological opportunities for new immigrants. Second, there appears to be an "empty niche" in the eastern Mediterranean, associated with water temperatures, with temperatures again being warm enough for warm water fishes.

Finally, many of the species that penetrated the canal are widespread species, adapted to a wide variety of living conditions. Consider the distributions of three of the invading species, a halfbeak and two mackerels. *Hemiramphus far* is the most widespread member of its genus, known from South Africa across the Indian Ocean north to Okinawa, south to Australia, and east to Tonga and Fiji. It, rather than the Red Sea-Persian Gulf *He. marginatus*, successfully moved through the canal and established populations that have now spread west and north as far as Albania. The two mackerels, the Narrow-barred Spanish Mackerel (*Scomberomorus commerson*) and the Indian Mackerel (*Rastrelliger kanagurta*), are the most widespread members of their genera, occurring from South Africa north to the Red Sea, east to China and Japan, and south to Australia and Fiji (Collette & Nauen 1983, maps on pp. 49 and 63). Such generally successful colonist species could have been predicted as the most likely taxa to take advantage of the opportunities in the eastern Mediterranean because they are adapted to a wide range of ecological conditions.

Arctic and Antarctic fishes

The diversity and adaptations of fishes of the far north and south are treated in Chapter 18 (Polar regions). Marine shore and continental shelf species down to 200 m from Arctic and Antarctic waters account for about 5.6% of the total fish fauna. The two polar regions contain 538 species of fishes, 289 in the Arctic and 252 in Antarctica (Møller et al. 2005). Only 12 of 214 polar fish genera and 10 of 72 polar fish families are found in both areas.

The Arctic region north of 60° in the Pacific (approximately Nunivak Island, Alaska) to Newfoundland and northern Norway in the Atlantic has 20–25% endemism (Briggs 1974) and contains 416 species in 96 families (Eastman 1997). Six groups dominate, comprising 58% of the fish fauna: zoarcoids, gadiforms, cottids, salmonids, pleuronectiforms, and chondrichthyans. Other groups include skates, herrings, greenlings, poachers, snailfishes, pricklebacks, wolffishes, and gunnels. Most of these groups have higher species diversity in the Pacific than in the Atlantic portions of the region (Briggs 1974, 1995).

Antarctica and the surrounding Southern Ocean contain 322 species of fishes in 50 families (Eastman 2005). The immediate Antarctic region has 174 species in 13 families, 88% of which are endemic. Antarctica has a higher level of endemism of fishes and invertebrates than the Arctic Ocean, although the Arctic contains 1.5 times the fish species and twice as many families (Briggs 1974). Of the fishes in the immediate Antarctic region, six families in the suborder Notothenioidei account for 55% of the species and more than 90% of the individuals. Primitive notothenioids, such as the Bovichtidae, occur in southern hemisphere habitats of Australia, New Zealand, and South America. Some families occur in both Antarctica and the surrounding continents (Nototheniidae and Channichthyidae), some occur in Antarctica and nearby oceanic islands such as Las Malvinas (the Falklands) (Harpagiferidae), and one family (Bathydraconidae) is restricted to Antarctica. Of the notothenioids, 97% are Antarctic endemics; even 70% of the non-notothenioids are endemic. Six other families that contribute multiple species to the region are, in order of species diversity (Eastman 2005): snailfishes (70 species), eel pouts (24), skates (eight), and eel cods, deepsea cods, and southern flounders (four species each).

In some cool water species, such as the chub mackerels *Scomber japonicus* and *S. colias*, distributions are interrupted by low-latitude regions. Such species are considered to have **antitropical distributions**, in that they are present in temperate waters on either side of the equator (Hubbs 1952). Other cold water species show **tropical submergence**, that is, they continue their ranges into tropical regions by submerging, moving into deeper waters that are the same temperature as the cold waters of Arctic and Antarctic regions.

Freshwater fishes

Freshwater fishes make a much larger contribution to biodiversity than might be expected based on area alone. Cohen (1970) was surprised to find that about 41% of the world's fish species live in fresh waters (see Fig. 16.1). But Horn (1972) demonstrated the real significance of this by pointing out that fresh waters comprise only 0.0093% of the water on the planet, which means that nearly half of all fish species live in less than 1% of the world's water supply. Another way of looking at this is to calculate the mean volume of water per species of marine versus freshwater fishes. The average marine species has 113,000 km^3 available to it, whereas the average freshwater species has only 15 km^3.

The probable causes of this 7500-fold disparity in biodiversity in the two major habitat types are undoubtedly very complex, involving ecological as well as historical (phylogenetic and geological) factors. Two likely influences are productivity and isolation. Shallow waters receive significant sunlight, allowing photosynthesis, which forms the base of food webs. Most fresh waters are shallow and relatively productive, whereas most water in the world's oceans lies well below the euphotic zone where primary productivity occurs (see Fig. 18.1). Shallow marine waters are productive and support a diverse fauna, as is evident in the coastal zones that support 45% of all fish species (see Fig. 16.1).

Also influencing diversity is the potential for isolation, an historical factor that differs greatly between marine and freshwater habitats. Marine habitats are broadly continuous; significant faunal breaks occur primarily where continental landmasses, large rivers, or sills occur, and where major oceanic currents act as geographic boundaries. Fresh waters, in contrast, are frequently and readily broken up into isolated water bodies. Drought, volcanoes, landslides, tectonic uplifting, glacial retreat, and dam building by beavers are some of the agents that can lead to a body of water losing its connections with other bodies, which in turn isolates the fishes in that body from gene flow with other areas. Genetic isolation is a driving force of evolution, leading to such dramatic events as explosive speciation and formation of species flocks (see Box 15.2). Isolating events are, therefore, much more common in fresh waters, and it is therefore not surprising that so many species of freshwater fishes have arisen in such little space.

Freshwater fishes versus fishes in fresh waters

Up to this point in our discussion, we have used the term *freshwater fishes* a little carelessly. Historically, there was also much confusion surrounding the term until George Myers (1938) clarified the problem. He distinguished between **primary** freshwater fishes, whose members are very strictly confined to fresh water, and **secondary** freshwater fishes, whose members are generally restricted to fresh water but may occasionally enter salt water. Most families of primary freshwater fishes have had a long evolutionary history of physiological inability to survive in the sea. The term **peripheral** is used for a number of genera and species of marine families that have taken up more or less permanent residence in fresh water or that spend part of their life cycle in fresh water and another part in marine habitats (such **diadromous** fishes are discussed in Chapter 23, Diadromy). There are about 85 families of primary freshwater fishes, 11 of secondary, and more than 30 of peripheral freshwater fishes (Table 16.2).

The origins of freshwater fishes, and the importance of distinguishing among the different types, become particularly clear when the composition of fishes in the fresh waters of islands is considered. Continental islands that have been connected to the adjacent mainland, such as Trinidad, have the same kinds of fishes as are present on the adjacent mainland of South America. Oceanic islands such as Bermuda, the West Indies, and Hawaii, which have never been connected with continents, have no native primary freshwater fishes. All the native fishes in their fresh waters are secondary or peripheral species.

Freshwater zoogeographic regions

One effective way to understand the distribution of freshwater fishes is to recognize six regions or realms, as Alfred Russel Wallace proposed in 1876: (i) Nearctic (North America except tropical Mexico); (ii) Neotropical (Middle and South America, including tropical Mexico); (iii) Palearctic (Europe and Asia north of the Himalayan Mountains); (iv) African (or Ethiopian); (v) Oriental (Indian subcontinent, Southeast Asia, the Philippines, and most of Indonesia); and (vi) Australian (Australia, New Guinea, and New Zealand). A detailed discussion of the fauna of these regions was provided by Darlington (1957), and maps of the distributions of freshwater fish families are presented by Berra (2007).

Nearctic region

The Nearctic region consists of North America south to the Mexican plateau. The North American freshwater fish fauna is the best known and has been mapped by Lee et al. (1980) and discussed thoroughly by Hocutt and Wiley (1986) and Mayden (1993). There are 14 families of primary freshwater fishes (see Table 16.2) and a total of about 950 species of fishes in the region. The most speciose families include three families of ostariophysans – the Cyprinidae, Catostomidae, and Ictaluridae (the only North American family of Recent catfishes) – plus two percoid families – the Percidae (especially the darters) and the Centrarchidae. The ranges of five Nearctic families – the Cyprinidae, Catostomidae, Ictaluridae, Percidae, and

Table 16.2

Primary, secondary, and selected peripheral freshwater fish families and the geographic areas where they occur.

Family*	Division	Nearctic	Neotropical	Palearctic	Ethiopian	Oriental	Australian
Petromyzontidae	per	x		x			
Geotriidae	per		x				x
Mordaciidae	per		x				x
Potamotrygonidae	per		x				
Ceratodontidae	1st						x
Lepidosirenidae	1st		x				
Protopteridae	1st				x		
Polypteridae	1st				x		
Acipenseridae	per	x		x		x	
Polyodontidae	1st	x		x			
Lepisosteidae	2nd	x	x				
Amiidae	1st	x					
Denticipitidae	1st				x		
Osteoglossidae	1st		x		x	x	x
Pantodontidae	1st				x		
Hiodontidae	1st	x					
Notopteridae	1st				x	x	
Mormyridae	1st				x		
Gymnarchidae	1st				x		
Salmonidae	per	x		x			
Plecoglossidae	per			x			
Osmeridae	per	x		x			
Salangidae	per			x		x	
Retropinnidae	per						x
Prototroctidae	per						x
Galaxiidae	per		x		x		x
Aplochitonidae	per		x				x
Lepidogalaxiidae	?						x
Esocidae	1st	x		x			
Umbridae	1st	x		x			

Table 16.2

Primary, secondary, and selected peripheral freshwater fish families and the geographic areas where they occur.

Family*	Division	Nearctic	Neotropical	Palearctic	Ethiopian	Oriental	Australian
Kneriidae	1st				x		
Phractolaemidae	1st				x		
Characidae	1st	x	x		x		
Erythrinidae	1st		x				
Ctenoluciidae	1st		x				
Hepsetidae	1st				x		
Cynodontidae	1st		x				
Lebiasinidae	1st		x				
Parodontidae	1st		x				
Gasteropelecidae	1st		x				
Prochilodontidae	1st		x				
Curimatidae	1st		x				
Anostomidae	1st		x				
Hemiodontidae	1st		x				
Chilodontidae	1st		x				
Distichodontidae	1st				x		
Citharinidae	1st				x		
Ichthyboridae	1st				x		
Gymnotidae	1st		x				
Electrophoridae	1st		x				
Apteronotidae	1st		x				
Rhamphichthyidae	1st		x				
Cyprinidae	1st	x		x	x	x	
Gyrinocheilidae	1st					x	
Psilorhynchidae	1st					x	
Catostomidae	1st	x		x			
Homalopteridae	1st					x	
Cobitidae	1st			x	x	x	
Diplomystidae	1st		x				
Ictaluridae	1st	x					

Table 16.2

Primary, secondary, and selected peripheral freshwater fish families and the geographic areas where they occur.

Family*	Division	Nearctic	Neotropical	Palearctic	Ethiopian	Oriental	Australian
Bagridae	1st			x	x	x	
Cranoglanididae	1st					x	
Siluridae	1st			x		x	
Schilbeidae	1st				x	x	
Pangasiidae	1st					x	
Amblycipitidae	1st					x	
Amphiliidae	1st				x		
Akysidae	1st					x	
Sisoridae	1st			x		x	
Clariidae	1st			x	x	x	
Heteropneustidae	1st					x	
Chacidae	1st					x	
Olyridae	1st					x	
Malapteruridae	1st				x		
Mochokidae	1st				x		
Doradidae	1st		x				
Auchenipteridae	1st		x				
Aspredinidae	1st		x				
Pimelodontidae	1st		x				
Ageneiosidae	1st		x				
Hypophthalmidae	1st		x				
Helogeneidae	1st		x				
Cetopsidae	1st		x				
Trichomycteridae	1st		x				
Callichthyidae	1st		x				
Loricariidae	1st		x				
Astroblepidae	1st		x				
Amblyopsidae	1st	x					
Aphredoderidae	1st	x					
Percopsidae	1st	x					

Table 16.2

Primary, secondary, and selected peripheral freshwater fish families and the geographic areas where they occur.

Family*	Division	Nearctic	Neotropical	Palearctic	Ethiopian	Oriental	Australian
Oryziatidae	2nd			x		x	
Adrianichthyidae	2nd					x	
Horaichthyidae	2nd					x	
Cyprinodontidae	2nd	x	x	x	x	x	
Goodeidae	2nd	x					
Anablepidae	2nd		x				
Jenynsiidae	2nd		x				
Poeciliidae	2nd	x	x				
Melanotaeniidae	2nd						x
Neostethidae	per					x	
Phallostethidae	per					x	
Gasterosteidae	per	x		x			
Indostomidae	per					x	
Channidae	1st			x	x	x	
Synbranchidae	per		x	x	x	x	x
Cottidae	per	x		x			
Cottocomephoridae	per			x			
Comephoridae	per			x			
Percicthyidae	per	x	x	x			x
Centrarchidae	1st	x					
Percidae	1st	x		x			
Toxotidae	per					x	x
Scatophagidae	per				x	x	x
Enoplosidae	per						x
Nandidae	1st		x		x	x	
Embiotocidae	per	x		x			
Cichlidae	2nd	x	x		x	x	
Gadopsidae	per						x
Bovichthyidae	per		x				x
Rhyacichthyidae	per					x	x

Table 16.2

Primary, secondary, and selected peripheral freshwater fish families and the geographic areas where they occur.

Family*	Division	Nearctic	Neotropical	Palearctic	Ethiopian	Oriental	Australian
Kurtidae	per					x	x
Anabantidae	1st				x	x	
Belontiidae	1st			x		x	
Helostomatidae	1st					x	
Osphronemidae	1st					x	
Luciocephalidae	1st					x	
Mastacembelidae	1st			x	x	x	
Chaudhuriidae	1st					x	

*The following widely distributed peripheral families (mostly marine) are omitted from this analysis. Carcharhinidae, Elopidae, Megalopidae, Anguillidae, Clupeidae, Engraulidae, Chanidae, Ariidae, Plotosidae, Batrachoididae, Gadidae, Ophidiidae, Hemiramphidae, Belonidae, Atherinidae, Syngathidae, Alabetidae, Centropomidae, Ambassidae, Teraponidae, Kuhiiidae, Sparidae, Sciaenidae, Monodactylidae, Mugilidae, Polynemidae, Gobiidae, Soleidae, Tetraodontidae.
1st = primary; 2nd = secondary; per = peripheral.
From Berra 1981.

Centrarchidae – extend south well into Middle America. Included in this area are the Southern Appalachian river drainages, with about 350 species, the richest diversity of temperate freshwater fishes of any continent (e.g., Lydeard & Mayden 1995).

This region can be divided into 10 provinces (Fig. 16.8) based mainly on distribution data for freshwater fishes, mussels, and crayfish (Abell et al. 2000, as modified by Lévêque et al. 2008).

1. The **Pacific Coastal Province** contains the Pacific drainages from the Yukon River to Mexico and also the interior drainages west of the Rocky Mountains. It includes the Columbia River drainage with 61 freshwater species including two endemic relict species, a mudminnow (Umbridae) and a trout-perch (Percopsidae). The province also includes the Klamath and Rogue rivers along the border of California and Oregon, with about 30 freshwater species and the Sacramento–San Joaquin drainage system of California that contains 43 species of freshwater fishes. About 42% of these are endemic, including 10 species of minnows and the Sacramento Perch (*Archoplites interruptus*), the only centrarchid occurring natively outside of eastern North America.
2. The **Great Basin Province** contains 150 internal drainage systems that are now very arid but contained large lakes during periods of the Pleistocene. There are about 50 species, mostly minnows, suckers, killifishes, and whitefishes, with about 80% endemism (Miller 1958).

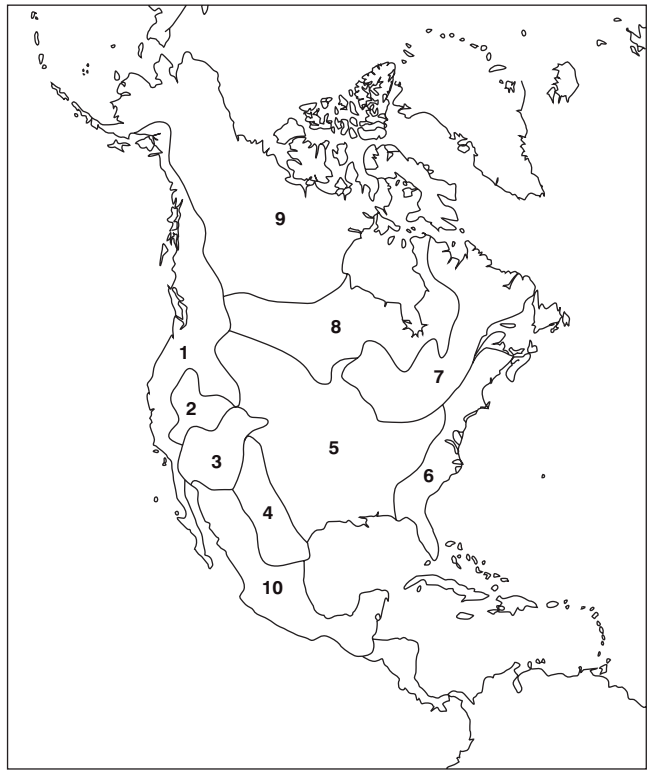


Figure 16.8
Main ichthyological provinces in North and Middle America. Numbers refer to regions in the text. From Lévêque et al. (2008).

3 The **Colorado Province** contains about 32 species of freshwater fishes, 75% of which are endemic, with many species threatened by dams, water extraction, and introduced species (see Chapter 26, Dam building).
4 The **Rio Grande Province** is essentially the Rio Grande River and its tributaries. It contains 154 species (about 80 endemic), including the northernmost species of two Neotropical families, the Characidae (*Astyanax mexicanus*) and the Cichlidae (*Cichlasoma cyanoguttatum*).
5 The **Mississippi Province** is the largest Nearctic province, comprising the area drained by the Mississippi and Missouri rivers, and contains the most species, about 375 (about 130 of which are endemic).
6 The **Atlantic Coastal Province** contains the rivers that drain into the Atlantic Ocean from New Brunswick to Florida and continues through Florida's gulf-draining rivers. The northern part of the province has a relatively high proportion of anadromous fishes, while the southern portion has numbers of secondary fishes that have invaded from marine waters.
7 The **Great Lakes–St. Lawrence Province** is largely derived from the Mississippi Province.
8 The **Hudson Bay Province** includes most of central Canada and part of the United States. Its fish fauna of about 100 species (Crossman & McAllister 1986) is most similar to that of the Mississippi Province. Minnows are an important component in the southernmost part of the province but are largely replaced by trouts, sculpins, suckers, and pickerels in the northern part of the province.
9 The **Arctic Province** includes Canadian and Alaskan rivers that drain into the Arctic Ocean. More than half of the 66 freshwater species (Lindsey & McPhail 1986) belong to diadromous families, one-third are primary freshwater species, and 11% belong to marine families. This province shares some species, such as the Alaskan Blackfish (*Dallia pectoralis*), with Siberia, which belongs in the Palearctic region.
10 The **Mexican Transition Province** is a mosaic of xeric rivers, lakes and springs, subtropical coastal rivers, volcanic crater lakes, sink holes, and extensive wetlands. It contains about 200 endemic species.

Neotropical region

The Neotropical region consists of South America and Middle America, into which some North American species have moved. South America has the largest freshwater fish fauna in the world, with 32 families of primary freshwater fishes, 4475 valid described species plus at least another 1550 still to be described (Reis et al. 2003). There are no minnows or suckers in South America, but their ecological equivalents may be in the eight families of characins with over 1200 species. Other ostariophysans include 13 families of catfishes with about 1300 species, and six families of Gymnotiformes. Cichlids (about 150 species) are the most speciose perciform group. Representatives of many marine families have also invaded South America: freshwater stingrays (Potamotrygoninae), which are endemic to South America; herrings (Clupeidae); toadfishes (Batrachoididae); needlefishes (Belonidae, three endemic genera and seven species); croakers (Sciaenidae); and soles (Achiridae). Gery (1969) recognized eight faunistic regions but Lévêque et al. (2008) modified this into 10 ichthyofaunal provinces (Fig. 16.9):

Figure 16.9
South American ichthyological provinces. Numbers refer to regions in the text. From Lévêque et al. (2008).

1 The **South Patagonian Province** with12 species (one endemic).
2 The **North Patagonian Province** with 23 species (five endemic).
3 The **Trans-Andean (South) Province** with 19 species (13 endemic).
4 The **Lake Titicaca Province** with 32 species, 30 endemic including the endemic fauna of the cyprinodontoid *Orestias*.

5 The **Paranean Province** consisting mainly of the coastal rivers of Argentina plus two large rivers, the La Plata and the Sao Francisco from Brazil, with 847 species (517 endemic).
6 The **South-East Brazilian Province** with 194 species (90 endemic).
7 The **East Brazilian Province**, comprising the smaller coastal rivers of eastern Brazil, with 131 species (50 endemic).
8 The **Guianean-Amazonian Province**, the richest basin, with about 2400 species and more than 2000 endemics.
9 The **North Venezuelan Province** with 61 species (nine endemic).
10 The **Trans-Andean Province**, with 423 species (326 endemic).

Palearctic region

The Palearctic region of northern Europe and Asia contains only 14 families of primary freshwater fishes with many minnows and loaches but only about 10 species of catfishes from four families. Non-ostariophysans include perches (Percidae), pickerels (Esocidae), and a mudminnow (Umbridae, *Umbra krameri*). Europe itself was historically thought to be relatively depauperate in freshwater fishes, but recent reanalysis suggests Europe has a rich fauna of 546 native species, with considerable endemism in the southern regions (Kottelat & Freyhof 2007). Lévêque et al. (2008) modified the ichthyological regions defined by Reyjol et al. (2007) based on species lists for 233 species from 406 basins to define seven European provinces (Fig. 16.10):

1 **Ponto-Caspian Province** with 98 species (36.7% endemic).
2 **Northern Europe Province** with 42 species (9.5% endemic).
3 **Western Europe Province** with 47 species (6.4% endemic).
4 **Central Europe Province** with 57 species (1.8% endemic).
5 **Central Peri-Mediterranean Province** with 93 species (64.5% endemic).
6 **Eastern Peri-Mediterranean Province** with 64 species (31.2% endemic).
7 **Iberian Peninsula Province** with 50 species (60% endemic).

African region

The African region has a diverse freshwater fish fauna that includes 27 families of primary freshwater species and a number of primitive species as discussed below under archaic distributions. The region contains a total of about

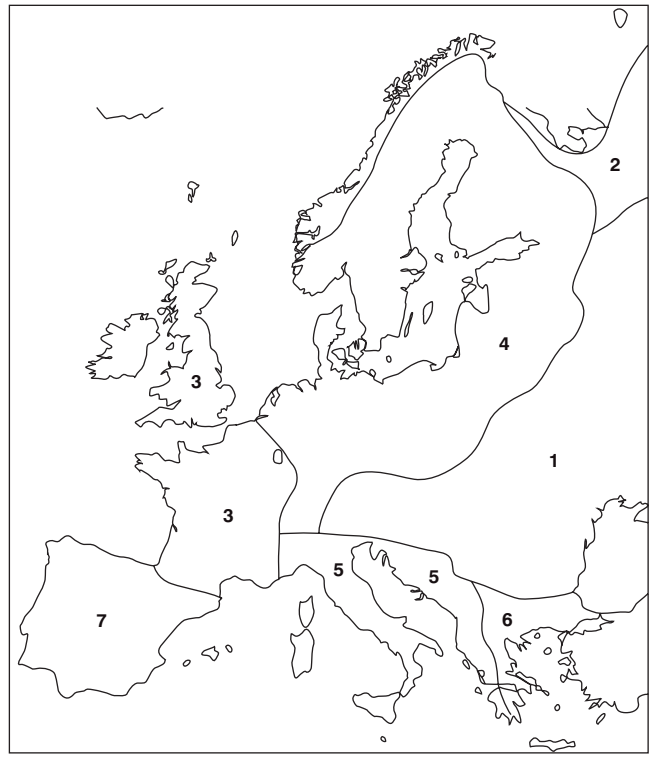


Figure 16.10
Main ichthyological provinces in western Europe. Numbers refer to regions in the text. From Lévêque et al. (2008).

2000 species of primary and secondary fishes belonging to about 280 genera and 47 families (Roberts 1975c). Almost half the species are ostariophysans (300 species of minnows, 190 characins, and more than 360 catfishes from six families). Roberts recognized 10 ichthyofaunal provinces (although these were modified into nine by Lévêque et al. (2008)) (Fig. 16.11):

1 **Maghreb Province.**
2 **Nilo-Sudan Province.**
3 **Upper Guinea Province.**
4 **Lower Guinea Province.**
5 **Congo Province.**
6 **Quanza Province.**
7 **Zambezi Province.**
8 **East Coast Province.**
9 **Southern Province** or Cape of Good Hope.
10 **Madagascar Province.**

Oriental region

The Oriental region includes India, southern China, South-east Asia, the Philippines, and the East Indies out to Borneo and Bali (Fig. 16.12). Alfred Russel Wallace (1860, 1876)

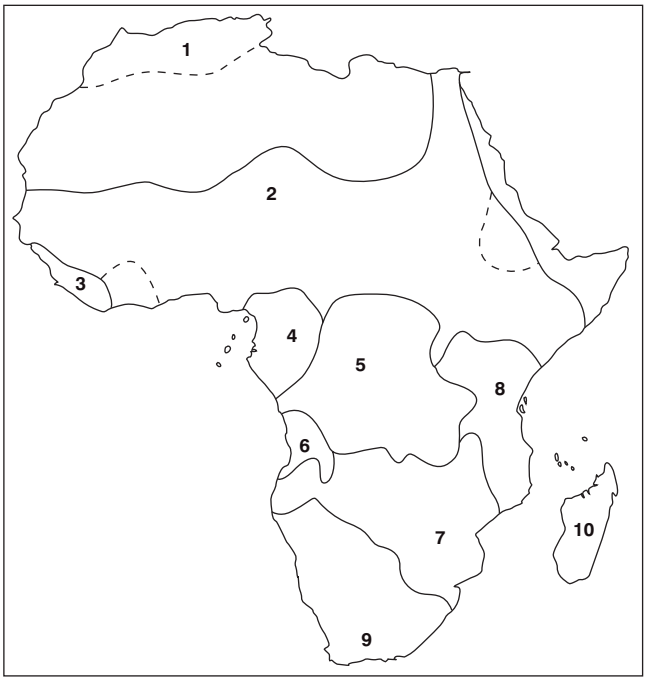


Figure 16.11
Main ichthyological provinces in Africa. Numbers refer to regions in the text. From Lévêque et al. (2008).

proposed a boundary between the Oriental and Australian faunas that Thomas Huxley named for him as **Wallace's Line**. Some authors extend the line even farther to the east (Weber's Line) to also include the Celebes (now Sulawesi) and some other Indonesian Islands in the Oriental region. The region contains 28 families of primary freshwater fishes with 12 families of catfishes and four families of cypriniform ostariophysans: minnows (Cyprinidae), loaches (Cobitidae), algae eaters (Gyrinocheilidae), and river loaches (Balitoridae), which are endemic to the region. Non-ostariophysan families include snakeheads (Channidae), spiny eels (Mastacembelidae), labyrinth fishes (Anabantoidei), and a few cichlids. Only two species of primary freshwater fishes occur east of Wallace's Line. All other fishes in fresh waters east of the line have been derived from marine groups, such as the catfishes and rainbowfishes.

Australian region

The Australian region has only two species of primary freshwater fishes, both ancient relicts of a much wider archaic distribution pattern (see below). Two families of secondary and 16 families of peripheral freshwater fishes of marine origin include freshwater species of catfishes (two marine families, Ariidae and Plotosidae), silversides (Atherinidae), rainbowfishes (Melanotaeniidae), halfbeaks (Zenarchopteridae), needlefishes (Belonidae), Teraponidae, Centropomidae, Percichthyidae, and gobies (Gobiidae).

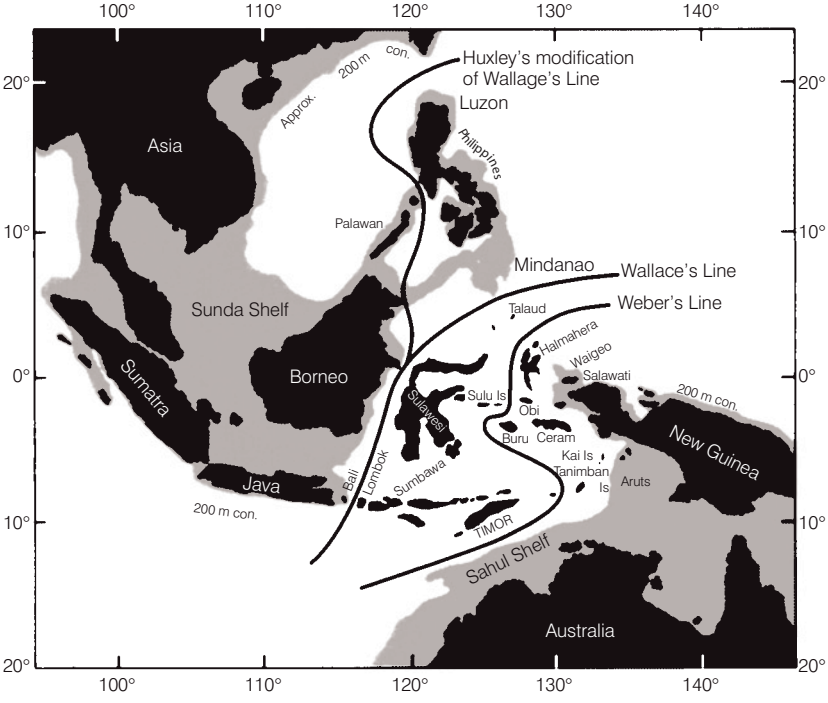


Figure 16.12
Wallace's and Weber's lines separating the Oriental and Australian regions. The shaded areas show how the major landmasses would be connected if the sea retreated to the 200 m line. Adapted from Berra (2007).

Archaic freshwater fish distributions

The term **archaic** is used to refer to the distribution of six groups of primitive primary freshwater fishes (see Chapter 13) that date back long enough that their present distribution may be based on a different arrangement of the continents. These groups include lungfishes (Dipnoi), Polypteriformes, Polyodontidae, Lepisosteidae, Amiidae, and Osteoglossomorpha.

There are three living genera of lungfishes (see Fig. 13.10): the South American *Lepidosiren*, African *Protopterus*, and Australian *Neoceratodus*. Placement of *Lepidosiren* and *Protopterus* together in a single family, Lepidosirenidae, instead of in separate families, emphasizes their close relationships (Lundberg 1993). *Neoceratodus* is the most different lungfish, morphologically and physiologically, and has a relict distribution, restricted to portions of the Burnett and Mary rivers in southeastern Queensland (see Chapter 13, Subclass Dipnoi, Order Ceratodontiformes: the lungfishes).

Other archaic groups include the bichirs, Polypteridae, which consist of two living African genera – *Polypterus* with 10 species and the monotypic *Erpetoichthys* (previously *Calamoichthys*) – and a fossil genus (†*Dajetella*) from the Late Cretaceous and Paleocene of Bolivia (Lundberg 1993). There are two species of paddlefishes, family Polyodontidae: one (*Polyodon spathula*) from the Mississippi River of North America and the other (*Psephurus gladius*) from the Yangtze River of China. The seven species of gars, Lepisosteidae, are usually considered as secondary freshwater fishes and comprise two genera, *Lepisosteus* and *Atractosteus* in North America, Central America, and Cuba, plus fossils known from India and Europe. Only one Recent species of Bowfin, Amiidae, is still extant: *Amia calva* of the United States; fossil species have been found on all the continents except Australia (Grande & Bemis 1998). Fossils show that the present-day distribution of these groups is a relict of their original, much wider distribution.

Another archaic group is the Osteoglossomorpha, the most primitive subdivision of the Teleostei. It is more speciose and more widespread than the Dipnoi. It includes six families (Fig. 16.13). There are four genera in the Osteoglossidae, two in each of two subfamilies (or families; Lundberg 1993): Heterotinae, *Heterotis niloticus* in the Nilo-Sudan Province of Africa and *Arapaima gigas* from the Amazonian lowlands and Guianas of South America; and Osteoglossinae, two species of *Osteoglossum* from South America and three species of *Scleropages* from Queensland, New Guinea, and Southeast Asia. The lungfish *Neoceratodus forsteri* and *Scleropages* are the only native primary freshwater fishes found in Australia.

Other osteoglossomorphs include the African freshwater butterflyfish *Pantodon* (Pantodontidae), sister group of the Osteoglossidae; the North American Hiodontidae, the Goldeye *Hiodon alosoides* and the Mooneye *H. tergisus*; the African knifefishes (Notopteridae), and the African Mormyriformes, Mormyridae (elephantfishes), with 150 species; and the monotypic Gymnarchidae (*Gymnarchus niloticus*). Archaic fish distributions are summarized in Fig. 16.14.

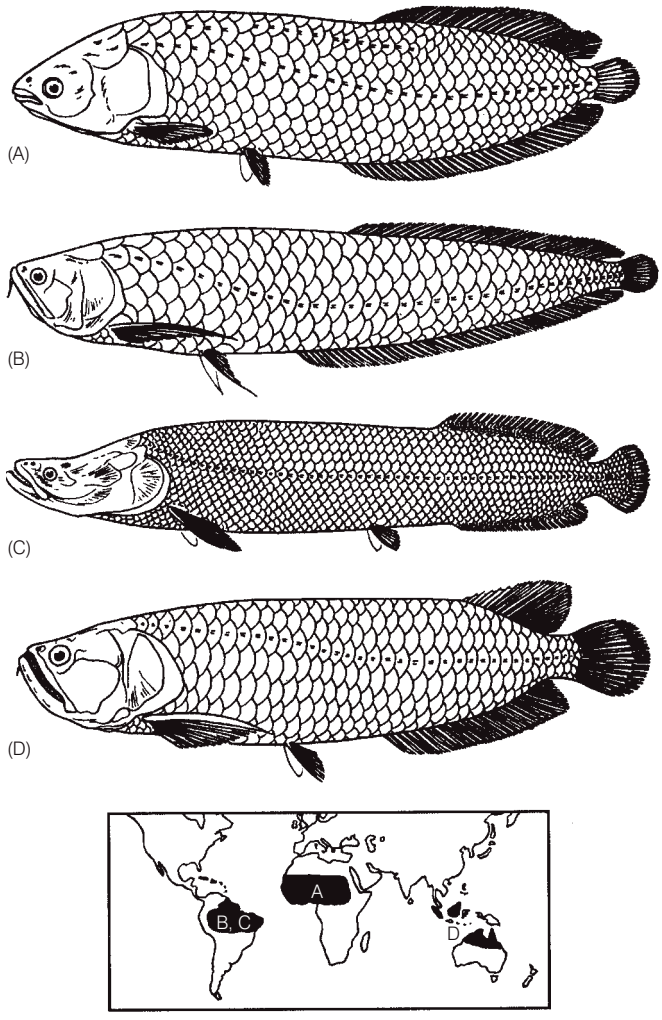


Figure 16.13
Osteoglossidae and their distribution (inset below). (A) *Heterotis*. (B) *Osteoglossum*. (C) *Arapaima*. (D) *Scleropages*. From Norman and Greenwood (1975).

More recent distributions

Five groups of primary freshwater fishes have more recent distributions than the six archaic groups. These include the pickerels and relatives, the darters and perches, the sunfishes, the cichlids, and the Ostariophysi.

The suborder Esocoidei contains two families – Esocidae, the pickerels from North America and Eurasia, and Umbridae, the mudminnows from eastern and western

Figure 16.14
Summary of archaic freshwater fish distributions.

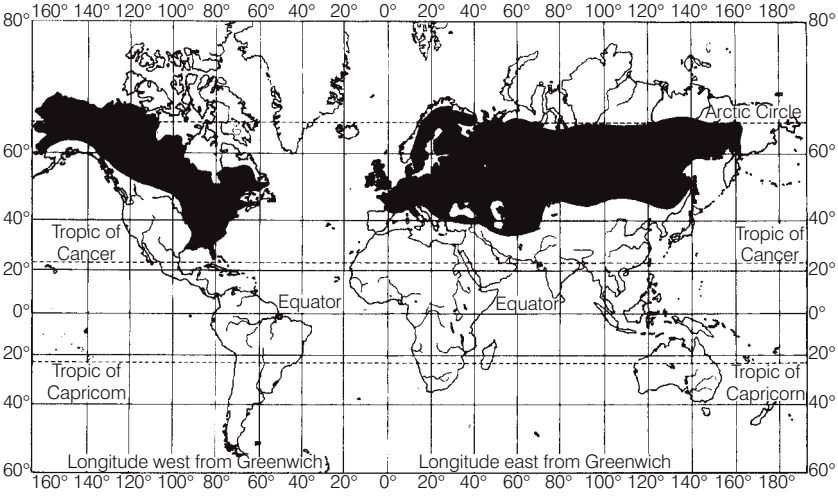


Figure 16.15
Distribution of the pickerels, Esocidae. Adapted from Lagler et al. (1977).

United States – and one relict species, *Umbra krameri*, from the Danube River in Europe (Fig. 16.15). The Northern Pike, *Esox lucius*, ranges across northern North America, Europe, and Asia, giving it the broadest natural distribution of any fish in the northern hemisphere.

Three families of acanthopterygian fishes are of major importance in fresh waters. The Percidae, the perches and darters, includes about 175 species, 15 of which are European and 160 of which are American, including all the darters, tribe Etheostomatini (Fig. 16.16). The black basses and sunfishes (Centrarchidae) include 25 species, 24 from eastern North America and one relict species, *Archoplites interruptus*, from California (Fig. 16.17). The Cichlidae ecologically replaces the Centrarchidae and Percidae in the southern continents of South America, Africa, Madagascar, and southern India (Fig. 16.17). This large family, which may have more than 2000 species (see Box 15.1), is usually considered a secondary freshwater family because some species show salinity tolerance. Distributions of the first four groups are summarized in Fig. 16.18.

The largest group of freshwater fishes is the series Otophysi of the superorder Ostariophysi, which includes four orders: Cypriniformes, Characiformes, Siluriformes, and Gymnotiformes.

The Cypriniformes includes three large and two small families found primarily in the northern continents. The Cyprinidae, the carps and minnows, is one of the largest families of freshwater fishes, with about 2000 species. It is found in North America, Africa, Europe, and Asia (Fig. 16.19). The highest diversity of cyprinids is found in Asia. The 75 species of suckers, Catostomidae, are confined to North America, except for a relict genus in China, *Myxocyprinus*, and a recent reinvasion of Siberia by *Catostomus catostomus* (Fig. 16.20). The loaches, Cobitidae, are found in Eurasia. The two smaller families, the Gyrinocheilidae and the Balitoridae, occur in Southeast Asia.

Figure 16.16

Distribution of the darters and perches, Percidae. Adapted from Norman and Greenwood (1975).

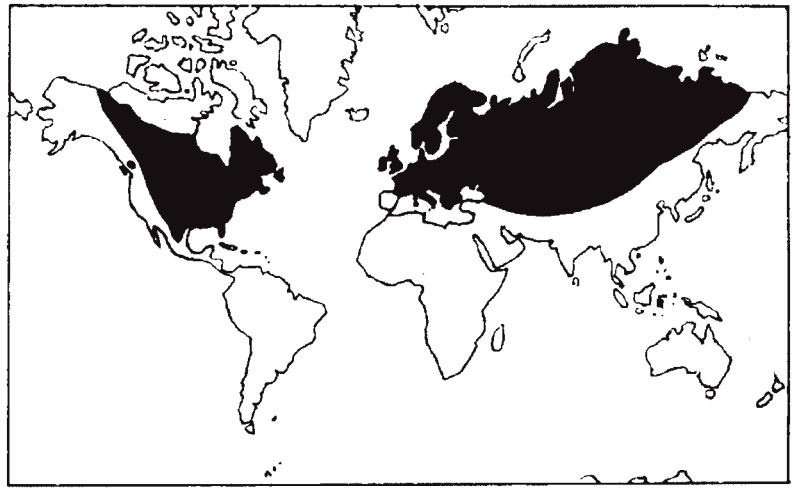


Figure 16.17

Distribution of the sunfishes, Centrarchidae, and cichlids, Cichlidae. Adapted from Lagler et al. (1977).

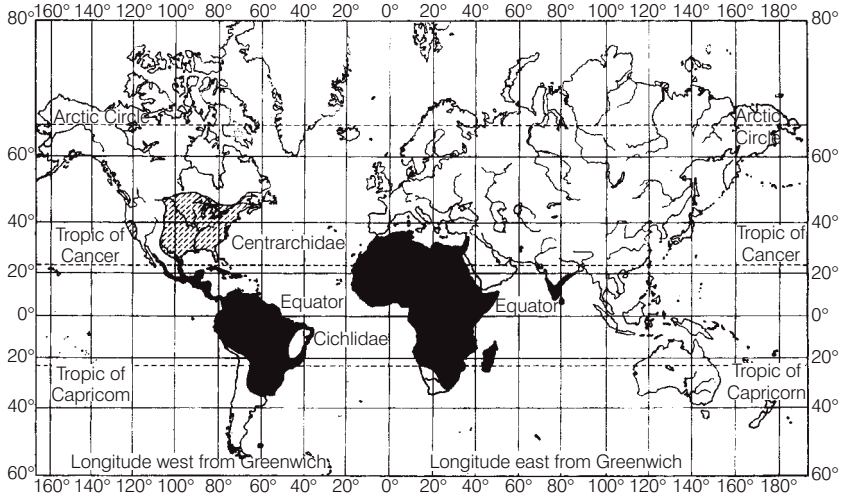
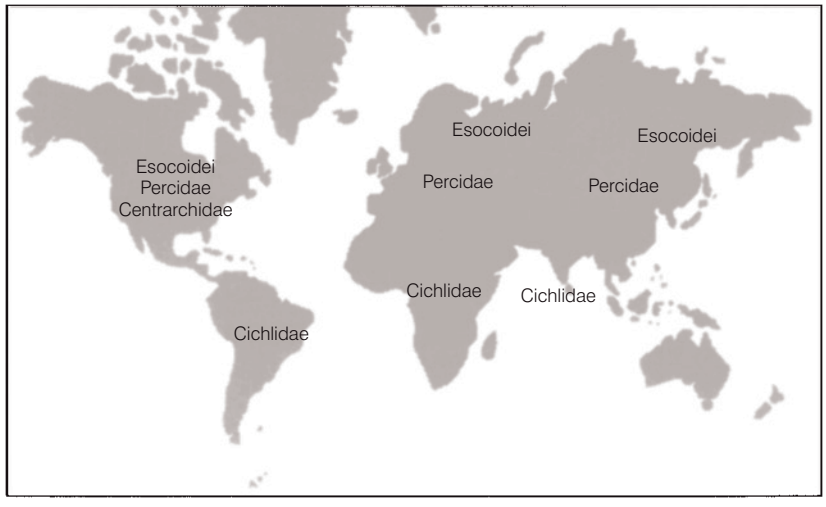


Figure 16.18

Summary of recent primary fish distributions (other than Ostariophysi).



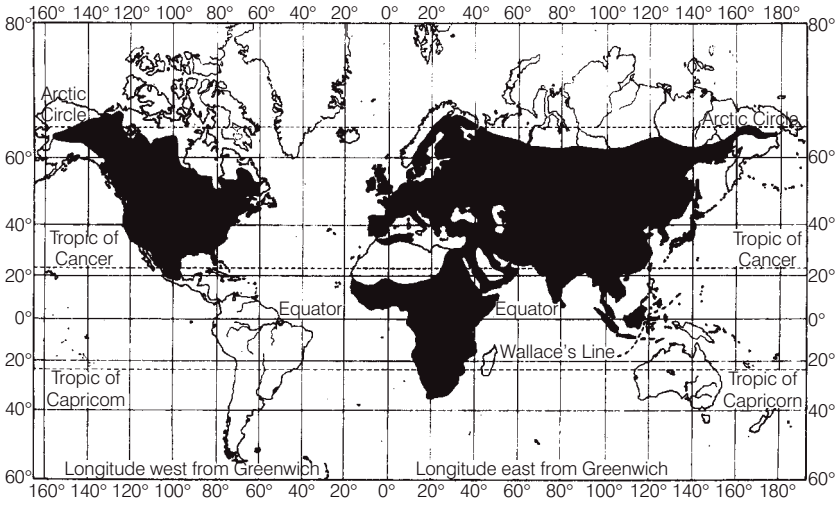


Figure 16.19
Distribution of the minnows and carps, Cyprinidae. Adapted from Lagler et al. (1977).

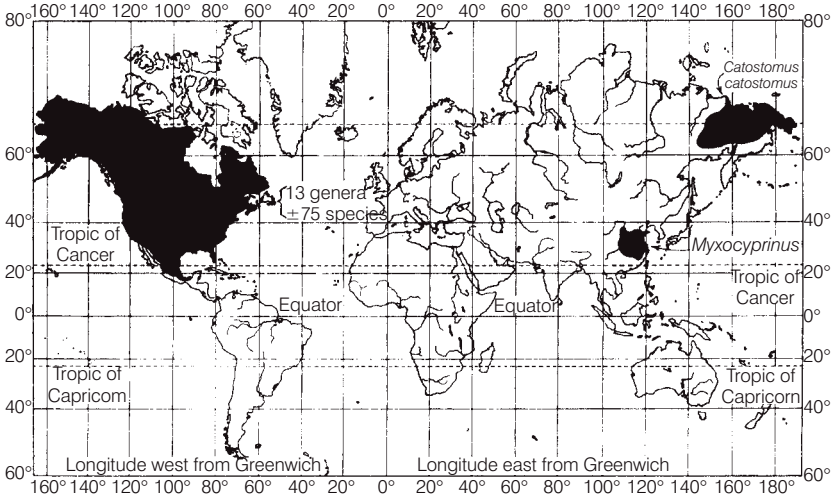


Figure 16.20
Distribution of the suckers, Catostomidae. Adapted from Lagler et al. (1977).

The Characiformes, the characins, comprises 10–16 families of tetras and relatives. The greatest diversity of the order is in South America, with 200 genera and over 1000 species. Characins are also widespread in Africa, with 23 genera and 150 species, currently placed in four families.

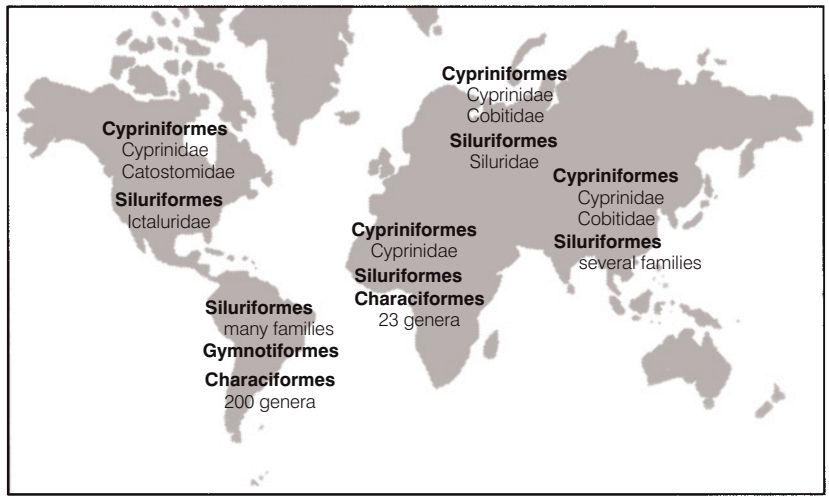
The Gymnotiformes comprises five families and more than 100 species of electric fishes restricted to South America.

The catfishes, Siluriformes, include about 34 families of diverse fishes and about 2000 species. There is only one freshwater family in North America, the Ictaluridae, including *Ictalurus*, *Ameiurus*, and madtoms of the genus *Noturus*. There are 14 endemic families and more than 1200 species in South America (Lundberg 1993). Some of the families are the suckermouth catfishes, Loricariidae and Astroblepidae, the popular aquarium fishes in the Callichthyidae, and the parasitic catfishes in the Trichomycteridae. Africa has six freshwater siluriform families with about 400 species. Europe has only the Siluridae with two species of *Siluris*, including the huge *S. glanis*, reaching 5 m in length and 300 kg. There are several families in Asia. The catfishes also contain two marine families, Ariidae and Plotosidae, making them exceptions to the primary freshwater fish nature of the Siluriformes. To further complicate the issue, the Plotosidae has secondarily invaded fresh waters of Australia and New Guinea. The dominance of otophysans among primary freshwater fishes is summarized in Fig. 16.21.

Similarities between South American and African freshwater fishes

The primary freshwater fishes of South America and Africa are remarkably similar. The Dipnoi and Osteoglossomorpha among archaic fishes link South America, Africa, and Australia. The more recent distributions of the

Figure 16.21
Summary of otophysan distribution.



Characiformes and Cichlidae also link South America and Africa. A question arising from these parallels is whether this similarity is due to dispersal or vicariance. Some researchers believe that the Ostariophysi originated in Southeast Asia and dispersed to South America from Africa across a direct land bridge. However, land bridges work particularly poorly for freshwater fishes because rivers seldom run lengthwise along such bridges. Other researchers favor dispersal of Ostariophysi through North America, but this is not supported by recent distributions or by fossil evidence. Among 13 putative African–South American clades, only three clades – lepidosirenid lungfishes, polypterid bichirs, and doradoid catfishes – clearly fit the simple continental drift–vicariance model, with a common ancestor inhabiting fresh waters of the African–South American landmass before the opening of the Atlantic Ocean (Lundberg 1993). Distributions of other groups, such as cichlids and characins, are more difficult to explain this way because they have evolved more recently, so perhaps some dispersal has taken place in addition to vicariant events. An explanation for the distribution of a freshwater galaxiid in South America and Australia is a good example of the argument over dispersal versus vicariance (Box 16.3).

Box 16.3

Vicariance versus dispersal: *Galaxias maculatus*

Vicariance and dispersal have been postulated by different sets of authors to explain the distribution of *Galaxias maculatus*, a small diadromous fish with a highly disjunct distribution in streams in eastern and Western Australia, New Zealand, South America, and some oceanic islands (Berra et al. 1996). The argument over whether vicariance or dispersal best explains the distribution of *G. maculatus* started over 100 years ago and was particularly vociferous from the late 1970s through the mid-1990s (see summary in Berra et al. 1996).

Rosen (1978) considered galaxiid fishes to be part of a pan-austral Gondwanan biota that was fragmented by the movement of the southern continents during the Mesozoic. Rosen concluded that the present distribution resulted from vicariant events. *Galaxias maculatus* is the only galaxiid that breeds in brackish not fresh water, and its transparent whitebait larvae grow in the ocean before returning to fresh water. McDowall (1978), therefore, found it simpler to accept a relatively recent oceanic dispersal by a fish with a marine juvenile stage. Recent allozyme electrophoresis shows that *G. maculatus* is a single species with surprisingly little genetic variation across its entire range (Berra et al. 1996). These data tend to support a dispersal hypothesis in this case, but mitochondrial DNA analysis is needed to further test this hypothesis.

Middle American freshwater fishes

The freshwater fish faunas of North and South America are very different. Minnows, suckers, ictalurid catfishes, darters, and sunfishes predominate in the north, whereas cichlids, characins, gymnotoids, and a wide array of different catfish families are common in the south. What happens in the region between North and South America, in Middle America?

Middle America acts partly as a **filter barrier** slowing the movement of North American fishes south and South American fishes north, thus allowing invasion by marine groups. A few representatives of North American families such as Ictaluridae, Catostomidae, and *Lepisosteus* extend south to Costa Rica (Fig. 16.22). A few representatives of South American families such as Cichlidae (*Cichlasoma*) and Characidae (*Astyanax*) extend north to the Rio Grande. Of the approximately 456 species of freshwater fishes in Central America, over 75% comprise secondary freshwater fishes such as Cyprinodontidae, Poeciliidae, Cichlidae, and marine invaders, and only 104 species are primary freshwater fishes (Miller 1966).

The general pattern of contributions from both major regions and of many secondary freshwater fishes also holds for more localized faunas in the region. For example, the **Usumacinta Province**, comprising the Grijalva and Usumacinta rivers of Guatemala and Mexico, contains a mix of North American and South American fishes totaling over 200 species (Miller 1966). Two secondary groups, the cyprinodontoids and the cichlids, comprise about 90 species. There are also a large number of marine derivatives (18 species in nine families). Among these are a few endemics, including species from three marine families, Belonidae (*Strongylura hubbsi*), Hemiramphidae (*Hyporhamphus mexicanus*), and Batrachoididae (*Batrachoides goldmani*). Freshwater species of these three families occur elsewhere, but what factors have led to this remarkable parallel derivation of endemic freshwater species? Part of the explanation is due to the depauperate nature of the primary freshwater fishes of the region, but this is true of many other rivers south through Panama. More information is needed on the nature of the water in the Usumacinta Province. Is it high in ions, as is true of southern Florida fresh waters that also contain a number of marine species (but not endemics derived from marine species)? Have there been historical factors or vicariant events involved? Here is an interesting problem involving phylogeny, biogeography, and physiology that awaits solution.

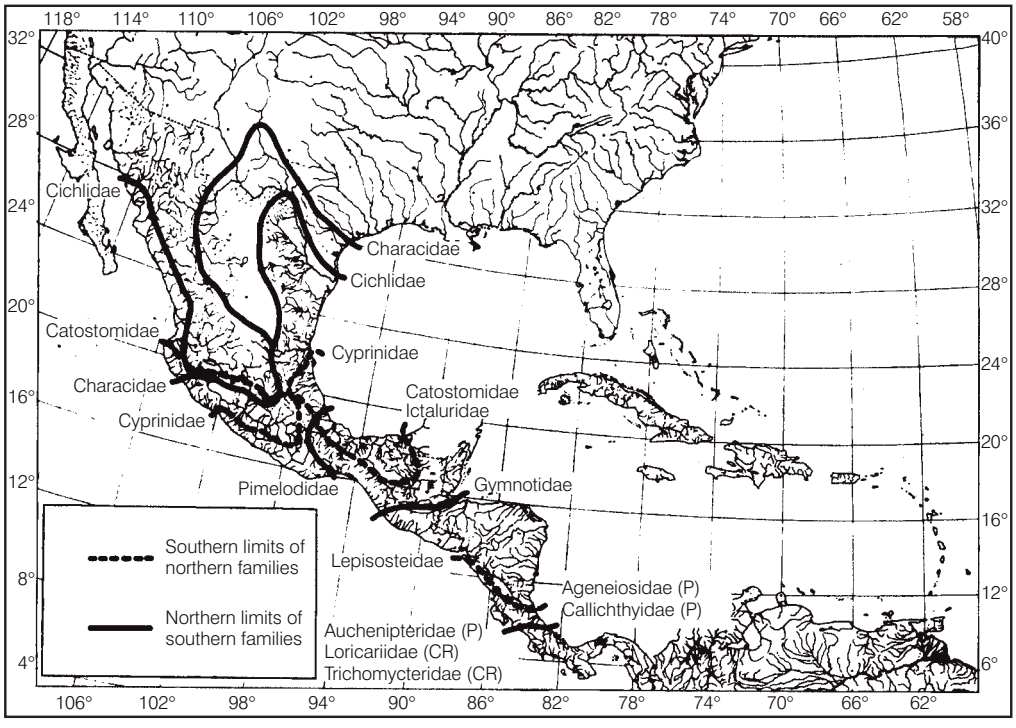
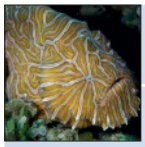


Figure 16.22

Distributional limits of certain primary and secondary freshwater fishes in Central America. A single characin (*Astyanax mexicanus*) and a single cichlid (*Cichlasoma cyanoguttatum*) reach north to the Rio Grande. CR, Costa Rica; P, Panama. Adapted from Miller (1966, fig. 1).



Summary

SUMMARY

1. Zoogeography is the study of the distribution of animals. About 58% of the 28,000 species of fishes are marine, 41% are freshwater species, and 1% move between the two habitats.
2. Four main ecological divisions of marine fishes are: (i) epipelagic, surface-dwelling species (about 1% of all fishes); (ii) deep pelagic species (5%); (iii) deep benthic species (6%); and (iv) inshore, littoral, or continental shelf species (46%).
3. Inshore marine fishes occur in four major regions, in order of decreasing biodiversity: Indo-West Pacific, western Atlantic, eastern Pacific, and eastern Atlantic.
4. Vicariance biogeography combines phylogenetic information with distribution patterns to assess relative movements of biota or habitat. Vicariant events (historical events such as the movement of continents, stream capture, etc.) that divided populations often explain present distributions.
5. Freshwater fishes are surprisingly diverse, accounting for 41% of the world's fish species, although fresh water constitutes only 0.0093% of the planet's water.
6. Six freshwater regions are the: (i) Nearctic region (North America except tropical Mexico), with 14 families and about 950 species; (ii) Neotropical region (South and Middle America), with 32 families and more than 4500 species; (iii) Palearctic region (Europe and Asia north of the Himalayas), with 14 families, with many minnows and loaches; (iv) African (or Ethiopian) region, with 47 families and 2900 species, including many primitive species; (v) Oriental region (India, southern China, Southeast Asia, the Philippines, and the East Indies to Wallace's Line), with 28 families, including 12 families of catfishes and four cypriniform families, and about 3000 species; and (vi) Australian region (Australia, New Guinea, and New Zealand), with only two primary freshwater species, both ancient relicts of a much wider archaic distribution pattern.
7. Six groups of primitive primary freshwater fishes have ancient distributions best explained by continental drift: lungfishes, bichirs, paddlefishes, gars, Bowfin, and bonytongues.
8. Most primary freshwater fishes belong to the Ostariophysi, which includes the Cypriniformes, Characiformes, Siluriformes, and Gymnotiformes. Cypriniform carps, minnows, loaches, and suckers are found primarily on the northern continents. Characiform characins comprise 10–16 families, with greatest diversity in South America (200 genera, more than 1000 species) but with 23 genera and 150 species in Africa. Siluriform catfishes, which include 34 families and about 2000 species, occur on all continents. Gymnotiform electric fishes comprise six families restricted to South America.

Supplementary reading

SUPPLEMENTARY READING

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Website

http://research.amnh.org/ichthyology/congo/.

Chapter 17

Fish genetics

Chapter contents

CHAPTER CONTENTS

DNA is the blueprint of life, and evolution is the architect. Across the 530 million year history of fishes, natural selection has continually modified the blueprint to accommodate challenges and new opportunities. The result today is about 28,000 species with unique genetic features, and within each species are thousands or millions of genetically unique individuals. Scientists have learned to read the DNA blueprint in recent decades, and have begun to resolve the history written there. Genetic studies can resolve relationships from family pedigrees to the most ancient vertebrate lineages. Between these extremes, genetic surveys are useful for discovering new species, and resolving biogeographic patterns (see Chapter 16) and management units in conservation (see Chapter 26).

Genetics contains many specialties. For example, cytogenetics is the study of chromosomes, ecological genetics can reveal breeding behavior, population genetics is used to define management units (or stocks) for fisheries, evolutionary genetics demonstrates the basis of novel organismal traits, and molecular phylogenetics is the application of DNA data to resolve branches in the tree of life. Accordingly, this chapter is divided into six sections on genomics, molecular ecology, population genetics, phylogeography, molecular evolution, and conservation genetics.

The jargon barrier

To many students of fish biology, the topic of genetics can seem dry, jargon-laden, and (worst of all) lab based. It is true that some fish geneticists wear lab coats instead of scuba gear, and discuss base pairs instead of bait, sufficient to raise suspicions about their motives. However, genetics is also a diverse and exciting field that has a lot to offer ichthyologists, especially in the focal point of this book, the diversity of fishes. Like many disciplines, the field of genetics has a vocabulary that can be challenging to those unfamiliar with the concepts and terminology. Therefore, the first five sections of this chapter begin with a box briefly introducing the concepts and terms needed to understand the reading that follows.

Fish genomics

Genomics is the study of the entire DNA sequence of an organism, which in fishes includes the small mitochondrial genome and the enormous nuclear genome that can contain over a billion **base pairs (bp)**. The earliest explorations of fish genomics were **chromosome** counts and **karyotypes**, but genomics now refers primarily to the intensive efforts to record the entire nuclear genome for many species. In the late 1990s, the technology applied to the Human Genome Project was redirected towards fishes and other vertebrates, and a cottage industry of fish genome projects is emerging. As of this writing, four fish genomes are completely described: Zebrafish (*Danio rerio*), Medaka (*Oryzias* sp.), and two pufferfishes. Carp (*Cyprinus carpio*), cichlid (genus *Tilapia*), and salmon (genus *Oncorhynchus*) are the subject of upcoming genome projects, and doubtless this list will be expanded over the next several decades.

DNA Deoxyribonucleic acid, composed of four building blocks known as **nucleotides**: adenine, cytosine, guanine, and thymidine, usually abbreviated as A, C, G, and T. These building blocks form long strings called **DNA sequences** that can be compared to learn interesting things about fishes. DNA sequences are usually high-quality data because they are verifiable and replicable.

Base pairs (**bp**) These are the units of double-stranded DNA (paired nucleotides). The length of a DNA sequence is usually measured in base pairs or nucleotides, which mean the same thing in this context. Fragments as small as 100 bp can be informative in population genetics and pedigree analyses, and for identifying the species present in stomach contents and feces. For phylogenetic comparisons, fragments in excess of 500 bp are preferred, and fragments longer than 1000 bp are the current standard. Variants on bp include **kb** (thousands of base pairs) and **mb** (millions of base pairs). As DNA analyses get faster and cheaper, the data sets get larger and now include whole genomes.

Diploid nuclear DNA (**nDNA**) Nuclear DNA includes the chromosomes that are typically inherited in pairs, one copy from each parent (except for those fishes with separate sex chromosomes). In this **diploid** state (often refered to as **2N**), every cell has two copies of each DNA sequence that may be identical (**homozygous**) or slightly different (**heterozygous**). Studies of fish evolution have employed **intron** sequences (see below) including intron six of lactate dehydrogenase-A (LDHA6), and intron seven of creatine kinase (CKA7) (Quattro & Jones 1999; Hassan et al. 2002). Other commonly used sequences include the recombination activation genes (RAG-1 and RAG-2), and the ribosomal gene 28S rDNA. Some nuclear sequences such as Tmo-4C4 have been discovered and used for genetic comparisons without prior knowledge of their function (Karl & Avise 1993; Streelman & Karl 1997).

Haploid mitochondrial DNA (**mtDNA**) This is a closed circle of double-stranded DNA, usually around 16,500 bp in fishes and other eukaryotes. This small genome is believed to be descended from a bacterium that entered the cells of a metazoan ancestor on the order of 600 million years ago, long before the first fishes arose (Margulis 1970). This genome is in the mitochondria, the energy-producing organelles of the cell that reside outside the nucleus. There can be hundreds of mitochondria in each cell, so mtDNA usually exists as many copies of a single identical sequence (**haploid**, denoted as **1N** in contrast to diploid 2N nDNA). This genome has protein-coding genes that mutate faster than most nDNA genes, and these provide good resolution of populations as well as evolutionary lineages at the taxonomic level of genus and species. Typical fish studies will use mtDNA sequences from cytochrome *b* or cytochrome oxidase, two genes that code for proteins. The more slowly evolving ribosomal genes (12S and 16S rDNA) are used for phylogenetic studies on the deeper taxonomic scale of genera, families, and orders. Another mtDNA segment, known as the **control region**, does not code for a protein product, but is a scaffold for DNA replication. Like introns (see below), this area can accumulate mutations more rapidly than protein-coding regions, and for that reason is favored for resolving fine-scale **population structure** (see below, Population genetics).

Gene A segment of DNA that is the blueprint for a particular protein or ribosomal RNA. There are over 30,000 genes in fishes.

Karyotype These are chromosomes visualized by histological staining, and characterized by comparing their number, shape, and size. Rare genomic rearrangements can be detected, and these are valuable for discerning evolutionary history, usually above the taxonomic level of species and genus.

Intron and exon Many genes are made up of segments that are translated into transfer RNAs (tRNAs), ribosomal RNAs (rRNAs), and proteins. These functional units are called exons, and they are separated by segments of noncoding DNA known as introns. While the functional significance of this arrangement is not completely understood, the introns usually accumulate mutations more rapidly than the exons. Intron sequences are used to construct evolutionary trees and assess the relationships between species; however they have also been used for population surveys.

Polymerase chain reaction (**PCR**) This is a method that allows researchers to make millions of copies of a DNA sequence in a few hours. PCR requires short DNA **primers** (usually about 20 nucleotides long) that attach to each end of the DNA sequence of interest. Hence one limitation is that you need information about the DNA sequence in order to design primers. Fortunately there are now mtDNA and intron primers that work on a broad range of fishes. PCR is the indispensable starting point for most molecular genetic surveys of fishes. It also allows DNA sequence information to be recovered from very small amounts of tissue (fin clips, scales, muscle biopsy, a drop of blood; see Box 17.1) and

partially degraded tissues such as stomach contents and feces.

Automated DNA sequencing DNA sequencing previously was performed with cumbersome polyacrylamide gels, using a number of toxic and radioactive chemicals. Starting about 1990, this methodology was replaced with automated machines that could use much less hazardous chemicals. A DNA sequence that used to cost more than US$50 to produce can be obtained for less than $10 with the automated technology, and the price continues to fall. Where previously a hard working scientist could produce perhaps 500 DNA sequences per year, machines like the Applied Biosystems Prism® 3100 Genetic Analyzer can produce over 600 sequences per day. DNA data are now readily accessible for a modest budget, and fish phylogeography studies of 200–500 specimens may entail less than $10,000 in lab costs.

Genbank http://www.ncbi.nlm.nih.gov/Genbank/ is a repository for DNA sequence data. The online service includes a search option that will find the closest matches to a DNA sequence provided by the user. This can be very useful for identifying an unknown specimen, or for finding the closest relative to a fish.

Genome size

Fish genomes include 21 to 100+ chromosomes in the nuclear genome (nDNA) with two copies of every gene in most (diploid) species. Some 58% of examined teleosts (334 out of 580 species) have 48 or 50 chromosomes (Naruse et al. 2004), and 48 is believed to be the ancestral state for ray-finned fishes. Despite this conservation of chromosome number, overall genome sizes can differ by more than two orders of magnitude, with the lungfish having the largest fish genome (81.6 pg of DNA in a set of chromosomes), the bichir having the largest actinopterygian (ray-finned fish) genome (5.85 pg), and the tetraodontiforms (such as pufferfish) having the smallest genomes (0.35 pg (Table 17.1), compared to 3.4 pg in the human genome. The number of chromosomes and genome size can vary even within a single genus (see the *Oncorhynchus* examples in Table 17.1). Three trends in genome size are apparent:

1. There is a progressive reduction in DNA content from the earliest to the most advanced bony fishes.
2. Apart from lungfishes, elasmobranchs have the largest fish genomes, with 3–34 pg of DNA (Stingo & Rocco 2001). In contrast, the holocephalians (the other major group of cartilaginous fishes) have among the most compact genomes (1.2–1.9 pg; Venkatesh et al. 2005).
3. In general, freshwater fishes have larger genomes than marine fishes (Yi & Streelman 2005). This is attributed to smaller population sizes in freshwater fishes, which can reduce the power of natural selection to produce a compact genome.

It is notable that fishes with the most radically derived morphology (tetraodontiforms) have the smallest nuclear genome. The pufferfish (genus *Fugu*) provided an ideal candidate for the first fish genome study, having much the same set of genes observed in mammals, but in a package eight times smaller than the human genome. The insights from the first round of fish genome studies are many, and highlights include:

- Genomes are dynamic with many rearrangements between species and sometimes within species. Segments of the genome that are similar between fishes and mammals are rarely longer than four genes.
- Previous estimates of the vertebrate genome ranged from 60,000 to 150,000 genes, but that number now appears to be 30,000–40,000 genes.
- There are regions of the genome of unknown function that are high conserved (very similar) between fishes and mammals. High similarity between fishes and mammals indicates that these gene regions have important functions that are under strong natural selection.

Polyploidization and evolution

Polyploidization is the wholesale duplication of the nuclear genome, and most authorities agree that such an event lies near the base of the ray-finned fish (Actinopterygian) evolutionary tree. Such events are rare but important in the evolution of fishes. Ohno (1970) proposed that gene duplication is essential for major evolutionary innovations in vertebrates, as opposed to the single nucleotide mutations that can distinguish populations and species. In this view, the duplicated genes are under relaxed selection pressure, because there are now four copies (instead of two) available to get the job done. When polyploidy occurs, the original function of the gene can be maintained, freeing the extra copies to develop new functions (**neofunctionalization**), or they can double the capacity of a crucial metabolic pathway. Over tens of millions of years, some of the duplicated genes will prove to be redundant and lose their function in a process known as **diploidization** (returning to the diploid state). The few genes that are retained may allow evolutionary innovations.

Table 17.1

Chromosome number, nuclear genome size, and mitochondrial genome size in select fishes. C-values indicate the amount of DNA in a haploid complement (a single copy of the chromosomes), measured in picograms per cell. References for chromosome number and C-value are available from the Animal Genome Size database (http://www.genomesize.com). The nuclear genome sizes, in millions of base pairs (mb), are from Roest Crollius and Weissenbach (2005). References for mitochondrial genome sizes are given, and sizes are presented in thousands of base pairs (kb). In some cases the chromosome number could not be obtained from the same species used to estimate genome size, so values are obtained from congeners (fish in the same genus) as follows: the chromosome number for *Anguilla japonica* is based on congeners *A. rostrata* and *A. anguilla*; for *Sardinops* it is based on *S. sajax*; for *Fugu* on *F. niphobles*; and for *Tetraodon* on *T. palembangensis*. The mtDNA genome size for dogfish is based on *Scyliorhinus canicula*.

Species	Number of chromosomes	Nuclear genome size (C-value/mb)	Mitochondrial genome size (kb)
Sea lamprey *Petromyzon marinus*	168 (Vialli 1957)	2.44/n.a.	16.201 (Lee & Kocher 1995)
Great White Shark *Carcharodon carcharias*	82 (Schwartz & Maddock 1986)	6.45/n.a.	n.a.
Dogfish *Squalus acanthias*	60 (Pedersen 1971)	6.88/n.a.	16.696 (Delarbre et al. 1998)
Coelacanth *Latimeria* spp.	48 (Cimino & Bahr 1974)	3.61/n.a.	16.446 (Inoue et al. 2005)
Lungfish *Protopterus dolloi*	68 (Vervoort 1980)	81.6/n.a.	16.646 (Zardoya & Meyer 1996)
Bichir *Polypterus ornatipinnis*	36 (Bachmann 1972	5.85/n.a.	16.624 (Noack et al. 1996)
Eel *Anguilla japonica*	38 (Hinegardner & Rosen 1972)	1.40/n.a.	16.685 (Inoue et al. 2001)
Sardine *Sardinops melanostictus*	48 (Ida et al. 1991)	1.35/n.a.	16.881 (Inoue et al. 2000)
Carp *Cyprinus carpio*	100 (Hinegardner & Rosen 1972)	1.70/n.a.	16.575 (Chang et al. 1994)
Zebrafish *Danio rerio*	48 (Hinegardner & Rosen 1972)	1.8/1700	16.596 (Broughton et al. 2001)
Stickleback *Gasterosteus* spp.	42 (Hinegardner & Rosen 1972)	0.70/675	
Chinook Salmon *Oncorhynchus tshawytscha*	56 (Ojima et al. 1963)	3.04/3100	16.644 (Wilhelm et al. 2003)
Rainbow Trout *Oncorhynchus mykiss*	60 (Rasch 1985)	2.60/2700	16.660 (Zardoya et al. 1995)
Medaka *Oryzias* sp.	48 (Uwa 1986)	0.95/800	
Pufferfish *Fugu rubripes*	44 (Ojima & Yamamoto 1990)	0.42/380	16.447 (Elmerot et al. 2002)
Green Pufferfish *Tetraodon nigroviridis*	42 (Hinegardner & Rosen 1972)	0.35/350	

n.a., not available.

Dramatic support for Ohno's model of evolution came from the Zebrafish (*Danio rerio*) genome, and the discovery of seven **HOX genes** (important regulators of morphological development during embryonic growth). In mammals there are four HOX genes on four chromosomes, whereas the Zebrafish lineage apparently had eight HOX genes on eight chromosomes, followed by the loss of one copy (Amores et al. 1998). The pufferfish genomes provide additional evidence of gene duplication and neofunctionalization.

When did this early genome duplication occur? The duplication does not appear in sturgeon or gar, but is shared by all surveyed teleosts (Hoegg et al. 2004). Hence this event must have occurred in the basal teleost lineage, on the order of 300–400 million years before present (mybp). This genome duplication may have provided a powerful toolkit for diversification of the teleosts, by providing twice as many genes as existed in ancestral fishes (Roest Crollius & Weissenback 2005).

The ancient polyploidization in teleosts is not the only genome duplication in bony fishes. Additional whole-genome duplications have occurred in the ancestors of modern salmon 25–100 mybp (Allendorf & Thorgaard 1984), in catostomids (suckers) about 50 mybp (Uyeno & Smith 1972), and in carp about 12 mybp (David et al. 2003). Partial duplications of the genome are probably more common, either as unequal exchanges during genetic recombination, or the unequal sorting of chromosomes during meiosis. This phenomenon can occur when two species hybridize, as observed in Pocilliiform fishes (guppies and mollies), occasionally giving rise to parthenogenic (unisexual) species (Vrijenhoek 1984; see Chapter 21).

Sex chromosomes

Gender in most vertebrates is determined by either chromosomes or hormones. In fishes both can occur. Most bony fishes and all elasmobranchs investigated to date have an XX/XY chromosome system, with males being the **heterogametic** (XY) sex (Maddock & Schwartz 1996; Devlin & Nagahama 2002). These include the diverse families Cichlidae, Gobiidae, Percidae, Fundulidae, Balistidae, and Salmonidae. A minority of fishes have the ZZ/ZW system, in which females are heterogametic. This arrangement dominates in some widespread families including Serranidae, Characidae, and Synodontidae. Both XY and ZW systems are found in the speciose families Cyprinidae and Poeciliidae, indicating that changes in sex determination systems can occur over relatively brief evolutionary timescales of a few million years (Devlin & Nagahama 2002). In contrast, the sex determination mechanisms in mammals (XY) and birds (ZW) are conserved across tens of millions of years (Mank et al. 2006).

As indicated by the many forms of hermaphroditism in fishes (see Chapter 21), gender defined by chromosomes can be altered by hormonal responses to environmental cues including temperature, season, and social status. For example, sex in the Atlantic Silverside (*Menidia menidia*) is determined by temperature; populations in cool weather can be 25% male, whereas the same population will be 50% male at the peak of summer (Conover & Kynard 1981). Overall, most fishes are **gonochoristic** (hard wired for one sex by chromosomes), but many others are flexible, and sex determination in these species may also be disrupted by organic pollutants that mimic sex hormones (Sumpter 1997; see Chapter 26, Pollution).

Mitochondrial genome

In the first decades of molecular genetic studies, the mitochondrial genome was much more accessible than the nuclear genome because it has more copies per cell, a small size, and is constructed like a single chromosome. Hence the study of mitochondrial genomics has proceeded much more rapidly than nuclear genomics, with over 100 complete fish mtDNA genomes resolved at this time (Miya et al. 2003). In contrast to the nuclear genome, the mtDNA has retained the same genes in the same locations and genome size is very similar across the vertebrates (Table 17.1). In fishes and most other vertebrates, the mtDNA genome encodes the information to construct 13 different proteins, 22 tRNAs, 2 rRNAs, and has a distinct segment for the origin of gene replication known as the control region.

Transgenic fishes

There is growing interest in genetically modified fishes to produce pharmaceutical products, novel aquarium pets, and faster growing strains for human consumption. This was originally attempted by "shotgunning", injecting many copies of the desired gene into the nucleus of the eggs, a process with a very low success rate. Subsequent methods have grown more sophisticated, using viruses that can insert desired genes into a chromosome (Dunham 2004).

The first genetically modified fish was announced in 1984, based on Rainbow Trout (*Oncorhynchus mykiss*) eggs injected with a metallothionein (toxic metal resistance) gene (Maclean & Talwar 1984). Another early success was a transgenic Nile Tilapia (*Oreochromis niloticus*) modified with a gene for growth hormone. It attained three times the size of normal tilapia (Martinez et al. 1996). Rainbow Trout and Coho Salmon (*Oncorhynchus kisutch*) have also been modified with a salmon growth hormone gene that produced larger fish (Devlin et al. 2001). The first transgenic aquarium fish is the **glofish®**, a Zebrafish (*Danio rerio*) with red, green, and orange fluorescent colors (http://www.glofish.com/). This fluorescence gene may eventually be used to detect aquatic pollution by switching on a bright color in fishes that are exposed to environmental contaminants.

Many authorities regard transgenic fishes as a potential boon to aquaculture, allowing higher survival, faster growing fishes, and larger yields. Indeed, genetically modified fishes have the potential to alleviate hunger and promote human health in impoverished corners of the globe. However, other authorities warn of the hazards of transgenic fishes escaping into the wild (Muir & Howard 2002). These hazards are similar to those of alien fish introductions (see Chapter 26), with the additional threat that transgenic fishes could breed with native stocks. In a study of a transgenic Medaka (*Oryzias latipes*), the modified males had greater mating success when introduced into a natural population, presumably because of their larger size, but their offspring had significantly lower survival. In these circumstances, accidental introduction of transgenic fishes might jeopardize future reproduction, possibly leading to extinction (Muir & Howard 1999). Clearly the benefits of this technology have to be balanced against significant risks.

Molecular ecology

Terrestrial zoologists are fortunate in that they can observe the behavior of study organisms with relative ease. Yet when molecular assays are applied, it becomes apparent that these studies can miss important facets of life history, especially in breeding biology. Perhaps terrestrial zoologists are complacent, or sleep too much. Regardless of the explanation, these problems are compounded in the aquatic medium, as observations of natural behavior are more difficult to make and are often limited in duration.

Locus (plural **loci**) This is a segment of DNA, usually corresponding to a gene (for allozymes) or a segment of repeat sequences (for microsatellites). If a paper describes results from 10 loci, it means the study surveyed 10 distinct segments of the genome.

Alleles These are different versions of a gene, locus, or DNA sequence. They can diverge by many mutations or as little as one mutation. A typical allozyme survey may reveal one to six alleles at a locus, whereas a microsatellite locus can have upwards of 30 alleles at a locus. Gene flow between populations can be estimated by the differences in frequency of alleles.

Allozymes This is the workhorse methodology for fish genetics over the last 30 years. Allozymes are the protein products of individual genes in the nDNA. Proteins are loaded on a gel and subjected to an electric field. The gel acts like a sieve to separate molecules based on differences in amino acid composition (and corresponding electric charge). Distinct alleles can be identified because they move through the gel at different rates. For example, alcohol dehydrogenase (an enzyme that breaks down ethanol) can exist in three versions in salmon. Allozyme surveys have been widely applied to test for **population structure** (see below, Population genetics) and to assess genetic differentiation among congeneric species (Shaklee & Tamaru 1981), but less frequently used to resolve deeper evolutionary separations.

Microsatellites These are nDNA segments composed of short repeats of two, three, or four nucleotides, such as CA-CA-CA. When the DNA is copied during cell replication, sometimes mistakes are made, and a "CA" is added or deleted. Microsatellite loci are also known as **VNTRs** (variable-number tandem repeats) because the alleles differ by the number of repeats. Differences in the length of a microsatellite allele can be detected with gel separation. A high mutation rate and very high **heterozygosity** (see below, Population genetics) make these microsatellites the method of choice for resolving relationships from family pedigrees to closely related populations, and have provided valuable insights into the breeding systems of fishes. This is the most widely used genetic marker in the category of **DNA fingerprints** that can diagnose individuals with a high degree of certainty. However, the high mutation rate entails a risk of misinterpretation at higher evolutionary levels, so microsatellites are generally not an appropriate tool for phylogenetics.

Genotype This is the description of the alleles at a locus, indicating which two alleles occur at a diploid locus. For example if a microsatellite locus has 31 repeats of a simple two-base sequence (CA-CA-CA . . . for example) on one allele, and 33 repeats on the other allele, then the genotype is described as 31/33.

Haplotype This is the same as a genotype, but applied to the haploid mtDNA genome. Different haplotypes are distinguished by one or more mutations, and are typically given letter or number designations. For example, if haplotype 6 is observed in a reef fish at high frequency (80%) in a Caribbean population, but at low frequency (20%) in a Brazilian population, this would indicate a strong population genetic separation.

Tissue collections for genetic analysis: get involved!

In the period when allozyme studies dominated population genetics, practitioners had to carry dry ice or cumbersome vats of liquid nitrogen to their field locations to collect and preserve fresh tissue. Many older ichthyologists remember this era of difficult methods, and they shunned collections of genetic materials as part of their field activities.

These days the collection of material for genetic analysis could hardly be easier. The PCR process (see above) requires only small quantities of intact DNA. No freezing or refrigeration is necessary to preserve specimens, and a tiny amount of tissue (less than 0.5 g) is sufficient for DNA analyses. The field collector only has to prevent DNA degradation by bacteria, fungi, or harsh environmental conditions. This can be accomplished by storing tissue in isopropyl alcohol (>50% preferred), ethanol (>70% preferred), or a saturated salt (NaCl) solution (Box 17.1). In a pinch, ichthyologists have used distilled spirits, which are usually available at even the most remote field sites.

Today's collecting kit for fish genetics is no larger than a lunch box, and contains no toxic or corrosive materials that might complicate air travel. Any field expedition can include one. Even if the field researchers are not directly interested in genetic analysis, they can support tissue collections that advance many areas of ichthyology. The University of Kansas Natural History Museum maintains one of the oldest and largest fish tissue collections (http://nhm.ku.edu/fishes/).

Genetic resolution of breeding systems

Molecular genetics in general, and microsatellite markers in particular, have launched a renaissance in the field of reproductive biology. Previous conclusions about breeding systems that have accrued over many decades, often requiring labor-intensive observations, can now be efficiently tested with individual-specific genetic markers. Questions about **monogamy** (couples mating only with each other), multiple paternity and maternity in egg clutches, egg thievery, and cuckoldry can be resolved. Microsatellites also allow genetic reconstructions of family pedigrees with a high degree of certainty. These genetic tools have highlighted the distinction between social mating systems, as defined by behavior, and genetic mating systems, as defined by relationships in a DNA-based pedigree. For example, social monogamy in nesting fishes is often coupled with genetic cuckoldry, indicating that fidelity among mates is less widespread than previously assumed.

Multiple paternity or maternity in a clutch of eggs can be readily detected based on the number of alleles observed at microsatellite loci. The methodology is straightforward in diploid organisms: survey individuals in a brood (eggs or offspring) with microsatellite markers. At each **autosomal** (not sex-linked) locus, the maximum number of alleles in the offspring of a monogamous brood is four (two from the mother, two from the father). If five or six alleles are detected, at least three parents (usually including two fathers) are contributing, if seven or eight alleles are detected then at least four parents are contributing. Usually these assays are conducted with three or more microsatellite loci to attain reliable estimates of the number of parents.

To accurately reconstruct family relationships and corresponding breeding systems, it is preferable to genetically survey all candidate parents for a brood of offspring. While this may be achievable in large mammals (including humans), it is seldom a practical goal with fishes, and is impossible in pelagic-spawning marine fishes. In these cases, statistical methods can be employed, particularly maximum likelihood, to estimate parental assignments (Bernatchez & Duchesne 2000).

Marine fish with pelagic larvae

The level of multiple paternity/maternity in marine fishes with **pelagic** (oceanic; see Chapter 16) larval dispersal is unknown. In fishes that spawn in aggregations (including many pelagic fishes), monogamy could be uncommon. On the other hand, fishes that breed as stable pairs (including many coral reef fishes) could have a high degree of monogamy. For these cases, researchers have long wondered whether siblings could stay together during the pelagic larval phase, and recruit to the subadult habitat as a group of related individuals (Shapiro 1983). This runs counter to the long-held view that marine fish larvae are highly dispersive. Indeed the first genetic test of kinship in young-of-year reef fishes, based on three allozyme loci, found no evidence of related individuals in the Red Sea serranid *Anthias squamipinnis* (Avise & Shapiro 1986), and the same conclusion was forwarded recently for the clownfish *Amphiprion percula*, based on seven microsatellite loci (Buston et al. 2007).

However, several recent lines of evidence indicate that fish larvae have advanced swimming and navigational skills (Leis & Carson-Ewart 2000b) and some can recruit back to their region of origin (Jones et al. 2005). These observations resurrect the possibility that kin groups (siblings) can remain together in the pelagic phase and settle out on the same reef habitat. Three recent studies provide evidence for this behavior. Planes et al. (2002) used allozymes to survey juveniles of the Unicornfish (*Naso unicornis*) recruiting to Pacific reefs and observed high relatedness within these groups. Pujolar et al. (2006) found high relatedness within some cohorts of the catadromous eel (*Anguilla anguilla*) recruiting to European streams. These findings are remarkable given that European eel larvae may spend more than a year in the pelagic zone prior to transforming

Box 17.1

Protocol for collecting genetic material using SED buffer

A saturated salt (SED) buffer can be prepared in any basic lab. This SED buffer contains salt (NaCl), EDTA (ethylene diamine tetra-acetic acid) to maintain pH 7.5, and DMSO (dimethyl sulphoxide) to increase the penetration of the salt buffer. Note that the EDTA and DMSO are not strictly necessary for short-term storage (weeks or months). A simple saturated NaCl solution will suffice, however the full buffer is recommended for long-term storage and optimal DNA recovery. No refrigeration or freezing is required.

Materials

- SED buffer in tubes. We recommend screw-cap 2 ml tubes arranged in boxes of 100 tubes. Both tubes and boxes are inexpensive and readily available from lab suppliers.
- Tweezers and single-edge razor blade (or scalpel).
- XMarker pen, tube labels, and data sheets to record species, date, and location information.
- Disposable gloves (optional).

Tissue source

Almost any tissue will suffice. Typical DNA sources are fin clips or gill rakers, but tissue plugs work well and may be desirable for nonlethal sampling. Muscle, liver, blood, or gonad are also good sources. Tissues that have been previously frozen will work, and even dried tissue may work. Several researchers have managed to get DNA data from archived scale collections, presumably due to attached bits of dried tissue. Note that tissues immersed in formalin usually do not work. Formalin degrades DNA, so museum specimens may not be usable.

Collecting tissue

1. Take a tissue sample about half the size of a pencil eraser-head or 0.5 cm^2 of fin or other tissue.
2. Add tissue to numbered tube with SED buffer.
3. Record species, location, date, and specimen number if available.
4. Clean or rinse cutting tools between each specimen.
5. Avoid extended exposure to intense heat or sunlight.

Protocol notes

1. To make 1 L of SED buffer use the following procedure
   - Dissolve 95 g tetrasodium EDTA in 700 ml distilled water (or cleanest source).
   - Adjust pH to 7.5 with glacial acetic acid.
   - Saturate with NaCl, about 200 g. Allow salt to dissolve completely.
   - Add 200 ml DMSO, bring up to 1 L with distilled water.

This protocol is modified from Proebstel et al. (1993).

2. SED buffer is nontoxic, nonflammable saline solution. It can be carried in airline luggage without special permits and can be stored indefinitely at room temperature. Since this buffer contains saturated salt (NaCl), you may find a white precipitate in some tubes. This does not affect the ability of the buffer to preserve tissue.
3. Handling SED buffer without disposable gloves may result in exposure to DMSO, which is absorbed into skin very rapidly. It is a common remedy for muscle aches, so it should not be hazardous at these concentrations. However, it will produce a garlicy taste in your mouth along with a comparable breath odor. If you anticipate a romantic encounter in the near future, we recommend that you wear latex gloves when handling DMSO.

into juveniles. Selkoe et al. (2006) conducted microsatellite surveys to assess recruits of the Kelp Bass (*Paralabrax clathratus*) on the West coast of North America. The application of kinship tests, not available to previous studies, revealed siblings and half-siblings (sharing one parent) in seven out of 40 samples. Hence evidence of kinship among recruits of marine fishes is increasing. However, these studies indicate that the phenomenon is not consistently observed in all groups of recruits, even within a single species and region.

Nesting fishes

Among the egg-laying (**oviparous**) fishes, nest guarding (usually by males) occurs in marine and anadromous fishes but is most common in freshwater species. Here the genetic surveys support previous suggestions that monogamy is frequently subverted by **sneaker males** (those that do not maintain a nest but deposit sperm into other nests) and other forms of cuckoldry, nest takeovers, and egg thievery. Furthermore, genetic studies have begun to reveal the success rate of these alternative breeding strategies. In a review of the genetic literature on the mating systems of fishes, DeWoody and Avise (2001) reported that when males guard the nest, on average they retain about 70–95% of paternal contributions. The remainder can be either from males that maintain nearby nests, or sneaker males. In this review of 10 species and 177 nests, one-third of nests showed evidence of cuckoldry, and no species was without some level of multiple paternity within nests.

In addition to multiple paternity in male-guarded nests, egg contributions from multiple females are common. In those genetic surveys, microsatellite surveys were augmented with maternally inherited mtDNA, whereby the number of haplotypes indicates a minimum number of mothers. Based on a summary of 10 species, DeWoody and Avise (2001) reported a range of one to 10 mothers per nest, with an average of 3.1 females/nest. In the same survey, the authors reported that eggs from a single female are routinely found in multiple nests. In nesting fishes, cuckoldry works both ways but is rarer in females (Avise et al. 2002).

Egg thievery is a puzzling phenomenon wherein nesting males steal clumps of fertilized eggs from other nests – eggs that have no genetic contribution from their new guardian. In a survey of 24 nests in the 15 spine sticklebacks (*Spinachia spinachia*), four had eggs that were probably stolen, as indicated by no maternal or paternal affiliation with nest mates (Jones et al. 1998). Why would a male deliberately guard and hatch eggs that are not his own? The most accepted explanation is that stolen eggs "prime" the nest for subsequent egg laying. Neophyte males may pose as successful breeders and guardians, thereby increasing their attractiveness to discriminating females.

Live-bearing (viviparous) fishes

Internal fertilization guarantees that the caretaker is the biological mother in all cases. However, rates of multiple paternity are variable across the (primarily freshwater) fishes that bear live young. Chesser et al. (1984) used allozymes to survey broods of the Mosquitofish (*Gambusia affiinis*), concluding that 56% of females contained embryos from multiple males. However, a re-examination of this species with microsatellites revealed that the multiple paternity rate is near 100% (Zane et al. 1999). The available evidence indicates that multiple paternity is common and widespread in the live-bearing fishes, as originally predicted by Chesser et al. (1984).

All elasmobranchs have internal fertilization (but see Box 17.2), and most give birth to live young, although a minority, including skates (Rajiformes), horn sharks (Heterodontiformes), and Chimaeras (Chimaeriformes), lay egg sacks. Regardless of the oviparous or viviparous pathway, internal fertilization again guarantees that the female is the biological mother, and also seems to promote multiple paternity. Daly-Engel et al. (2006) used microsatellite data to detect multiple paternity in two out of three surveyed members of genus *Carcharhinus* (requiem sharks), indicating that the phenomenon may be widespread in elasmobranchs. Microsatellite surveys demonstrated that about 40% of Sandbar Shark (*Carcharhinus plumbeus*) litters in Hawaii are multiply sired (Daly-Engel et al. 2007), compared to 86% of Lemon Shark (*Negaprion brevirostris*) litters in the Bahamas (Feldheim et al. 2004), and about 19% of Bonnethead (*Sphyrna tiburo*) litters in the Gulf of Mexico (Chapman et al. 2004). Hence the limited data indicate that multiple paternity is common but highly variable in elasmobranchs.

Mouth-brooding (oviparous) fishes

Fishes in the family Cichlidae have independently evolved mouth brooding in several genera, wherein fry are retained (primarily in the mother's mouth) after hatching (Goodwin et al. 1998). The few genetic surveys conducted to date demonstrate both multiple paternity and (more surprisingly) multiple maternity in female mouth-brooders. In the Blue Cichlid (*Pseudotropheus zebra*), microsatellite markers demonstrate multiple paternity in six of seven broods, and the female brooding the eggs was the mother in all cases (Parker & Kornfield 1996). In the Lake Tanganyika mouth-brooder *Tropheus moorii*, however, 18 of 19 broods examined with microsatellites had a single father (Egger et al. 2006). In the Lake Malawi mouth-brooder *Protomelas spilopterus*, microsatellite analyses reveal that four of six mouth-broods in females contained unrelated young at frequencies of 6% to 65% (Kellogg et al. 1998). In other words, females are brooding young from other members of their species. While this may be a simple mix-up between adjacent females, or maladaptive behavior, hypothesized benefits include attraction of mates, increased survivorship of siblings by dilution effect, and kin selection (aiding close relatives).

It is not clear that the mating behavior of mouth-brooders should be different from other egg-laying (oviparous) fishes. However, mouth brooding apparently confers much stronger population genetic structure than other reproductive behaviors, by eliminating the larval stage and reducing juvenile dispersal (see below, Population genetics). Both the mouth-brooding Banggai Cardinalfish (*Pterapogon*

Box 17.2

Parthenogenesis and the virgin shark

The diversity of fish reproductive strategies is reviewed in Chapter 21, including hermaphroditism and parthenogenesis. In the latter cases, the parthenogenetic (all-female) species requires a sperm contribution from a closely related species to initiate egg development (Vrijenhoek 1984). Genetic studies reveal that the male contribution via sperm is either discarded during egg development (**gynogenesis**) or discarded in the next generation (**hybridogenesis**). Hence these parthenogenetic fishes are closely related to sexually reproducing congeners, and are reliant on their sexual mode of reproduction to persist.

Given these circumstances, the scientific world was surprised by the recent discovery of virgin birth in a captive Bonnethead Shark (*Sphyrna tiburo*). There were previous reports of female sharks producing young after long periods in captivity, but these were attributed to cryptic mating activity or long-term sperm storage by females, because the genetic tools to assess parenthood were unavailable until recently. In the case of the virgin birth, the mother was taken from the wild at an age of less than 1 year and maintained in captivity with two other females. Analysis at four microsatellite loci confirmed the parthenogenetic origins of the offspring (Chapman et al. 2006). Notably, all four loci were homozygous for one of the maternal alleles, indicating **automictic parthenogenesis**, wherein two of the mother's (haploid) postmeiotic cells fuse. Rather than reproducing the mother's genome intact, this is analogous to self-fertilization, with a corresponding drop in genetic diversity. Note that the previous cases of parthenogenesis were all-female species, and for that reason relatively easy to detect. This automictic parthenogenesis, in species with two sexes and typical sexual reproduction, is very difficult to detect in the wild. The phenomenon may be more common than scientists realize, especially in rare species with low mate encounter rates.

kauderni, one of the few marine mouth-brooders) and the mouth-brooding tilapia (*Sarotherodon melanotheron*) show strong genetic separations between populations (Pouyaud et al. 1999a; Hoffman et al. 2005).

Pouch brooding and sex role reversal

The remarkable natural history of the family Syngnathidae (pipefishes and seahorses) has elicited much attention because of the "pregnant" (pouch-brooding) males. Just as internal fertilization guarantees that the viviparous female is the mother of offspring, the pouch brooding by male syngnathids assures that cuckoldry is effectively absent. However, microsatellite studies indicate that the rate of monogamy varies from 10% to 100%, as males may carry eggs from a single female or from as many as six females (Jones & Avise 2001). These same studies indicate that females may contribute eggs to more than one male pouch (polyandry).

In most fish species, females make the greater investment in reproduction, and males must compete for the limiting resource, specifically access to egg-laying females. Sexual selection theory maintains that the gender competing for the limited resource will have more pronounced secondary sexual characteristics (such as bright coloration), will be under stronger sexual selection, and will show a tendency towards multiple mating. The sex role reversal of the syngnathids offers a rare mirror image of typical sex roles, and an opportunity to test sexual selection theories (Vincent et al. 1992). In most (but not all) syngnathids, the males' pouches, rather than the females' eggs, are the limiting resource. Hence females compete for space in these pouches and, consistent with theory, display characteristics that are usually associated with males:

1. When sexual dimorphism is apparent in syngnathids, it is usually the females that display the conspicuous ornamentation (Dawson 1985).
2. In the few cases where sexual selection (for reproductive success) has been measured in sygnathids, it is higher in females than males (Jones et al. 2001).
3. Although there is considerable variation in sygnathid mating systems, microsatellite surveys show a range from monogamy to **polyandry** (multiple males mating with a single female), rather than the predominant **polygyny** (multiple females mating with a single male) observed in nesting fishes (Avise et al. 2002).

The research to date generally confirms sexual selection theories that were originally formulated in the realm of male sexual selection and polygyny.

Population genetics

This area of study uses genotype frequencies to distinguish populations. Populations (in the genetic sense) are groups of interbreeding individuals that rarely exchange members with other populations. Population genetic principles are often applied to fisheries' management, to define the **stocks** that are the units of harvest and management. Populations are important **management units** because if one population is depleted, it must recover alone, without being replenished from other populations.

Genetic differences between populations of fishes can range from restricted gene flow between adjacent locations (**shallow population structure**, see below) to ancient separations indicated by diagnostic differences in DNA sequences (**deep population structure**, see below). At the lower end of this spectrum, population-level separations are indicated by significant differences in the frequency of alleles (in nDNA) or haplotypes (in mtDNA). Populations separated by habitat discontinuities (especially in fresh water) or great distances (especially in the ocean) will not freely interbreed, and the consequence of this restriction is usually that the populations "drift" apart in terms of genetic composition. Sometimes these separations are reinforced by natural selection, but often the changes in allele frequencies are due to chance, when one allele at a given locus increases or decreases in one population, and a different allele increases or decreases in another population. As noted below, the level of separation is commonly measured with **F statistics** (F_{ST}, see below) and various analogs, especially ϕ_{ST} for DNA sequence data, with larger values indicating greater genetic isolation.

F statistics These come in many forms, but they all measure departures from random mating, the essence of population structure. $\mathbf{F_{ST}}$ is used with allele frequency data (Wright 1951) and is the most common measure of population structure. F_{ST} basically measures differences in allele frequencies between populations. F_{ST} values range from 0 to 1, with $F_{ST} = 0$ indicating that the two populations are frequently interbreeding, while $F_{ST} = 1$ would indicate that the populations each have a different allele at 100% frequency. $\mathbf{G_{ST}}$ is a modification for haploid data such as mtDNA (Takahata & Palumbi 1985), and $\boldsymbol{\phi_{ST}}$ incorporates both the allele frequency shifts (like F_{ST}) and the DNA sequence divergence between alleles or haplotypes (Excoffier et al. 1992). ϕ_{ST} is the preferred method for most comparisons of DNA sequence data. R_{ST} is used with microsatellite data, to incorporate expectations about how microsatellites mutate (Slatkin 1995). Values as low as $R_{ST} = 0.01$ can indicate a significant restriction on gene flow between populations. An F_{ST} or ϕ_{ST} value above about $\phi_{ST} = 0.10$ would indicate strong population structure and distinct management units (see below, Conservation genetics) in a fishery.

H statistics These are measures of **heterozygosity** (the level of genetic diversity) within populations, and at any locus can range from H = 0 (all individuals have the same identical allele) to H = 1 (all individuals have two different alleles). The corresponding value for haploid mtDNA is ***h***, which is the probability that two individuals drawn at random will have different haplotypes (Nei 1987). The average value derived from fish studies is about H = 0.05 for allozymes (Ward et al. 1994), but about H = 0.60 for microsatellites (DeWoody & Avise 2000), reflecting the much higher mutation rate, and higher diversity, in microsatellites.

Nucleotide diversity, π or θ_π These measure the average DNA sequence divergence (***d***; see below, Phylogeography) between individuals (Nei 1987). These values start at $\pi = 0$ (all members are genetically identical) and rarely exceed $\pi = 0.05$ within fish populations. For example, the Lake Trout (*Salvelinus namaycush*) has $\pi = 0.000$, no measurable mtDNA diversity, in Trouser Lake, Labrador (latitude 56° 32′), an area that was under glacial ice 15,000 years ago. In contrast, the Lake Trout in Seneca Lake, New York (latitude 42° 45′) have $\pi = 0.019$ (Wilson & Hebert 1998). The low genetic diversity in Labrador indicates colonization by a few individuals after the glacial period, ending about 12,000 years ago, whereas the higher genetic diversity in New York indicates an older population.

Effective population size, N_e This is the number of individuals in a population that pass their genes on to the next generation (i.e., the number of successful breeders in the population). This is usually estimated based on the level of nucleotide diversity (π) within populations, wherein high diversity indicates a large stable population. In the marine fishes that produce hundreds of thousands of eggs, N_e can be two orders of magnitude lower than the current population size, probably because of the high variance in reproductive success: most eggs and larvae perish, and few adults contribute to the next generation (Grant & Bowen 1998).

Migration rate, $N_e m$ This is effective population size (N_e) multiplied by the proportion of migrants in a population (m), producing an estimate of the effective

number of migrants per generation, an estimator of gene flow. This is often used without the "e" subscript, or sometimes with an additional "f" subscript ($N_{ef}m$) to denote female effective population size as measured with maternally inherited mtDNA. $N_e m$ can be approximated from F statistics with the equation (Wright 1951):

$$N_e m = (1 - F_{ST})/4F_{ST}.$$

A value higher than $N_e m = 1$ (one effective migrant per generation) is *in principle* sufficient to maintain genetic connectivity among diploid populations, so that populations are unlikely to differ genetically (Hartl & Clark 2006). The critical level of exchange for mtDNA is somewhat higher ($N_e m = 4$) due to maternal inheritance and haploid state. Like effective population size, effective migrants are individuals that migrate to a new population and contribute genes to that population. In most circumstances there are far fewer effective migrants than actual migrants.

Shallow population structure This term refers to groups of individuals that have significantly different haplotype (or allele) frequencies. For example, the soldierfish *Myripristis berndti* is distributed across the Indian and Pacific oceans, and there is a common mtDNA haplotype shared across this range, but it occurs at 45% frequency in the West Pacific, and 15% frequency in the Indian Ocean. The corresponding F statistic ($\phi_{ST} = 0.58$; Craig et al. 2007) indicates that the Indian Ocean and West Pacific contain distinct management units (see below, Conservation genetics). However, the fact that they share this haplotype indicates that they are closely related with shallow population structure, rather than distinct evolutionary lineages (subspecies or species).

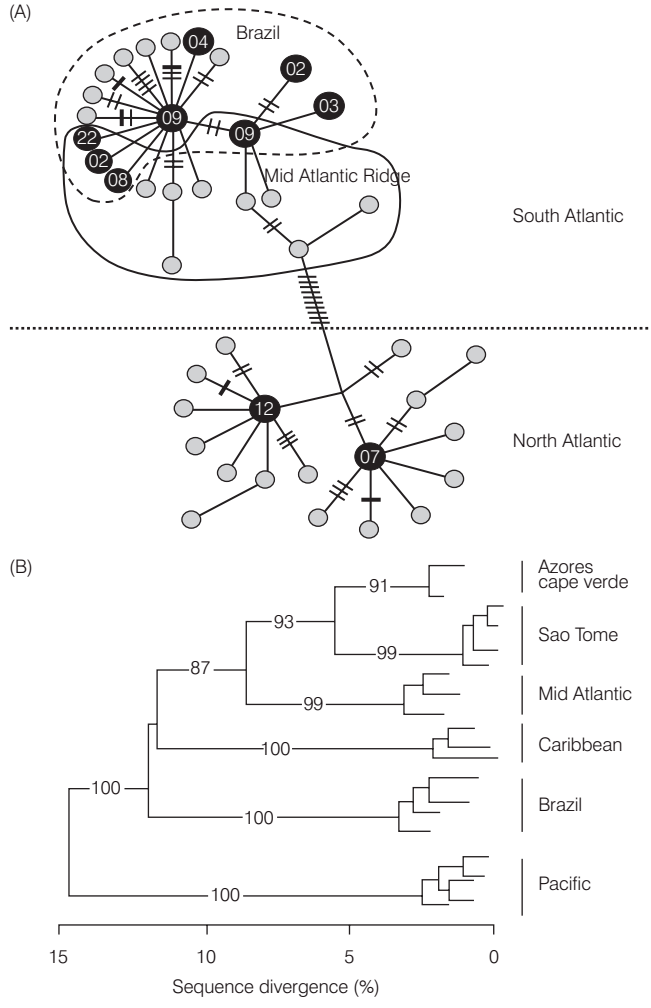


Figure 17.1

(A) A parsimony network (see below, Molecular evolution) for the Ocean Surgeonfish (*Acanthurus bahianus*), based on 608 bp of mtDNA cytochrome *b*. Parsimony networks are one method for describing relationships among mtDNA haplotypes. Each branch (regardless of length) indicates a single mutation. Branches interrupted by hash marks indicate additional mutations. Geographic segregation of haplotypes among regions of the tropical Atlantic (Brazil, Mid-Atlantic Ridge, North Atlantic) is indicated with dotted and solid enclosures. Haplotypes observed in more than one individual are dark (number of individuals shown inside the circle). The Mid-Atlantic Ridge and Brazil share haplotypes, indicating shallow population structure (F statistic $\Phi_{ST} = 0.064$), whereas the North Atlantic population is separated by 11 mutations ($d = 0.024$ sequence divergence; $\Phi_{ST} = 0.724$), indicating deep population structure and possibly an evolutionary separation. (B) Another method for describing relationships among haplotypes is a phylogenetic tree. This is a neighbor joining tree for the Redlip Blenny (*Ophioblennius atlanticus*) from five locations in the Atlantic Ocean, with bootstrap support (see below, Molecular evolution) indicated as a percentage value on each of the major branches. The scale at the bottom indicates the sequence divergence for each branch. The sister species *O. steindachneri* (Pacific) is used as an outgroup (see Chapter 2). Note that the oldest Atlantic branches are in the West Atlantic (Brazil and Caribbean) followed by progressively younger branches in the central Atlantic (Mid-Atlantic) and eastern Atlantic (Sao Tome, Cape Verde, Azores). This suggests a pathway of colonization from West to East Atlantic (see Chapter 16), with the Mid-Atlantic island of Ascension serving as a stepping stone. (A) from Rocha et al. (2002), used with permission; (B) from Muss et al. (2001), used with permission.

Deep population structure This term refers to cases where differences between populations are not based on haplotype (or allele) frequencies, but on accumulated differences in DNA sequences. These populations have been isolated for so long that they do not share any haplotypes due to accumulated mutations (Fig. 17.1A). These are identified by **diagnostic** differences in DNA sequences or alleles that indicate a population is **monophyletic** (every member shares DNA differences not found elsewhere; see Chapter 2). For example, if allozyme studies reveal that population one has allele A at 100% frequency, and population two has allele B at 100% frequency ($F_{ST} = 1$), and this monophyletic pattern recurs across several loci, this indicates deep population structure and an ancient separation between populations, on the order of hundreds of thousands to millions of years ago (Avise 2004). With DNA sequence data, differences between these deep populations are measured in sequence divergence (*d*; see below, Phylogeography) and diagnostic mutations: at one site on the DNA sequence, all the individuals in population one have nucleotide C, all the individuals in population two have nucleotide T, and this pattern is repeated at many sites along the DNA sequence. This condition implies some evolutionary depth, and the relationships between populations can be visualized with a phylogenetic tree rather than expressed with F statistics (Moritz 1994). This is a common condition in surveys of freshwater species, because of the imposing geological barriers between drainages (Roman et al. 1999). Deep population structure may indicate the presence of **cryptic species**, different species that were previously thought to be the same but are distinguished by DNA data. For example, the Atlantic Redlip Blenny (*Ophioblennius atlanticus*), previously thought to be a single species, may include up to five species (Muss et al. 2001) (Fig. 17.1B). Discovering new evolutionary lineages is one of the exciting aspects of fish phylogeography.

Dispersal and population structure

Certain life history traits correspond to shallow or deep population structure, especially those that influence the ability of the fish to disperse, as larva, juvenile, or adult. Hence the first generalization is that levels of population genetic structure are lowest in marine fishes, intermediate in **anadromous fishes** (see Chapter 23), and highest in freshwater fishes (Table 17.2). Sonoran topminnows (*Poeciliopsis occidentalis*) in the southwestern United States, that occupy desert springs separated by a few kilometers, can be isolated for thousands of years (Quattro et al. 1996). In this topminnow and other desert fishes, dispersal opportunities are limited to rare flooding events. At the other end of the spectrum, the Whale Shark (*Rhincodon typus*) has population structure only on the global scale of Atlantic versus Indo-Pacific oceans (Castro et al. 2007).

Genetic diversity (heterozygosity H) also shows a rank order among freshwater (lowest), anadromous (intermediate), and marine (highest) fishes. This is an expected consequence of tremendous differences in population size. Freshwater populations may number in the thousands to millions, whereas their marine counterparts, with much larger ranges, may number in the millions to (in the case of anchovies and sardines) billions. Larger populations will accumulate more genetic diversity (Kimura 1983). There are many exceptions to these trends, but the conclusion of a rank order in genetic diversity is supported by both allozymes and microsatellite surveys (Table 17.2).

If populations are isolated for thousands of generations, they will eventually reach **monophyly** (see Deep population stucture entry above). The rate at which populations diverge depends on the **effective population size** (N_e), with a high probability of monophyly after $4N_e$ generations (Neigel & Avise 1986). Often the condition of monophyly is accompanied, upon closer examination, by morphological differences that indicate previously unrecognized **cryptic species.** However, this is not invariably the case, and scientists may prefer to retain a single taxonomic label that recognizes multiple evolutionary (subspecific) units within a species. The term **evolutionary significant unit** (ESU) was coined for subspecific evolutionary entities that show morphologi-

Table 17.2

Population genetic diversity averaged across three types of fishes, for allozymes (113 species; Ward et al. 1994) and for microsatellites (32 species; DeWoody & Avise 2000). Heterozygosity (H) values are progressively higher in freshwater, anadromous, and marine fishes. Population structure (F_{ST}) values from the allozyme survey are progressively lower in freshwater, anadromous, and marine fishes.

Habitat	H allozymes	H microsatellites	F_{ST} allozymes
Freshwater	0.046	0.54	0.22
Anadromous	0.052	0.68	0.11
Marine	0.059	0.77	0.06

Table 17.3

Comparison of pelagic larval duration and population structure in 15 Atlantic reef fishes. Pelagic larval duration does not have a significant correlation with population structure (ϕ_{ST} values). Surveys are based on mtDNA cytochrome *b* sequences except for the Pygmy Angelfish, which employed mtDNA control region sequences. The pelagic larval duration for Trumpetfish, Rock Hind, Soapfish, and Pygmy Angelfish are estimates from other members of the genus or family. An asterisk indicates species with deep population structure and suspected cryptic evolutionary lineages. From Bowen et al. (2006b).

Species	Mean pelagic duration (days)	Population structure (ϕ_{ST})	Reference for pelagic duration	Reference for population structure
Slippery Dick *Halichoeres bivittatus*	24	0.77*	Sponaugle & Cowen 1997	Rocha et al. (2005a)
Black-ear Wrasse *H. poey*	25	0.23	Sponaugle & Cowen 1997	Rocha et al. (2005a)
Pudding Wife *H. radiatus*	26	0.83*	Sponaugle & Cowen 1997	Rocha et al. (2005a)
Clown Wrasse *H. maculipinna*	29	0.88*	Sponaugle & Cowen 1997	Rocha et al. (2005a)
Pygmy Angelfish *Centropyge* spp.	33	0.62*	Thresher & Brothers 1985	Bowen et al. (2006a)
Redlip Blenny *Ophioblennius atlanticus*	38	0.93*	D. Wilson, pers. comm.	Muss et al. (2001)
Greater Soapfish *Rypticus saponaceous*	40	0.87*	Lindeman et al. 2000	Carlin et al. (2003)
Rock Hind *Epinephelus adscensionis*	40	0.93*	Lindeman et al. 2000	Carlin et al. (2003)
Ocean Surgeonfish *Acanthurus bahianus*	52	0.72*	M. Bergenius, pers. comm.	Rocha et al. (2002)
Blue Tang *A. coeruleus*	52	0.36	B. Victor, pers. comm.	Rocha et al. (2002)
Doctorfish *A. chirurgus*	55	0.02	Bergenius et al. 2002	Rocha et al. (2002)
Blackbar Soldierfish *Myripristis jacobus*	58	0.01	Tyler et al. 1993	Bowen et al. (2006b)
Longjaw Squirrelfish *Holocentrus ascensionis*	71	0.09	Tyler et al. 1993	Bowen et al. (2006b)
Goldspot Goby *Gnatholepis thompsoni*	89	0.47	Sponaugle & Cowen 1994	Rocha et al. (2005b)
Trumpetfish *Aulostomus strigosus*	93	0.59	H. Fricke & P. Heemstra, pers. comm.	Bowen et al. (2001)

cal, behavioral, or genetic differences (Ryder 1986). Moritz (1994) suggested that ESUs could be recognized for populations that are monophyletic with mtDNA sequences. ESUs are often applied in the context of conservation, with an emphasis on higher priorities for ESUs than for populations, as has been applied to Pacific salmonids (see below). While monophyly in DNA assays is not the only way to assign such conservation priorities, this criterion is valuable for distinguishing populations that may have novel genetic characteristics, and may be in the process of speciating. ESUs as defined by monophyly of mtDNA sequences are surprisingly common in fishes, as indicated in Table 17.3, where eight out of 15 surveys of Atlantic reef fishes show evidence of ESUs.

Pelagic larval duration and population structure

The low level of population structure in marine fishes is a consequence of high dispersal, although other factors such as large population size may contribute to this trend. With few hard barriers in the ocean, and with pelagic larval periods ranging from a few days to 2 years, marine fishes have tremendous potential for dispersal. However, recent modeling and field work have disputed the conclusion that all coastal marine fishes have large "open" populations (Cowen 2002; Mora & Sale 2002; Swearer et al. 2002; Jones et al. 2005). Mark/recapture studies have demonstrated a surprising retention of larvae near their region of origin. Taylor and Hellberg (2005) show genetic partitions on a scale of tens of kilometers in the Caribbean cleaner gobies (*Elacatinus* spp.), and as noted in the molecular ecology section above, marine mouth-brooders (family Apogonidae) and pouch-brooders (family Syngnathidae) can have very strong population differences due to limited dispersal as both young and adults (Lourie et al. 2005). On the other hand, some apparently sedentary reef fishes can have little population structure across huge swaths of ocean. The pygmy angelfishes (genus *Centropyge*) show no structure across the central and West Pacific, and across the entire tropical West Atlantic, apparently due to oceanic dispersal of larvae (Bowen et al. 2006a; Schultz et al. 2007). Some fishes may transform from larvae to juveniles but remain in the open ocean for an extended period, as is apparently the case for soldierfishes (genus *Myripristis*), which show no population structure across the entire tropical Atlantic, and across the central and West Pacific (Bowen et al. 2006b; Craig et al. 2007).

Several researchers have made multispecies comparisons of **pelagic larval duration (PLD)** and population structure (measured with F statistics) to forge the intuitive links between PLD, dispersal, and population structure. It seems obvious that if larvae are drifting with oceanic currents, the longer pelagic duration will yield greater dispersal and less population structure. Indeed the first comparisons of pelagic larval duration and genetic connectivity in marine fishes supported this connection. Waples (1987) surveyed 10 species in the eastern Pacific, Doherty et al. (1995) surveyed seven species on the Great Barrier Reef, and both of these allozyme studies found a correlation between PLD and population genetic structure. However, subsequent studies have not replicated this correlation. In surveys of eight reef fishes in the Caribbean Sea (Shulman & Bermingham 1995), eight species on the Great Barrier Reef (Bay et al. 2006), and 15 reef species in the tropical Atlantic (Bowen et al. 2006b), no significant correlation was observed between PLD and population genetic structure (Table 17.3).

What can explain these contradictory results? The explanation likely includes at least three components:

1. The two studies that report a significant correlation between PLD and genetic connectivity (Waples 1987; Doherty et al. 1995) are anchored by species that lack a pelagic dispersive stage, and the significant relationship is weakened or lost without these cases (Bohonak 1999; Bay et al. 2006). Therefore it appears that PLD has some influence on population structure, as is most apparent in the fishes with very short or very long pelagic stages. However, other life history factors such as habitat specificity and larval behavior (see below) are involved as well (Riginos & Victor 2001; Rocha et al. 2002).
2. Fish larvae are not "drift bottles" at the mercy of ocean currents. A growing body of evidence demonstrates that they can swim against currents, navigate, and in some cases remain in the vicinity of appropriate juvenile habitats (Leis & Carson-Ewart 2000b; Swearer et al. 2002).
3. Most of the comparisons are among reef fishes, a category that is not cohesive in any phylogenetic or taxonomic sense. The reef fishes includes lineages that diverged from one another 100+ million years before present (Bellwood & Wainwright 2002). Such relatively great age of separation in other taxonomic groups would mandate comparisons between wolves and baboons, for example. Marine fishes are too diverse to expect a simple relationship between larval duration and dispersal.

Habitat preference

In resolving population structure of marine fishes, most attention has focused on the dispersive larval stage. However the movements and feeding activities of adults play a role in shaping population structure, especially for fishes in the **pelagic zone** (see Chapter 16). For example, population structure in wide-ranging tunas, billfishes, and pelagic sharks is usually measured on the scale of ocean basins: East versus West Atlantic in the Bluefin Tuna *Thunnus thynnus* (Carlsson et al. 2007), North versus South Atlantic in the White Marlin *Tetrapturus albidus* (Graves & McDowell 2006), Indian versus Pacific in the Swordfish *Xiphias gladius* (Lu et al. 2006), and Atlantic versus Indian-Pacific in the Whale Shark *Rhincodon typus* (Castro et al. 2007).

A few **demersal** (bottom-dwelling) fishes conduct reproductive or seasonal migrations, but most are sedentary, and for this reason the corresponding habitat preferences are seldom considered in predicting population structure. However, habitat preference can have a strong influence on the distribution of genetic diversity in fishes. Usually ecosystem **specialists** (those with very specific feeding or habitat requirements) have more population structure than generalists, as demonstrated by genetic comparisons of reef

fishes across the **Amazon barrier**. This turbid plume of fresh water was long regarded as a barrier that divided the West Atlantic reef fauna into northern (Caribbean) and southern (Brazilian) provinces (see Chapter 16). However, fresh water is less dense than salt water, and may form a surface layer with a saltwater "wedge" below. Trawl surveys conducted under the Amazon plume demonstrated the presence of many marine fishes that are usually associated with coral reefs (Collette & Rützler 1977). An mtDNA survey of West Atlantic wrasses (genus *Halichoeres*) across the Amazon barrier demonstrates a strong connection between habitat use and genetic structure. *Halichoeres maculipinna*, a reef species with specialized diet and feeding morphology, has an ancient evolutionary separation between Brazil and the Caribbean (sequence divergence $d = 0.065$ in cytochrome *b*). In contrast, *H. bivittatus* is found in a variety of habitats in addition to coral reefs and shows no strong genetic separation across the Amazon barrier (Rocha et al. 2005a). Notably, *H. bivittatus* was collected in the trawl surveys under the Amazon plume, whereas *H. maculipinna* was not. Combined, these genetic and field studies indicate that habitat preference and species ecology can be as important as geography and larval dispersal in defining the distribution of genetic diversity in fishes (Choat 2006).

Complex population structure

In migratory fishes, the resolution of populations (and corresponding management units) can be confounded by two factors:

1. Migratory overlap, in which populations mingle in feeding habitats or during migrations. Examples of such overlap can be found in the anadromous Sockeye Salmon (*Oncorhynchus nerka*; Grant et al. 1980) and Striped Bass (*Morone saxatilis*; Wirgin et al. 1997), as well as marine species such as the Bluefin Tuna (*Thunnus thynnus*; Carlsson et al. 2007) and possibly cod (*Gadus morhua*; Svedäng et al. 2007). When independent breeding populations overlap at shared feeding habitats, a critical question is whether genetic exchange occurs. If fish are not breeding during the period of overlap, those populations could be isolated management units.
2. Sex-biased dispersal, in which gene flow between populations is accomplished primarily by one gender. For many mammals and birds, males disperse prior to reproduction, while females remain in natal areas (Greenwood 1980).

Both population overlap and sex-biased dispersal are common in migratory marine fishes. Female site fidelity can be countered by opportunistic mating by males, so that each gender yields a different population genetic signal. This is known as **complex population structure** (Bowen et al. 2005), and the most common outcome is that female-inherited mtDNA shows population structure while biparentally inherited nDNA surveys show no structure (Goudet et al. 2002). This pattern is apparent in the Brook Charr (*Salvelinus fontinalis*; Fraser et al. 2004), Patagonian Toothfish (*Dissostichus eleginoides*; Shaw et al. 2004), and Shortfin Mako Shark (*Isurus oxyrinchus*; Schrey & Heist 2003). In a survey of White Sharks (*Carcharodon carcharias*) in the Indian Ocean, the mtDNA sequences reveal significant population structure ($F_{st} = 0.81$ between South Africa and Australia), while a microsatellite survey indicated a single population (Pardini et al. 2001). For these cases, dispersal by males can readily explain the lower population structure registered in nDNA relative to mtDNA.

Phylogeography

Whereas population structure is defined by differences in allele (or haplotype) frequencies, the field of phylogeography is concerned with the geographic distribution of genetic lineages, usually at the level of deep population structure, species, and genera. This perspective was prompted by the advent of mtDNA technology for wildlife studies in the 1980s, culminating in a seminal publication titled *Intraspecific phylogeography: the mitochondrial DNA bridge between population genetics and systematics* (Avise et al. 1987). As the title implies, this field is at the junction of population genetics and systematics (phylogenetics), with additional foundations in biogeography (see Chapter 16). The key innovation with mtDNA sequence data, later extended to nDNA sequence data (Karl & Avise 1993), is that the differences between alleles or haplotypes are known. Previously, allozyme studies could compare the frequency of alleles, but the alleles were just dark bands on a gel. Researchers did not know whether the alleles were different by two mutations, or 20 mutations. Therefore allozyme studies could not determine whether those alleles arose 1 million years ago or 10 million years ago. The age of these alleles can reveal important information: When two different alleles are at 100% frequency in separate populations, the age of the populations can be estimated with a **molecular clock** (see below). Often these estimates of the age of populations (and species) are linked to known biogeographic events (see below, Panama barrier).

Dispersal and vicariance revisited

As noted in Chapter 16 (Box 16.2), modern biogeography has been dominated by the **vicariance** model, wherein species distributions are shaped by geographic isolation, rather than by active dispersal. In this framework, evolutionary history could be reconstructed due to breakthroughs in the study of **plate tectonics** (the movements of continents over millions of years). For the first time, the geographic distributions of organisms could be interpreted through the

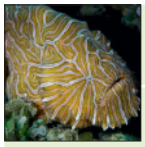
Sequence divergence This is usually expressed as *d*, the percent difference between two DNA sequences. For example, *d* = 0.10 means that an estimated 10% of the DNA sequence has changed between two individuals, populations, or species. The level of sequence divergence can vary from near zero between closely related species (such as the cichlid species flocks of East Africa), to upwards of *d* = 0.20. Above this range, sequences become **saturated**, meaning there are so many mutations that some nucleotide sites have changed two or three times, obscuring the true history. For example, a site that appears to have a mutation from G to C may actually have mutated from G to A to C. Saturated sequences cannot provide optimal resolution of evolutionary relationships, but may still be informative. A typical level of mtDNA sequence divergence between fishes in the same genus would be *d* = 3–15%, but differentiation in a few genera can exceed *d* = 30%, including *Galaxias* (Galaxiidae, mudfish and their relatives) (Johns & Avise 1998).

Molecular clocks Based on the assumption that isolated populations or species accumulate mutations at a predictable rate (Thorpe 1982), molecular clocks can be used to estimate divergence times, for example when **sister species** (those that are each other's closest relatives) stopped interbreeding and initiated separate evolutionary pathways. This is a valuable tool for reconstructing evolutionary divergence and speciation. For example, the mtDNA genomes of the Indonesian and African coelacanths differ by approximately *d* = 0.043, and the overall **divergence rate** may be about 0.1% per million years (0.001/MY), meaning 0.1% of their DNA sequence changes every million years. This yields an estimated divergence of 43 million years, indicating that the two coelacanths may have become isolated by the tectonic event when the subcontinent of India moved north and collided with Eurasia 50 mybp (Inoue et al. 2005). A typical rate for widely applied mtDNA fragments (cytochrome oxidase and cytochrome *b*) is 1%/MY to 2%/MY between species of bony fishes (Bermingham et al. 1997; Bowen et al. 2001). Elasmobranch mtDNA evolves more slowly, with a mtDNA control region clock rate of about 0.8%/MY (Duncan et al. 2006), and this may be true for primitive bony fishes as well. The reasons are still not clear but may include long generation time, efficient DNA repair mechanisms, or low metabolic rate (with less oxidative damage) or a combination of these factors (Martin & Palumbi 1993). Molecular clocks are analogous to the radioactive decay of a nuclear isotope. Any given radioactive molecule (or base pair) may not change in a million years, but others might change twice in the same interval, just by chance. Molecular clocks depend on assumptions about rate constancy that may not always be met. For these reasons, divergence times based on molecular clock estimates should be regarded as approximations, and interpreted with caution.

sequence of continental breakups and collisions. While this emphasis on vicariance revitalized the field of biogeography, it was also dominated by a radical element that denied the primary alternative, dispersal (and colonization), as a means to explain species distributions. Vicariance biogeographers regarded dispersal as trivial or unprovable (de Queiroz 2005). In particular, the advocates for vicariance biogeography claimed that plate tectonics and other geological processes provided a testable set of expectations because they could be linked to geological events, whereas rare dispersal events did not readily fit into a hypothesis testing format. On the vicariance side of this debate, Nelson (1979) described dispersal biogeography as "a science of the improbable, the rare, the mysterious, and the miraculous". In a courageous response to the radical view of vicariance, McDowall (1978) summarized the plight of adherents to dispersal theory:

> How can one test for [dispersal] events that may occur once, a few, or even many times but which leave no trace of having occurred? One can't. So we reach the point where, if we are going to insist on falsifiable theories, we must choose to exclude dispersal . . . but always we return to the fact that dispersal occurs.

Phylogeographic methods, and their immediate precursors in population genetics, provided a resolution to this dilemma (Box 17.3). While it is true, as McDowall (1978) notes, that dispersal events are very difficult to document directly (especially in fishes), nonetheless these events yield clear genetic signals. This was dramatically demonstrated by Rosenblatt and Waples (1986), who used allozymes to test the prediction of an ancient vicariant separation between marine fishes of the East Pacific and central Pacific. The Pacific Ocean sits atop a geological plate that is over 100 million years old, and corresponding genetic divergences should be very deep. Instead, the allozymes revealed much more recent connections, on the order of thousands of years rather than millions of years. Lessios and Robertson (2006) revisited the issue 20 years later with mtDNA data, and found that 19 of 20 species either shared haplotypes across the barrier, or had haplotyes that were a few mutations apart. The exception was the pipefish *Doryrhamphus excisus*, a member of the Syngnathidae, known to have low



Box 17.3

Dispersal and vicariance in the sardines (genus *Sardinops*)

Sardines (*Sardinops* spp.) occupy upwelling zones in the cold temperate corners of the Pacific and Indian oceans: South Africa (*S. ocellatus*), southern Australia (*S. neopilchardus*), Japan (*S. sagax melanostictus*), Chile (*S. s. sagax*), and California (*S. s. caeruleus*). The **antitropical** distribution (occurring on both sides of the tropics; Briggs 1987; see Chapter 16) of *Sardinops* provides an opportunity for testing biogeographic hypotheses. On an east–west axis across the Pacific Ocean, there are vast expanses of ocean that are inhospitable to sardines, but potentially breached by pelagic drifting larvae. On a north–south axis, tropical waters above 27°C are lethal to sardines and prohibit movement across the equator except during the coldest (glacial) conditions.

The dispersal model predicts recent separations or ongoing gene flow across the Indian and Pacific oceans (Parrish et al. 1989). The vicariance model mandates ancient separations based on the breakup of the continent Pacifica, on the order of tens of millions of years, between East and West Pacific (Nelson 1985).

In the **parsimony network** (see below, Molecular evolution) illustrating the relationships among sardine haplotypes (Fig. 17.2), South African and Australian "species" share haplotype C and Californian and Chilean "subspecies" share haplotype M, indicating shallow population structure rather than ancient species. A molecular clock for the mtDNA control region (15–20%/MY) indicates that all these sardines share a common ancestor at approximately 300,000–500,000 years ago (Bowen & Grant 1997). Based on the same comparisons with an allozyme molecular clock, the common ancestor is aged at 200,000 years ago (Grant & Leslie 1996). With either of these timeframes, the vicariance model of ancient separations is refuted. Sardines have crossed both the Pacific and the equator in recent evolutionary history. It is notable that the connection across the equator is in the East Pacific, which has a steep continental shelf and deep, cold water (even in the tropics). In contrast, the tropical zone between Japan and Australia is generally shallow, warm, and apparently impenetrable to cold-adapted sardines.

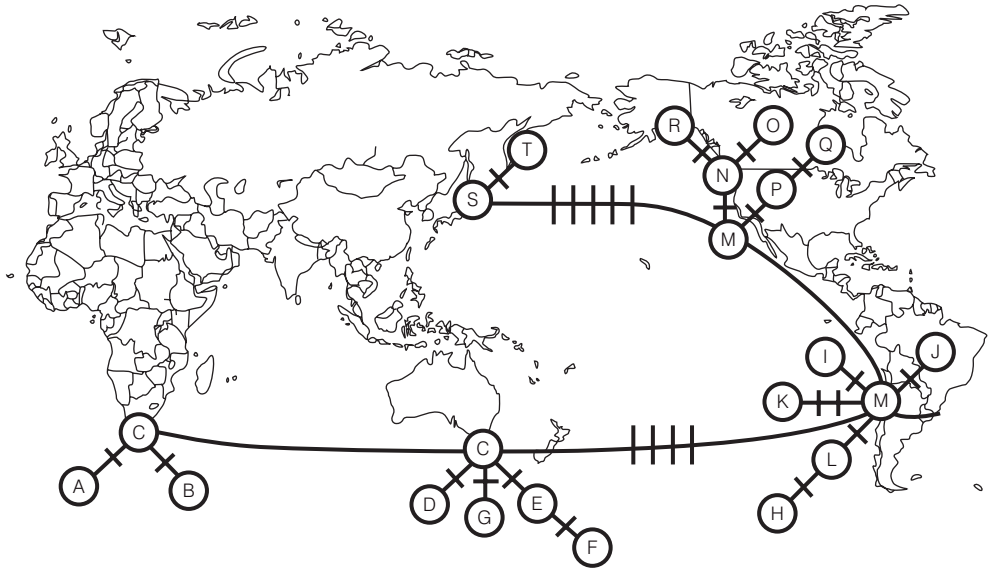


Figure 17.2

A parsimony network of mtDNA control region sequences, illustrating relationships among sardines (genus *Sardinops*) in five temperate upwelling zones of the Indian and Pacific oceans (hashmarks indicate multiple mutations along a branch). The 20 haplotypes are labeled A to T. Haplotype C occurs at both South Africa and Australia, and haplotype M occurs at both Chile and Mexico, indicating shallow population structure between these regions, and recent colonization around the rim of the Indian-Pacific Basin. The five regional forms were previously regarded as separate species, a taxonomy that is not supported by the mtDNA analysis. From Bowen and Grant (1997), used with permission.

dispersal ability from population genetic assessments (see above, Population genetics). Although vicariance is an excellent model for many freshwater fishes, dispersal models are a better fit for marine fishes, given their large ranges and high potential for dispersal as both larvae and (in the case of tunas, billfishes, and pelagic sharks) swimming adults. However, there are exceptions to this trend, especially among marine fishes that lack a pelagic larval stage, like the Spiny Damselfish (*Acanthochromis polyacanthus*; Bay et al. 2006), Banggai Cardinalfish (*Pterapogon kauderni*; Hoffman et al. 2005) and seahorses (genus *Hippocampus*; Lourie et al. 2005). Vicariance models work well when population structure is shaped primarily by geographic barriers rather than life history or ecology. Accordingly, the next section will explore the phylogeography of freshwater fishes.

Freshwater fishes

These fishes cannot get out of the water and travel over dry land to the next drainage, with rare exceptions such as "walking catfish" in the genus *Clarias*. For most freshwater fishes, opportunities for dispersal are few, the genetic differences between drainages are high, and vicariance models generally work well to explain evolutionary patterns. Geographic and oceanographic barriers can explain the majority of **sister species** (species that are each other's closest relative) relationships, although differences in freshwater characteristics (such as the Andes-derived white water, and the lowland-derived black water of the Amazon) may be a factor as well. Looking beyond these geographic and oceanographic barriers, four primary factors shape the phylogeography of freshwater fishes:

1. Changes in drainage routes. Stream captures are the most widely studied phenomenon, where erosion, earthquakes, or other geographic changes divert a stream from one drainage to another drainage. The high diversity of freshwater fishes in central North America may be due in part to streams in the Appalachian Mountain Range that switched from flowing toward the Atlantic coast to flowing toward the Mississippi River (Hocutt & Wiley 1986). Flooding, which in essence causes temporary stream capture, may also transfer fishes between drainages.
2. Glaciation. During these "ice ages" the temperate fishes (distributed between 25° and 65° latitude) were massively displaced by the cooling and advancing glaciers. At the end of each glacial epoch, enormous **proglacial lakes** formed at the retreating edge of ice sheets, some larger than the contemporary Great Lakes of North America. These large and shifting water masses provided extensive opportunities for dispersal (Hocutt & Wiley 1986; Behnke 1992).
3. Coastal opportunities for dispersal. Some freshwater fishes are tolerant of high salinity conditions and can survive for extended periods (days or weeks) in coastal waters. For example, the freshwater cichlids are members of the suborder Labroidei that includes surfperches, damselfishes, wrasses, and parrotfishes, all marine groups (Streelman & Karl 1997; see Chapter 15). Hence it is no surprise that some cichlid species can tolerate salt water. The other coastal opportunity for dispersal occurs during periods of heavy rainfall. Chesapeake Bay is a 300 km long estuary that usually contains ocean water at one end and fresh water at the other. However, in the aftermath of hurricane events, fresh water extends out of the mouth of the bay, as do the freshwater fishes that are usually confined to individual rivers.
4. Plate tectonics, wherein the movements of continents can separate or join populations of freshwater fishes. Chapter 16 contains several examples.

Here we briefly examine three of these phenomena, whereas the fourth (coastal dispersal) is covered in the next section (anadromous fishes).

Reconstructing stream captures

The South Island of New Zealand has two primary drainage systems, the Clutha in the north and Southland in the south. These two historically isolated drainages retain distinct faunas: a phylogeographic survey of galaxiid mudfishes reveals a number of **cryptic species** among taxa that were previously believed to span both drainages (Waters et al. 2001). Furthermore, these mtDNA studies have demonstrated two stream captures in this glacially influenced region. The older stream capture involved the Nevis River, which changed course from a southern to a northern drainage system, introducing a lineage of the mudfish *Galaxias gollumoides* that is characteristic of the Southland drainage (Waters et al. 2001). Molecular clock estimates indicate an ancient colonization, on the order of 300,000–500,000 years ago. In contrast, geological studies indicate that the Von River changed course (also from south to north) during the most recent glacial interval, about 12,000 years ago. The corresponding mtDNA survey indicates the presence of another mudfish derived from the Southland drainage (Burridge et al. 2007). These colonizations of the northern drainage are significant, as they comprise two of the nine native freshwater fishes.

Glacial eradication and recovery

The most recent glaciation affected North America severely, with a greater ice sheet than the Asian and European glaciations combined. This ice sheet reached as far south as the 44° latitude (where Toronto, Ontario and Bangor, Maine are today) about 23,000 years ago, followed by deglaciation 15,000 to 8000 years ago. The current distributions of several salmonids, in particular Lake Trout (*Salvelinus*

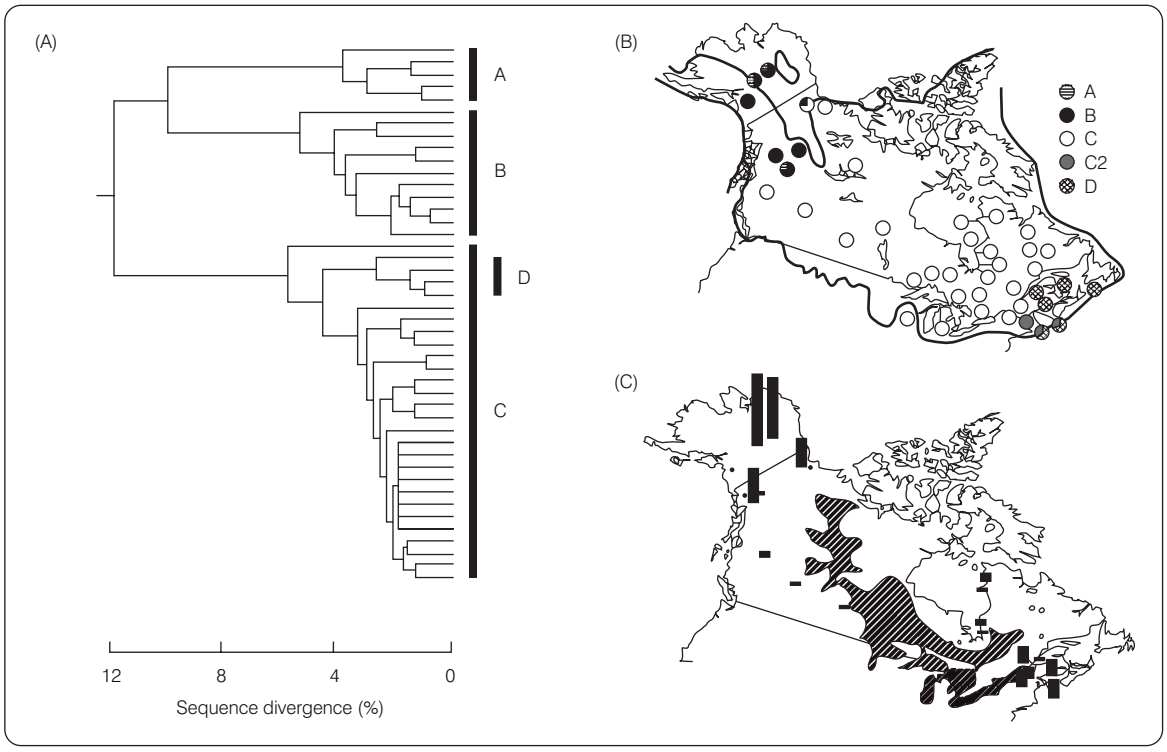


Figure 17.3

Phylogeographic data for the Lake Whitefish (*Coregonus clupeaformis*) based on mtDNA sequence data from 41 populations across the species range. (A) The phylogeny of Whitefish lineages corresponding to four glacial refugia. The scale bar indicates sequence divergence. (B) Distribution of the four lineages (A, B, C and C2, D) following postglacial dispersal. (C) Nucleotide diversity of sampled areas, in relation to the area formerly inundated by major glacial lakes (shaded area); the height of bars indicates the level of nucleotide diversity. From Bernatchez and Wilson (1998), used with permission.

namaycush) and Lake Whitefish (*Coregonus clupeaformis*), were almost completely covered by this ice sheet. These species, now broadly distributed from Alaska to the Atlantic drainages, must have persisted in refugia (perhaps at the fringe of their current range) for thousands of years. Hence patterns of genetic diversity can help to identify glacial refugial and recolonization pathways.

Bernatchez and Dodson (1991) used mtDNA to resolve four major lineages among populations of Lake Whitefish. These correspond to refugia in northern Eurasia, Beringia (Siberia-Alaska), the Mississippi valley, and perhaps two Atlantic locations (Fig. 17.3). The Mississippi haplotypes occupy the majority of the current range of Lake Whitefish, observed from New York to the Yukon. This is consistent with other fish distributions in indicating that the Mississippi fauna had the greatest opportunities for dispersal through proglacial lakes.

In a review of phylogeographic studies for 42 North American freshwater fishes, Bernatchez and Wilson (1998) observed a significant decline in mtDNA **nucleotide diversity** (see above, Population genetics) with increasing latitude, a clear indication of southern refugia during the last glacial period. Regression analysis indicates a steep (fivefold) drop in diversity from 25° to 46°N latitude, then consistently low diversity from 46° to 65°N (Fig. 17.4). It is remarkable that the analysis indicated the 46°N boundary for reduced genetic diversity, closely paralleling the southern limit of North American glaciers at 44°N. Almost universally, North American freshwater fishes are genetically depauperate in the deglaciated areas above the 44° to 46°N boundary. A similar pattern is apparent in Europe. Of the five mtDNA lineages observed in European Brown Trout (*Salmo trutta*), only one has colonized previously glaciated areas (Bernatchez 1995).

Plate tectonics: the mystery of the Asian Arowana (*Scleropages formosus*)

The distribution of arowanas (Osteoglossomorpha) has been a longstanding biogeographic mystery, as these primary freshwater fishes occur on four continents that are isolated by formidable marine barriers (see Fig. 16.13). Their distribution in South America, Africa, and Australia can be explained by the breakup of the southern supercontinent Gondwanaland (including South America, Africa, Antartica, Madagascar, and India) about 150 mybp. However, the distribution in Southeast Asia is hard to explain without a marine dispersal event from Australia. Despite the strict

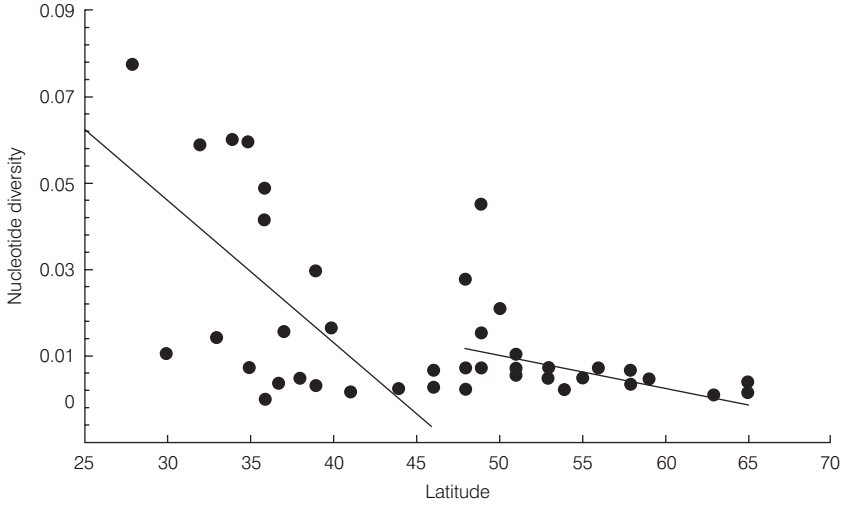


Figure 17.4

The relationship between nucleotide diversity and latitude for North American freshwater fishes, showing a general trend of reduced genetic diversity in areas that were under glacial ice. Two lines with two different slopes fit the data, with the break between the lines corresponding closely to the 46ºN latitude, near the southern limit of the most recent glaciation. Each dot represents a different species. From Bernatchez and Wilson (1998), used with permission.

freshwater requirements of arowanas, this was the favored explanation until recently. The Australia to Asia dispersal hypothesis was given further support by taxonomic studies based on morphology, which united in one genus the Asian *Scleropages formosa* with the Australian *S. jardinii* and *S. leichardtii*.

Based on a molecular clock for two mtDNA genes calibrated with several bony fishes, Kumazawa and Nishida (2000) estimate that the Asian and Australian arowanas actually diverged about 140 mybp. This timeframe coincides with the separation of India from the southern supercontinent, and subsequent transport into the northern hemisphere. India connected with Asia by about 40 mybp, and may have allowed the colonization of Asia at that time. This possibility is supported by the presence of fossil *Scleropages* in Sumatra, dating to the Eocene (35–57 mybp). Hence the biogeographic mystery of the arowanas unraveled when molecular clock data showed that the *Scleropages* species in Asia and Australia diverged in the Early Cretaceous, much farther back than typical congeners.

Anadromous fishes

These typically show strong site fidelity when they return from the ocean to natal streams to spawn, but with an error rate that is high enough to allow colonization of adjacent rivers. Anadromous salmon are the subject of much scientific interest because their life history (especially the site fidelity of spawning adults) is a compelling focus for ecological and genetic studies, and because of the wildlife management and conservation issues associated with salmon fisheries (see Chapter 26). Life history and population genetic studies provide a scientific foundation for resolving stocks, populations (in the genetic sense), and ESUs (see above, Population genetics).

The seven species of anadromous salmon and trout (genus *Oncorhynchus*) on the Pacific coast of North America are the most widely studied in the world, with extensive allozyme, mtDNA, and microsatellite inventories. Here there is a management mandate to define "distinct population segments" under the US Endangered Species Act, using ecology, life history, and genetics (Waples et al. 2001). Note that since genetics is not the sole criterion, differences in behavior (especially the timing of migrations to and from the ocean) are incorporated as well.

Currently the salmon and trout in US waters are divided into 12 ecologically distinct regions (Fig. 17.5), most corresponding to major tributaries and drainages. Within these 12 regions are a total of 58 designated ESUs (Table 17.4). Chinook Salmon (*O. tshawytscha*) and Steelhead Trout (*O. mykiss*) have the widest range and the most subdivisions, with 17 and 15 ESUs, respectively. Chinook, Steelhead, Sockeye (*O. nerka*) and Coastal Cutthrout (*O. clarki clarki*) also have considerable diversity in life history, particularly in the timing of smolting and spawning migrations, and all but Chinook have non-anadromous, "landlocked" populations. Some anadromous Sockeye populations use lakes for juvenile development, whereas others use a riverine habitat or migrate quickly to the sea. In contrast, Chum (*O. keta*), Pink (*O. gorbuscha*), and Coho Salmon (*O. kisutch*) are relatively inflexible in life history traits, including a very brief freshwater stage in the first two species (Groot & Margolis 1991; Quinn 2005).

Three species have anadromous and non-anadromous (remaining in fresh water) forms that inhabit the same drainages: Sockeye/Kokanee, Steelhead/Rainbow Trout, sea-run/freshwater Cutthroat Trout. The genetic surveys demonstrate that in each case, the two forms within each drainage are closely related populations, relative to populations with the same behavior in other drainages (Foote et al. 1989; Utter et al. 1989). These life history variants, including the option of remaining in fresh water, arose independently in each drainage.

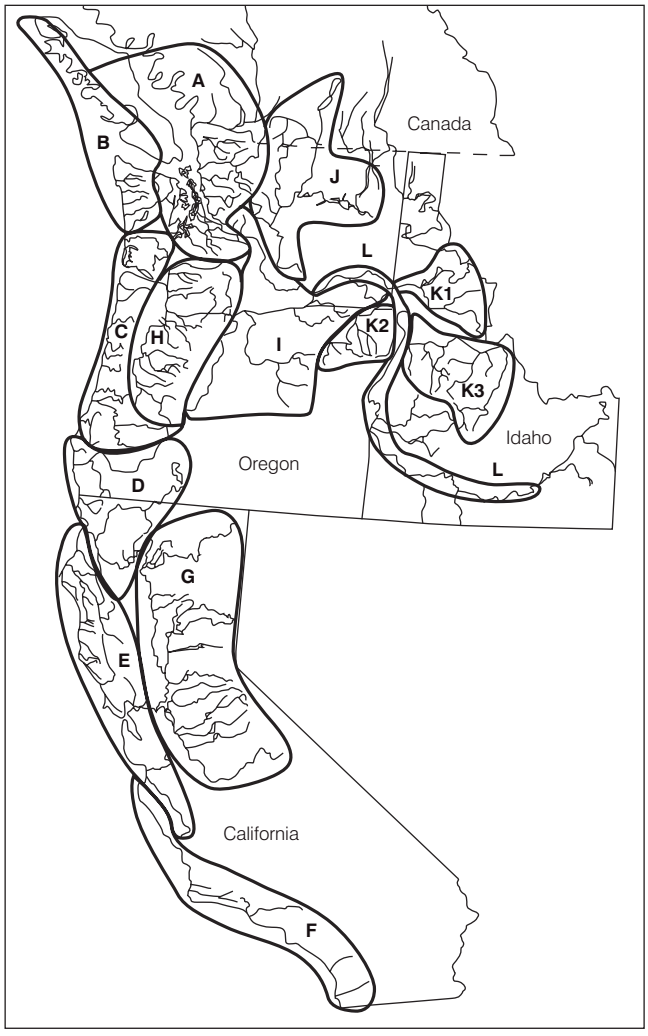


Figure 17.5
Drainage basins of western North America that support at least one spawning population of Pacific salmon (see Table 17.4). Letter codes correspond to the following ecosystems: A, Georgia Basin; B, temperate rainforest; C, north coast; D, Klamath Mountains; E, northern California; F, southern California; G, Central Valley; H, Willamette/Lower Columbia River; I, mid-Columbia River; J, upper Columbia River; K, Snake River tributaries; L, mainstem Snake River. From Waples et al. (2001), used with permission.

The exception to this pattern are the Chinook Salmon in the Columbia and Snake Rivers, where deep genetic partition exists between stream-maturing and ocean-maturing forms (Myers et al. 1998). Spring-spawning salmon of the stream-maturing type co-occur with fall-spawning salmon of the ocean type, but they do not interbreed, another example of complex population structure (see above, Population structure).

Pink Salmon are hard wired to a 2-year breeding cycle, so that even-year spawners never encounter odd-year spawners. The result is two distinct ESUs in a single species that inhabit the same feeding areas, mate in the same location at the same time of year, but never interbreed (Churikov & Gharrett 2002).

Sockeye and Cutthroat have strong population structure, and in both cases this structure is linked to higher dependence on freshwater habitat. The Sockeye is anadromous but requires lake habitat for juvenile development, whereas the Cutthroat is non-anadromous throughout much of its inland range. In the populations that have access to the ocean, many individuals stay in fresh water, and sea-running individuals do not migrate far from their river of origin (Johnson et al. 1999). Hence Cutthroat may be described as the least anadromous member of the genus *Oncorhynchus* in western North America. Recall the pattern in Table 17.2 wherein freshwater fishes have more population structure than anadromous fishes, which have more structure than marine fishes. In this hierarchy, it makes sense that the least anadromous fish would have the highest genetic structure (Waples et al. 2001).

Finally, the conservation genetics of these Pacific salmon are a matter of much concern. Perhaps 30% of the ESUs (corresponding to 27% of the genetic diversity) that existed prior to European contact are extinct, and another third are listed as endangered or threatened (Gustafson et al. 2007). Much has been lost, but enough remains to rebuild these stocks under prudent management regimes. However, widespread aquaculture of salmon has the potential to corrupt native populations. Interbreeding with fish that escape from captivity has the potential to introduce maladaptive genetic traits into local populations (Utter 2004).

Marine fishes

These fishes have few barriers to dispersal, and can show low population genetic separations across vast regions of the planet. This has implications for speciation that will be explored in the next section. Here we review a few of the major biogeographic barriers, and how genetic studies have illuminated the nature and history of these barriers.

Transarctic interchange between the North Pacific and North Atlantic

Approximately 3.5–4 million years ago the Bering Strait opened and allowed a cold temperate waterway between the North Pacific and North Atlantic basins, as indicated by paleontology and geology (Vermeij 1991). This opening persisted for more than half a million years and colonization proceeded in both directions, but with most movement of fishes from the highly diverse Northeast Pacific to the relatively depauperate Atlantic (Briggs 1970). The directionality of exchange is usually inferred from the fossil record, which shows that hundreds of species moved from

Table 17.4

The number of management units and evolutionary significant units (ESUs) within each species of salmon on the West coast of the United States. Note that management units can be defined with ecology and life history, as well as shallow population genetic structure. The higher level designation of ESU requires deep population structure or other evidence of evolutionary divergence. From Waples et al. (2001).

Species	Management units				ESUs
	Genetics	Ecology	Life history	Total	
Pink	2	2	1	5	2
Chum	2	4	1	7	4
Sockeye	9	4	6	19	7
Coho	2	6	1	9	7
Chinook	10	11	7	28	17
Steelhead	7	11	7	25	15
Cutthroat	3	6	2	11	6

the Northwest Pacific into the Atlantic. The initial interchange has been followed by perhaps three more openings of lesser duration and impact, including one event about 2 million years ago, and one after the last glacial period (<12,000 years ago) (Nikula et al. 2007).

Several widespread and abundant Atlantic fishes are the product of this Pacific invasion. The Atlantic Herring (*Clupea harengus*) is distinguished from the Pacific Herring (*C. pallasi*) in allozyme surveys, indicating a separation time of 3.6–6.6 million years (Grant 1986).

One important invasion may have occurred in the other direction: molecular clock estimates for allozymes and mtDNA indicate that Atlantic salmon (genus *Salmo*) invaded the Pacific during this interval, giving rise to the Pacific salmon genus *Oncorhynchus* (Kitano et al. 1997). For the anadromous and freshwater smelts (*Osmerus* spp.), mtDNA data indicate an exchange approximately 2–2.5 mybp, possibly linked to the second opening of the transarctic waterway (Taylor & Dodson 1994).

Regardless of the direction of exchange, it is clear that the transarctic interchange had a tremendous effect on biodiversity, especially in the North Atlantic. Genetic assays with allozymes and mtDNA complement the paleontological investigations, to provide a relatively complete picture of this great natural invasion.

The Panama barrier

The Isthmus of Panama eliminated contact between the Atlantic and Pacific about 3.5 mybp. This is an impassable barrier except for marine species that can tolerate the freshwater conditions of the Panama Canal (built by the United States and opened in 1914), such as the Atlantic Tarpon (*Megalops atlanticus*; McCosker & Dawson 1975). A number of studies have compared sister species across this barrier, first with allozymes and later with mtDNA, and these comparisons have been especially useful for calibrating molecular clocks against a reliable geological event (Lessios 1979; Bermingham et al. 1997). For example, the genetic differentiation between Atlantic and Pacific trumpetfishes (genus *Aulostomus*) fits a timeframe for the establishment of the Panama barrier (Box 17.4).

The Indian–Atlantic barrier

Southern Africa is another barrier to tropical species, where warm waters of the Indian Ocean (Agulhas Current) collide with cold upwelling in the South Atlantic (Benguela Current). However, the barrier is not absolute. Contemporary dispersal may be possible in warm-core gyres from the Indian Ocean that occasionally cross the frigid Benguela Current and transport tropical species into the Atlantic, as indicated by the occasional arrival of Indian Ocean biota at the island of St. Helena in the South Atlantic (Edwards 1990).

In addition to the trumpetfish example (Box 17.4), several studies have demonstrated colonization events from the Indian to Atlantic oceans. In the Blue Marlin (*Makaira nigricans*), Buonaccorsi et al. (2001) report two divergent mtDNA lineages. One lineage is restricted to the Atlantic, the other occurs in both the Atlantic and Indian-Pacific. Apparently Blue Marlin populations in the two ocean basins were isolated for an extended period, followed by a rare colonization of the Indian-Pacific lineage into the Atlantic. Molecular clock estimates put the initial Atlantic–Indian divergence at about 600,000 years ago.

Box 17.4

Global barriers to dispersal: the trumpetfishes (genus *Aulostomus*)

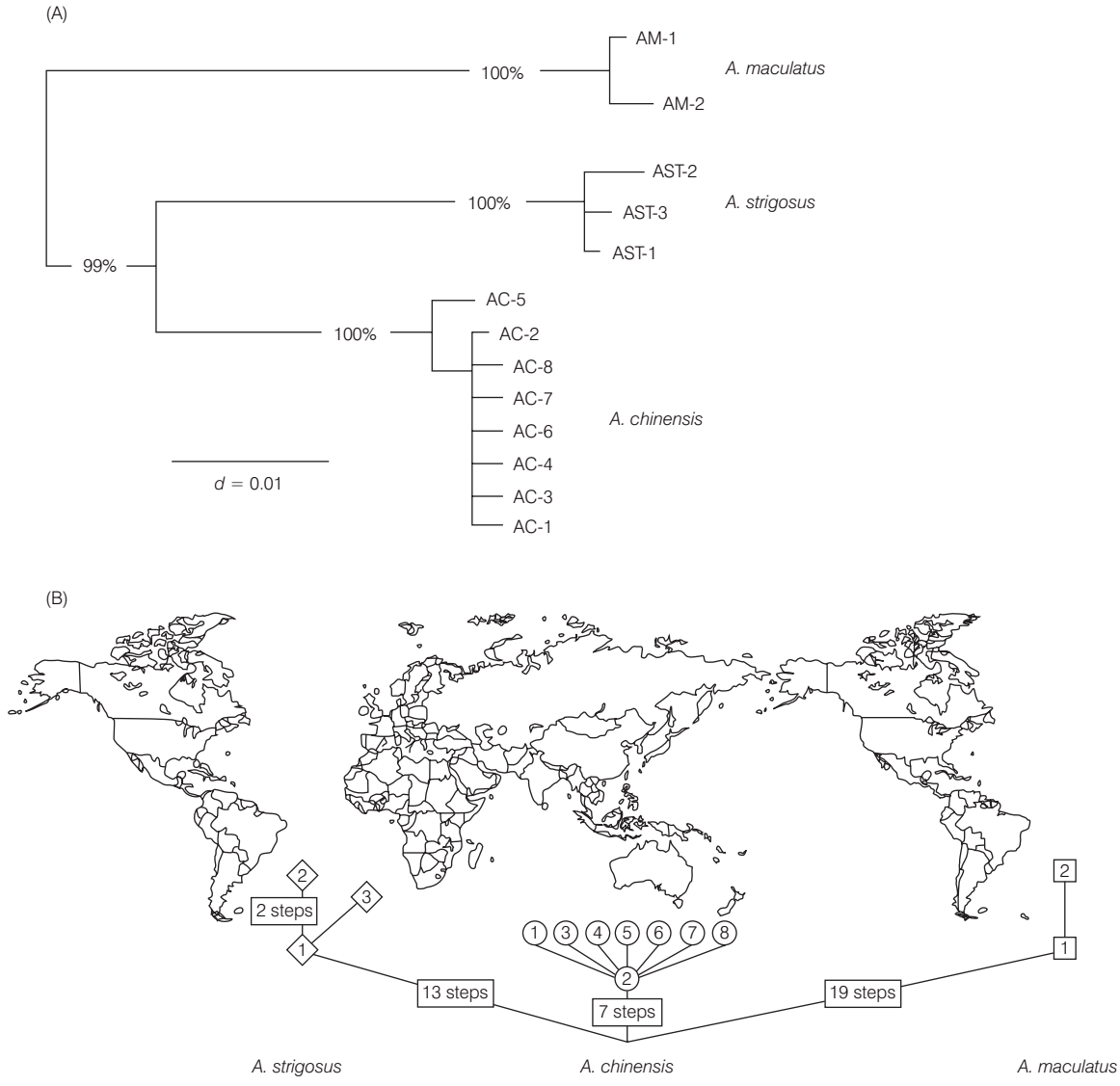


Figure 17.6

A neighbor joining tree (A) and parsimony network (B) based on mtDNA cytochrome *b*, showing the relationships among trumpetfish species across the range of genus *Aulostomus*. The scale indicates 1% sequence divergence. The data indicate a 3–4-million-year-old separation between West Atlantic (*A. maculatus*; haplotypes AM-1 and AM-2) and Indian-Pacific (*A. chinensis*; haplotypes AC-1 to AC-8) species, followed by approximately a 2.5-million-year separation between the Indian-Pacific and the East Atlantic species (*A. strigosus*; haplotypes AST-1 to AST-3). These separations correspond to major vicariant events separating the tropical fauna of each ocean basin (see text). From Bowen et al. (2001), used with permission.

The trumpetfishes (genus *Aulostomus*) inhabit tropical reefs and rocky habitats around the world. They have a long pelagic larval and juvenile stage that can exceed 100 days. Hence they have extensive potential for dispersal, and probably did not differentiate into West Atlantic and East Pacific populations until the last connection across the Isthmus of Panama was closed.

In the only modern appraisal of trumpetfish taxonomy, Wheeler (1955) recognized three species: West Atlantic *Aulostomus maculatus*, East Atlantic *A. strigosus*, and Indian-Pacific *A. chinensis*. He noted that the West Atlantic and Indian-Pacific species were well differentiated morphologically, but that the East Atlantic species was very similar to the Indian-Pacific species. In this biogeographic enigma, the closest relative to the East Atlantic species is not in the West Atlantic, as proximity would indicate, but in the Indian (and Pacific) Ocean.

What are the barriers that could produce this curious outcome? Tropical regions of the West Atlantic and Pacific oceans have been separated by the Isthmus of Panama for about 3.5 million years, whereas the tropical Atlantic and Indian oceans have been isolated for 2.5 million years by the frigid Benguela upwelling system in southern Africa (Shannon 1985). Prior to that time, roughly coinciding with the onset of modern glacial cycles 2.6–2.8 mybp (Dwyer et al. 1995), a warm water corridor connected the Indian and South Atlantic oceans.

The history of these two oceanic barriers, in combination with the morphological data, invoke a biogeographic scenario in which West Atlantic and Indian-Pacific trumpetfishes were initially isolated by the Panama barrier (3.5 mybp), followed by isolation of Indian-Pacific and East Atlantic populations by the Benguela Current (2.5 mybp). Bowen et al. (2001) tested predictions of this biogeographic model, both the timing and the order of events, with mtDNA cytochrome *b* and a conventional molecular clock (2%/MY). In a molecular phylogeny (Fig. 17.6), the deepest partition is between the West Atlantic and Indian-Pacific species (d = 6.3–8.2%), yielding a timeframe of about 3–4 million years. The divergence between Indian-Pacific and East Atlantic species (d = 4.4–5.4%) indicates a timeframe of about 2–2.5 mybp. In this case the mtDNA data confirm a vicariant model based on morphology and the timing of barriers between ocean basins. It is also notable that the 3.5-million-year separation of *A. maculatus* and *A. chinensis* is accompanied by diagnostic morphological differences, whereas the 2.5-million-year separation of *A. chinensis* and *A. strigosus* is not.

The goby genus *Gnatholepis* contains a single Atlantic member, the Goldspot Goby, *G. thompsoni*, that is indistinguishable from *G. scapulostigma* in the Indian Ocean (Randall & Greenfield 2001). Hence comparative morphology indicated a recent colonization event. Rocha et al. (2005b) determined that this Atlantic species was indeed closely related to *G. scapulostigma* ($d = 0.0054$ with mtDNA cytochrome *b*), indicating a colonization into the Atlantic approximately 150,000 years ago (Fig. 17.7).

Like the transarctic exchange described above, the route around southern Africa is an important biogeographic pathway for marine fishes, enhancing biodiversity in the Atlantic Ocean. Studies of the Indian–Atlantic barrier have focused on colonization into the Atlantic, consistent with prevailing currents. However, colonization in the other direction is possible for species that can overcome the water flow, as indicated by two recent examples from sharks. In the Scalloped Hammerhead Shark (*Sphyrna lewini*) and Blacktip Shark (*Carcharhinus limbatus*), haplotypes in the Indian Ocean are recently derived from the Atlantic populations (Duncan et al. 2006; Keeney & Heist 2006). Unlike most marine fishes, wherein dispersal is accomplished primarily by larvae, most sharks are active swimmers from birth. Swimming is the only form of dispersal available, and may eventually prove to be a fundamental difference between the phylogeography of bony fishes and elasmobranchs.

Phylogeographic studies continue to unravel the evolutionary history of fishes. They are most powerful when evidence from multiple species is assembled to resolve general trends (Lessios & Robertson 2006), and when the evidence from DNA is combined with biogeographic information (see Chapter 16), morphology, earth history, and ecology.

Molecular evolution

Access to DNA sequence information has revolutionized the field of phylogenetics. Using models of DNA sequence evolution, researchers can sort out the relationships among fishes from the earliest lineages to the most recent speciation events. Here we review a few of the many breakthroughs in recent years. More examples are accumulating in the scientific literature on a monthly basis. Indeed, it is a good time to be a fish phylogeneticist.

Phylogenies These are treelike diagrams that depict the evolutionary history of organisms. Since the advent of DNA data in phylogenetics, there has been accelerated progress in tree-building methods, but also considerable controversy. For a thorough treatment of this topic, the reader is encouraged to consult Li (1997) and Felsenstein (2004). Here we provide a limited introduction to this field, by outlining the primary methodologies. Four methods are widely used to assess molecular phylogenetic relationships: parsimony, neighbor joining, maximum likelihood, and Bayesian methods (see below).

Parsimony This is where the DNA sequences are assembled into a tree using the shortest number of mutational changes that can explain the data set (see Chapter 2). This is based on the philosophical point that the simplest explanation is the best one, and so parsimony methods are free of assumptions about how DNA mutates and evolves. **Parimony trees** are rooted with an **outgroup**, a sister taxon that shares an ancestral relationship with the species assembled in the phylogeny. The outgroup allows the resolution of shared ancestral characters (**symplesiomorphies**) and more recently derived advanced characters (**apomorphies**) in a cladistic analysis (see Chapter 2). **Parsimony networks** are unrooted arrangements that depict the number of mutations between DNA sequences. Several examples are provided in the phylogeography section above (see Figs 17.2, 17.6B, 17.7).

Neighbor joining (**NJ**) This is where trees are based on the divergence (sequence divergence *d*) between DNA sequences (Saitou & Nei 1987). This **phenetic** approach (see Chapter 2) is not employed in morphological systematics, but is popular in molecular systematics where the data consist of long strings of A, C, G, or T. This is a more sophisticated method than its predecessor, UPGMA (unweighted pair group with arithmetic averages) (Sneath & Sokal 1973) which is still used occasionally. NJ and UPGMA offer the advantage of providing branch lengths that are proportional to the divergence between sequences. If a mutation rate is known for these DNA sequences (see Molecular clocks entry above) then an approximate age of separation between species can be inferred from the tree.

Maximum likelihood (**ML**) This is where a model of DNA sequence evolution is used to assign a probability to alternative phylogenetic trees (Felsenstein 1981). For example, we know that a mutation of C to T is about 10 times more common than a mutation of C to G. Armed with this information, we can assign 10 times greater weight to the rare C to G mutation. Different branch orders in a tree are explored, and the one with the highest probability is deemed the correct one. Like parsimony, this methodology seeks to find the simplest arrangement, but ML methods allow us to incorporate knowledge about how DNA sequences change over time.

Bayesian methods Bayesian methods are closely related to ML methods, but they employ conditional probabilities: given a set of prior conditions X, the probability of this event is Y (Huelsenbeck et al. 2001). In this way, certain outcomes (or branching orders) can be ruled out based on independent information. For example, a *prior* condition for a molecular phylogeny could be a morphology-based phylogeny that indicates all sunfishes (genus *Lepomis*) are monophyletic (descended from a single common ancestor; see Chapter 2) when compared to other members of the family Centrarchidae. Baysian methods allow for ML analyses that are limited to outcomes where all sunfishes are united in a single branch of the tree. Because Baysian methods constrain the search for the most likely tree, they are somewhat controversial; if the prior information is wrong, the tree might be wrong.

Comparison of phylogenetic techniques ML and Bayesian methods are the current favorites for molecular phylogenetic studies, but all four methods have their merits. Parsimony methods are useful for describing networks of closely related haplotypes (see Figs 17.1A, 17.2). NJ is useful for describing the lengths of branches and visualizing the depth of corresponding evolutionary separations. In evaluating any particular phylogenetic study, the most important question is whether branch arrangements (also called **topology**) change across phylogenetic methods. If a branch moves around, depending on the type of analysis, don't bet the fish farm on that one.

Bootstrap support A method that resamples the data set to determine how robustly each branch in a phylogenetic tree is supported by the data. Branch arrangements that hinge on one or two mutations will have low bootstrap support. Generally a bootstrap support of >60% can be regarded as a tenable hypothesis, and values >90% can be considered very strong support. Other measures of branch support include **Bremer decay** (indicating how many mutations support a particular branch) and posterior probability in Baysian analyses (highest probability indicates branch order).

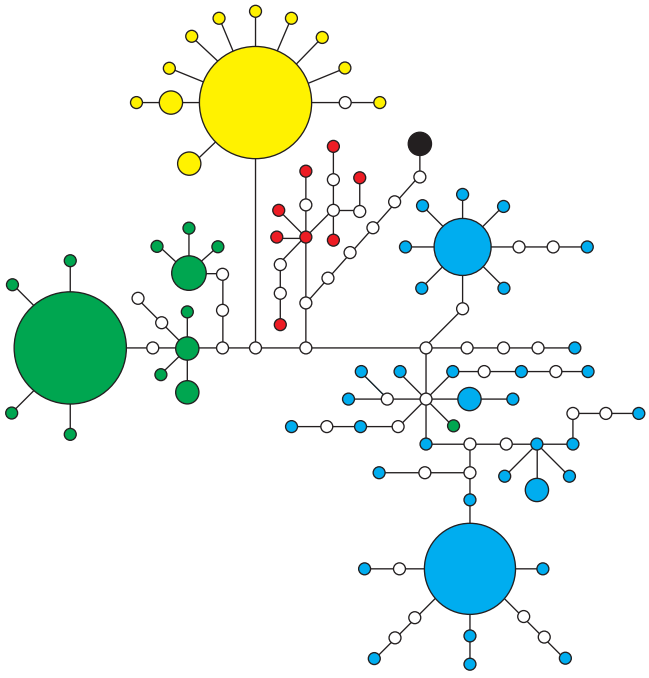


Figure 17.7

Parsimony network for mtDNA cytochrome *b* showing that the Atlantic Goby, *Gnatholepis thompsoni*, is the product of a recent colonization from the Indian Ocean. Populations in the western, central, and East Atlantic are indicated by blue, green, and yellow coloration. The sister species (*Gnatholepis scapulostigma*) is indicated in red (South Africa) and black (Pacific). Breaks in the branches (small circles) indicate mutation events, and unbroken branches indicate a single mutation regardless of length. The size of the circle indicates the frequency of each haplotype. From Rocha et al. (2005b), used with permission.

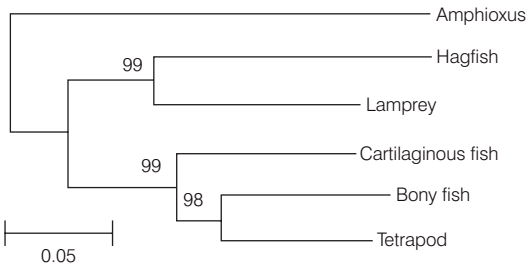


Figure 17.8

Phylogeny of the most ancient lineages of extant fishes. Previous studies had indicated that lampreys are more closely related to jawed fishes than hagfishes, based on shared primitive traits including features of the nervous system, osmotic regulation, and a lens apparatus in the eye. In contrast, DNA sequence data indicate that the two jawless fish taxa are sister lineages, followed by separation of the elasmobranch from the lineage that gave rise to modern bony fishes (actinopterygians) and tetrapods. The outgroup (Amphioxus) has a notochord but not a true vertebral column, is united with vertebrates in the phylum Chordata, and is considered to be the closest extant relative of the vertebrates (see Chapter 13). This is a maximum likelihood tree based on 35 nuclear gene sequences; the scale bar indicates percent divergence in amino acid composition. Bootstrap support values are indicated above the primary branches. From Takezaki et al. (2003), used with permission.

The deepest vertebrate radiations: are you a fish?

Fishes arose approximately 530 million years ago (reviewed in Chapter 11), and three deep lineages survive today: the lampreys (Petromyzontiformes), hagfishes (Myxiniformes), and jawed vertebrates (Gnathostomes). Notably, that last category includes cartilaginous fishes (Chondrichthyes), extant bony fishes (Actinopterygii), and tetrapods (amphibians, reptiles, birds, mammals). The fossil record indicates that all these groups arose in the first hundred million years of fish history, however the order in which they arose has been subject to extensive debate.

Takezaki et al. (2003) used over 27 kb of DNA sequence data from 35 nuclear genes to resolve the deepest lineages in the fish tree (Fig. 17.8). Despite fundamental morphological differences, the two jawless fishes (hagfishes and lampreys) appear to be each other's closest relatives. These data indicate that the cartilaginous fishes diverged next, followed by a bony fishes/tetrapod radiation. Based on molecular studies, the coelacanths appear to diverge near the base of the bony fish/tetrapod bifurcation (Zardoya & Meyer 1996). These studies illustrate two points: First, molecular systematics is especially valuable in cases where the morphology is too divergent (or too similar) to make robust phylogenetic conclusions. Second, the lineage that gave rise to terrestrial vertebrates was the most recent of the major branches in fish history, demonstrating that you, the reader, are really an odd fish (see Chapter 11; see also Shubin 2008).

The history of ray-finned fishes

The most successful modern fishes are the teleosts. However, ray-finned fishes include four additional lineages, known as the ancient actinopterygians. These include polypteriforms (bichirs and reedfish), acipenseriforms (sturgeons and paddlefish), lepisosteids (gars), and *Amia calva* (Bowfin). How they relate to teleosts, and each other, has been a matter of considerable debate, with systematists proposing almost every possible arrangement of relationships. However, most authorities have identified the polypteriforms as the oldest extant group of ray-finned fishes.

To address the evolutionary history of the ancient and modern ray-finned fishes, Inoue et al. (2003) analyzed entire mtDNA genomes from 12 of the ancient actinopterygians, 14 teleosts, and two elasmobranch outgroups (Fig. 17.9). This extensive DNA sequencing effort, approximately 16.5 kb per species, represents a growing trend in molecular phylogenetics fed by improvements in

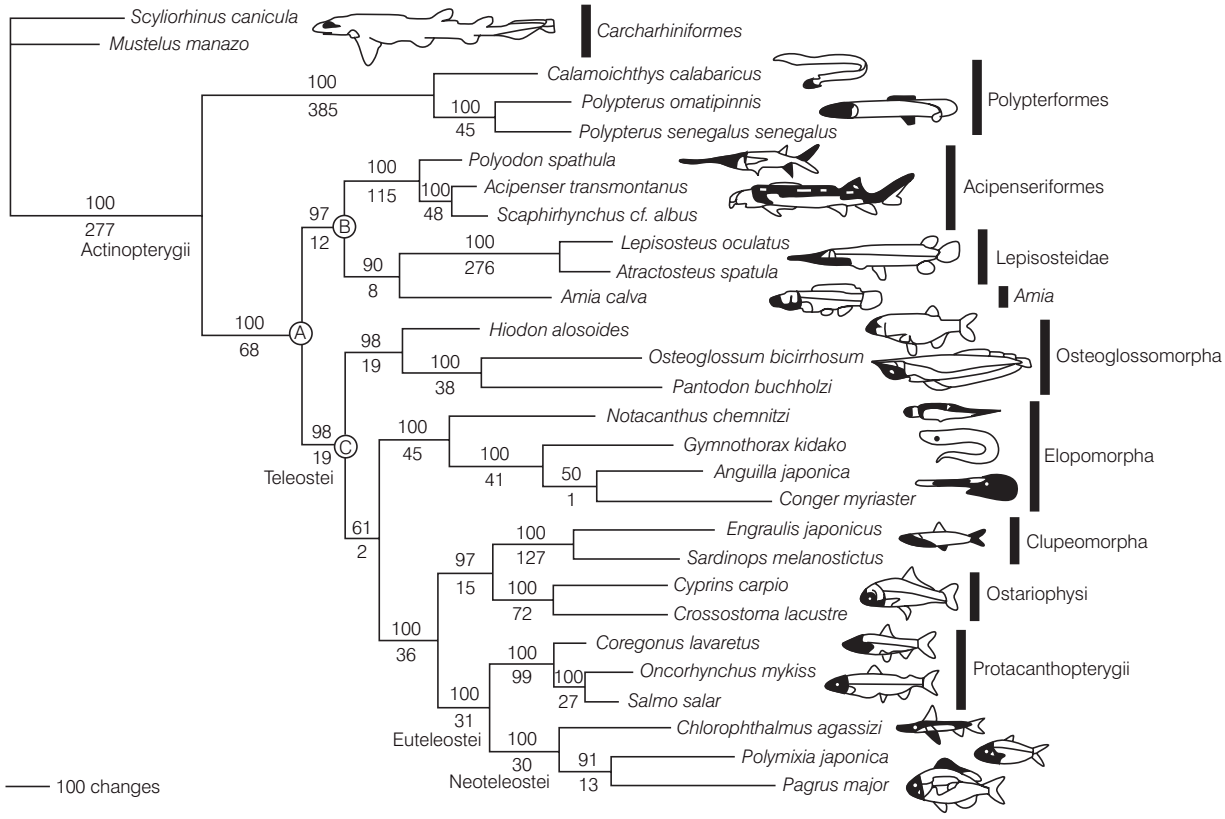


Figure 17.9

Phylogenetic relationships among actinopterygian fishes based on parsimony analysis of whole mtDNA genomes. The bar below indicates 100 mutational changes. Branch support is by bootstrap (above the branch) and Bremer decay (below the branch). Internal nodes A, B, and C denote the well-supported differentiation of teleosts from the other actinopterygian fishes. Tree topology indicates that the four lineages recognized as the ancient actinopterygian fish (polypteriforms, acipenseriforms, lepisosteids, and *Amia*) occupied the oldest positions in the phylogeny. These data do not support the proposal that the acipensiforms (sturgeons and paddlefish) are the sister group to the neopterygians (lepisosteids, *Amia*, and teleosts; Nelson 1969), but otherwise provide a good fit to previous phylogenetic hypotheses. From Inoue et al. (2003), used with permission.

automated DNA sequencing technology; using entire genomes to reconstruct evolutionary relationships.

In keeping with earlier hypotheses, the polypteriforms appear to be the most ancient of the living ray-finned fishes. No doubt their persistence into the modern era is aided by unusual adaptations to arid conditions; for example, the bichir live in semipermanent freshwater habitats in Africa and their gas bladder functions as a primitive lung. They can obtain oxygen from air during periods of stagnation and drought, and can move over land to another body of water if their lake or swamp dries up. Based on the mtDNA data, the sturgeons, paddlefish, gars, and Bowfin are a sister lineage to the teleosts.

The phylogeny of higher teleosts (Percomorpha) has been investigated with 100 complete mtDNA sequences, and these data indicate many unexpected relationships, including a phylogenetic affinity between Lophiiformes (goosefish, long assumed to be a primitive teleost) and Tetradontiformes (pufferfishes, long assumed to be among the most advanced teleosts) (Miya et al. 2003). Clearly these findings indicate a rich field for further investigation.

Mapping an evolutionary innovation in parrotfishes

Parrotfishes (Scaridae) are a group of herbivorous fishes that include *browsers* on seagrass, *excavators* on hard substrate, and *scrapers* on coral reefs. Using their beaklike jaws, individuals can consume tons of coral every year, and in undisturbed locations they promote a healthy balance between coral growth and erosion (Bellwood et al. 2003). For this reason they are regarded as ecosystem engineers, essential to ecosystem function.

Several recent studies have attempted to resolve the origin of the unusual "parrot" jaw morphology, in which the teeth are fused to form an efficient tool for removing algae and coral. The oldest known fossil example belongs to one of the seagrass grazers (genus *Calotomus*), prompting a hypothesis that parrotfish made a gradual transition from the less specialized browsers to the excavators and most recently to the coral scrapers (Bellwood 1994). These evolutionary hypotheses are testable with **trait mapping**, in

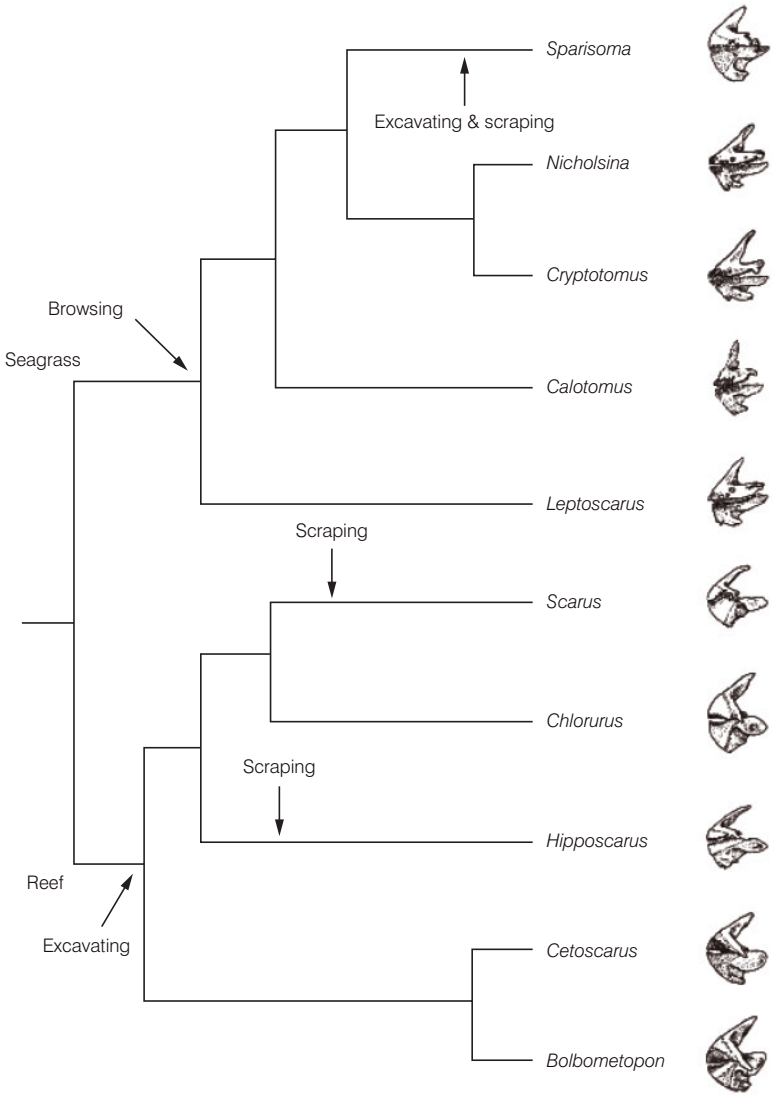


Figure 17.10
Molecular phylogeny of parrotfish genera based on a maximum likelihood analysis of nuclear and mitochondrial sequences. The jaw dentition for various feeding modes is indicated on the right. This tree shows that the key evolutionary innovation of feeding by excavating and scraping arose twice in the family Scaridae. This is an example of trait mapping (see text) to elucidate the evolution of fish diversity. From Streelman et al. (2002), used with permission.

which the key evolutionary innovations are assigned to the branches of a molecular phylogeny. In this case, browsing, excavating, and scraping can be mapped on a molecular phylogeny of Scaridae, to determine whether the oldest branches in the tree include browsers, and whether the youngest branches include scrapers.

Streelman et al. (2002) addressed this question with 2 kb of DNA sequence, including the nuclear intron Tmo-4C4 and three mtDNA segments (cytochrome *b*, 12S, and 16S genes) in 16 scarid species and two outgroups (Labridae). The resulting phylogeny (Fig. 17.10) shows an ancient separation between the grazers or browsers versus the excavators and scrapers. The grazer lineage has jaw morphology that is little modified from the ancestral condition, with no fused teeth. The notable exception in the grazer lineage is the genus *Sparisoma*, which contains browsers, excavators, and scrapers. The *Sparisoma* species that are excavating or scraping have independently evolved the fused teeth and corresponding jaw morphology. Hence the evolutionary innovation of excavation/scraping arose twice in the family Scaridae. The genus *Sparisoma* is estimated to be 14–35 million years old based on a molecular clock, providing a timeframe for the independent evolution of the excavating/scraping adaptation (Bernardi et al. 2000).

Cryptic evolutionary diversity: the case of the bonefishes

Bonefishes (genus *Albula*) inhabit sand flats in tropical and subtopical habitats, where they are widely sought by anglers because of their high-energy battles at the end of a fishing line. The bonefish was originally described by Linnaeus (1758). Subsequent taxonomic research contributed 23 species names for bonefishes around the world. However as scientific communication improved in the 19th and 20th century, it became apparent that these regional "species" were very similar or indistinguishable. These species were

synonymized (see Chapter 2) until most bonefish were recognized as a single species (Whitehead 1986).

The recognition of a single globally distributed bonefish began to unravel when Shaklee and Tamaru (1981) analyzed allozymes in Hawaiian bonefish. They discovered two genetically distinct forms that occupy similar habitats, and that only could be distinguished by careful examination of jaw structure. Subsequent comparisons with mtDNA cytochrome *b* revealed ancient genetic separations in the genus *Albula* ($d = 0.03–0.30$), indicating three species in the Caribbean, and three in the East Pacific (Pfeiler et al. 2006; Bowen et al. 2007). Hidaka et al. (2008) discovered subtle morphological differences among Pacific bonefishes, and split one widespread Pacific species into three regional species: *A. virgata* (a Hawaiian endemic), *A. argentea* (distributed from the central to West Pacific), and *A. oligolepis* (West Pacific to Africa). At this writing, there are probably 10 bonefish species, although several have not been formally described (Fig. 17.11). The deepest genetic separation in the genus is between the two sympatric Pacific species *A. glossadonta* and *A. argentea*, with an mtDNA cytochrome *b* sequence divergence of $d = 0.26–0.30$. Based on a molecular clock calibrated for bonefish cytochrome *b* (1%/Ma), this corresponds to 26–30 million years. It is a remarkable finding that these two fishes, which are identical to the untrained eye and were considered a single species until recently, are five times older than the separation of gorillas and humans.

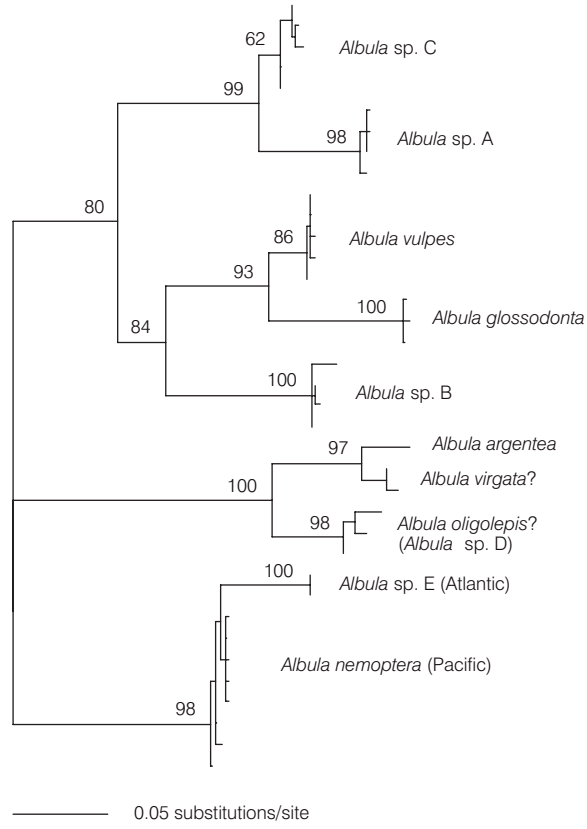


Figure 17.11

Phylogenetic relationships of bonefish species based on maximum likelihood analysis of mtDNA cytochrome *b*. Bonefish that occupy shallow sand flats were thought to be one species worldwide (*Albula vulpes*), with a second species occupying deeper water (*A. nemoptera*). However, allozymes and DNA studies demonstrate at least 10 evolutionary lineages in the genus *Albula*. Numbers above branches indicate bootstrap support. Some species have yet to be formerly described (species A, B, C, and E), whereas others are only tentatively linked to a branch in the tree (*A. virgata*, *A. oligolepes*) pending DNA sequence analysis from voucher specimens (see Chapter 2). The scale bar indicates 5% sequence divergence. From Bowen et al. (2007), used with permission.

The cichlid radiation of Lake Malawi

In the bonefish example above, genetic studies show that cryptic species can be revealed by mtDNA sequence divergence, most especially in cases where morphological differences are slight or absent. The reverse can also be the case, in which morphological divergence and speciation can outpace mtDNA divergence. The cichlid species flocks of the African Great Lakes have fascinated fish biologists and (more recently) evolutionary geneticists (see Box 15.2). According to some estimates, Lake Malawi in eastern Africa contains over 600 species, most in the lineage of haplochromine cichlids, with a diversity in form and function that includes eye biters, scale eaters, crab eaters, sediment sifters, plankton eaters, egg robbers, a species that picks parasites off catfish, and one that catches flies near the water's edge. Taxonomists spent decades sorting these fishes into genera and species, until mtDNA studies upended the whole classification scheme in the 1990s. First, genetic studies demonstrated that the haplochromine cichlids of Lake Malawi are very closely related, $d < 0.06$ in mtDNA sequence comparisons (Albertson et al. 1999). Second, these species descended from a single common ancestor that colonized the lake a few million years ago. Third, many of the species are indistinguishable in mtDNA surveys, indicating speciation events no older than a few thousand years (Kornfield & Parker 1997; Won et al. 2003).

Fish species flocks exist elsewhere in the world, but none are as diverse as the cichlids of Lake Malawi. What could promote such rapid and extreme diversification? Kocher (2004) describes two factors that seem to promote this process. In the first step, the cichlids move into habitats that require some specialization. Fishes in each habitat will benefit from breeding with similar individuals, to reinforce the genetic and morphological features that allow successful feeding and reproduction. This **ecological selection** promotes isolation from cichlids in other habitats, and promotes specialization of feeding morphology and other adaptive traits. The next step is diversification in coloration, a step that can apparently happen on a scale of dozens or hun-

dreds of generations. Malawi cichlids are nest builders and many are female mouth brooders (see above, Molecular ecology, and Chapter 21), behaviors that promote **sexual selection** wherein females choose a mate based on coloration and behavior. Hence coloration determines which fish interbreed and which ones do not, the foundation of speciation. When the genes for an ecological adaptation are co-inherited (perhaps on the same chromosome) with the genes under sexual selection (for distinct coloration), speciation can occur very rapidly. Therefore the composition of the cichlid genome is a third factor that promotes rapid speciation. Kocher (2004) concludes that this plurality of genetic, behavioral, and ecological factors, all of which drive speciation in other organisms, are combined in cichlids to produce the greatest diversity in freshwater fishes. Notably, the cichlid model of speciation does not require geographic isolation (allopatry).

In summary, molecular systematics has revealed much about the history of fishes (and ourselves), and also key points about fish diversity. First, molecular phylogenetics is especially valuable for determining the pattern and pace of evolutionary changes. In the last 20 years the field of systematics has switched from morphology-based trees, to mapping morphological changes on molecular trees. The molecular studies provide a time dimension for these morphological changes, if a calibrated molecular clock is available.

Second, speciation can occur very rapidly, as is the case for African cichlids. Some species of cichlids and other fishes are distinguished by morphology, behavior, and coloration, yet are indistinguishable with mtDNA sequences (Bowen et al. 2006a). A related point is that these rapidly evolving fishes are not isolated by physical barriers, defying the conventional model of allopatric speciation (Wiley 2002; Coyne & Orr 2004). Instead, much of the speciation in fishes seems to occur in adjacent habitats, along ecological rather than geological partitions (Rocha & Bowen 2008).

Third, some sister species may be unrecognized because they retain very similar morphology across millions of years, and these hidden species can be revealed with DNA surveys. Cryptic species continue to be discovered, even among the large and well-studied fishes: the numbers of species of ocean sunfishes (genus *Mola*), goliath groupers (genus *Epinephelus*), and hammerhead sharks (genus *Sphyrna*) have all expanded after genetic appraisals (Bass et al. 2005; Quattro et al. 2006; Craig et al. 2008). Very often the genetic difference is accompanied by subtle morphological differences that become apparent upon re-examination. Molecular genetic surveys have also been useful in identifying emerging species, those that seem to be in the process of speciation (McMillan & Palumbi 1995; Campton et al. 2000; Craig et al. 2006).

Finally, the discovery of unrecognized species and cryptic evolutionary diversity can be especially important if these species are scarce, endangered, or heavily exploited. Recall the case of Hawaiian bonefish, a favorite with anglers that was once thought to be a single species, now known to be two species. Consider the implications if the two species, one more common than the other, are managed as a single fishery stock. The less abundant species could be severely depleted without any sign of distress in the overall fishery. In the final section of this chapter, we discuss the application of genetics to the conservation of fishes.

Conservation genetics

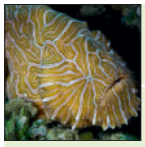
Genetics can contribute to conservation efforts in a number of ways (Box 17.5). Molecular phylogenetic assessments can identify the oldest lineages in the tree of life, which contain a disproportionately high fraction of overall genetic diversity due to their age and uniqueness. Ancient lineages are not always obvious based on morphological examinations, as demonstrated in the bonefish case above. Treating multiple species as a single species would be a fundamentally flawed premise for fish management, and could put the less abundant species at risk. To serve the conservation goal of preserving biodiversity, we need to know the fundamental evolutionary lineages, both above and below the species level.

A second way that genetics can support conservation objectives is in defining populations, the fundamental units of wildlife management. The examples discussed previously in this chapter illustrate how population genetics can assist these efforts. If two populations have significantly different allele frequencies, they are expected to be **demographically independent**, meaning they have differences in demographic parameters such as age structure, fecundity, survivorship, growth rate, and sex ratio. However, for wildlife managers the more pragmatic concern is if an isolated population is depleted, it will not be replenished by dispersal from other populations. Isolated populations must recover from catastrophes, both natural and human-caused, without significant input of individuals from elsewhere. If the population goes extinct, the habitat may eventually be recolonized by rare migrants, but these colonists are not sufficient to replenish populations over the timeframe of decades that concern wildlife managers.

Populations defined with genetics are often equated with stocks in fishery management, however they are not quite the same thing. If a group of fishes in one branch of a river is significantly different from elsewhere in terms of allele frequencies and F statistics, that genetically defined population can be regarded as an independent stock. However, the reverse is not always true. If fishes in two branches of the river are not significantly different in allele frequencies, then they may still be isolated stocks. It only takes a few migrants per generation to genetically homogenize breeding populations (but see Mills & Allendorf 1996). Ten

effective migrants (meaning those that succeed in migrating to a new population and contributing genes to that population) may prevent population genetic differentiation, but will not be sufficient to replenish depleted stocks. Hence a genetically isolated population is a stock, but a stock is not necessarily a genetically isolated population (Waples 1998). To assess contemporary movement and stock structure, tagging studies may be preferable. However, these are labor intensive, more expensive than most genetic assays, and impractical in many cases.

Fortunately this gap between demography and population genetics seems to be closing. New statistical methods allow researchers to identify individuals that move between populations by comparing microsatellite genotypes (Manel et al. 2005; Allendorf & Luikart 2006). Instead of relying on allele frequencies to define populations, these methods



Box 17.5

BOX 17.5

Species, ecosystems, or genes?

For decades scientists have argued about the conceptual basis of conservation biology. Is this a form of ecology? Many scientists maintain that ecosystems should be the primary focus of conservation, rather than individual species (Helfman 2007; see Chapter 25). Certainly ecosystems are the organic life-support machinery for all life. If ecosystems are healthy, species are at lower risk.

Alternately, is phylogenetics the basis for conservation? Many systematists and taxonomists maintain that individual species are the currency of wildlife management. They argue that we cannot protect species that are not identified and classified. Certainly the conservation focus on endangered species bears out this view, and the approach of saving the tree of life provides a valuable perspective (Purvis et al. 2005). Further, systematists argue that branch lengths in a phylogenetic tree can provide an impartial criterion for setting conservation priorities, with the longest branches deserving the highest priorities. For fish conservation, this would place a high priority on the lobe-finned coelacanth (see Chapter 13), and a lower priority on members of the recently derived cichlid species flocks of East Africa.

Both the ecological view and the taxonomic view have deep roots in human history. The philosophers of ancient Greece recognized some animals as special and worthy of protection. Likewise large tracts of land were set aside by the royalty of Medieval Europe as game reserves, and poachers who violated these boundaries were summarily executed, an early example of wildlife regulations in the service of protected areas.

A relatively new point of view is the evolutionary perspective. Evolutionists maintain that conservation efforts should protect the processes of speciation and adaptation (Frankel 1974; Erwin 1991; Fraser & Bernatchez 2001). In this view, maintaining genomic diversity allows adaptations and future evolutionary radiations. Corresponding conservation priorities include emerging species, evolutionary novelties, and speciose groups. Under these priorities, long solitary branches in the tree of life (living fossils) are the remnants of previous evolutionary radiations, dead ends that should not be subject to intensive conservation efforts. This view appears to directly contradict the phylogenetic viewpoint: evolutionists would protect the speciose cichlids rather than the ancient coelacanths.

Should conservation measures be based on taxonomic rank (a phylogenetic mandate), ecosystem health (ecological mandate), or genetic diversity (evolutionary mandate)? While these positions would seem to be irreconcilable, they are strikingly concordant when viewed in the temporal perspective of past, present, and future. The phylogenetic mandate is historical, with a focus on the successful products of past evolutionary radiations. The ecological mandate is contemporary, with a focus on healthy ecosystems for conservation efforts. The evolutionary mandate seeks to promote biodiversity in the future. In this temporal framework, the three biological disciplines that claim domain over conservation are not conflicting, rather they address three essential components: the preservation of the threads of life as they arrive from the past (phylogenetics), abide in the present (ecology), and extend into the future (evolution) (Bowen & Roman 2005) (Fig. 17.12). In this temporal perspective, the three scientific disciplines have complementary, rather than competing, roles in conservation. Notably, genetics has a vital role in all three disciplines. Molecular phylogenies reveal the deep branches and cryptic evolutionary partitions that may be missed in morphological surveys. Population genetic studies illuminate the level of connectivity among ecosystems, an essential prerequisite for designating protected areas. Genomic studies can reveal the genetic diversity and innovations that will promote future evolutionary radiations.

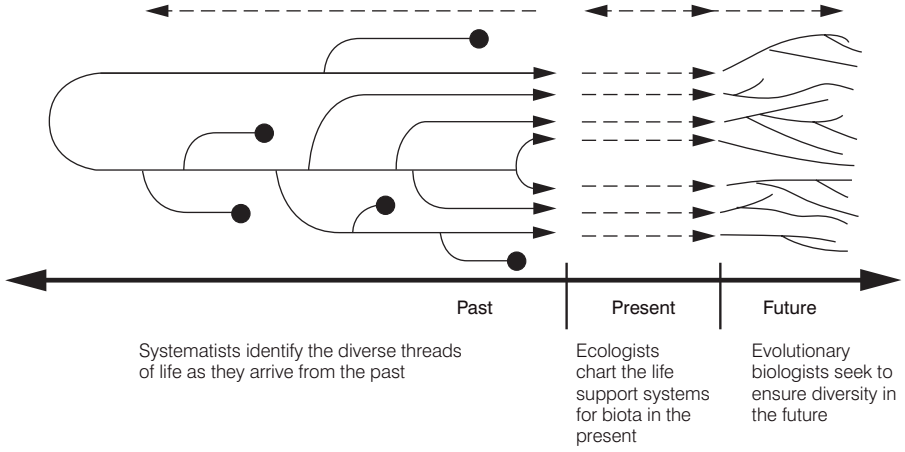


Figure 17.12

The complementary roles of three scientific fields (phylogeneticists, ecologists, and evolutionary biologists) in conservation. The process of conserving fishes begins with phylogenetic studies to identify the products of past evolutionary radiations. Subsequently, ecologists identify the key habitat features that allow fishes to persist in the present. Finally, evolutionary biologists identify the raw materials for future diversification. The black circles represent extinction events. From Bowen and Roman (2005), used with permission.

infer pedigrees among closely related individuals or their extended families, and identify individuals at one location whose closest relatives are in another location. Hence microsatellites may close the gap between traditional population genetics, which assesses gene flow averaged across thousands of generations, and tagging studies that assess contemporary movement but may miss the rare or episodic exchanges.

The third major application of genetics in conservation is in the maintenance of evolutionary potential. This field has roots in the captive breeding programs that seek to retain genetic diversity and viability in endangered species (Frankham et al. 2002), and will draw on the emerging field of genomics. One goal is to preserve the genetic variants that will allow species to persist and survive future environmental challenges. This emphasis on adaptive evolutionary conservation (Fraser & Bernatchez 2001) can also include an assessment of novel genetic properties that confer selective advantages or higher survival, or could be the wellspring of new species.

Many technical challenges remain in the field of conservation genetics, such as developing the tools to read meaningful genetic changes among the millions of nucleotides that constitute a genome. Other challenges await in the realm of ethics and environmental responsibility. For example, when is it a good idea to clone endangered species? The first such clone was reported in 2000, a wild ox (Lanza et al. 2000); can fishes be far behind? Another challenge concerns the aquaculture of genetically modified fishes (Helfman 2007; see above, Fish genomics). Transgenic Zebrafish (*Danio rerio*) are now in routine development for commercial production of pharmaceuticals. What are the risks of using transgenic fish in aquaculture? Should we use transgenic technology to introduce pollution-resistant fishes? These ethical quandaries are right around the corner.

Molecular identification in the marketplace

The PCR technology that allows researchers to recover DNA data from small bits of tissue is now recognized as a major forensic tool, both in criminology and wildlife management. The first organized effort at species identification in the marketplace with PCR technology was directed at the Japanese and South Korean whale fisheries (Baker et al. 1996). To date the applications of forensic genetics to fish products have been few, but these cases are instructive.

Sturgeon caviar represents the ultimate luxury product from fishes, commanding prices upwards of US$50 per ounce. However, native stocks of the most prized species have crashed in the aftermath of the Soviet Union, as poorly regulated fisheries and high price have driven up the harvest, while pollution and dams have reduced habitat. In these circumstances, there is strong incentive to find substitutes

for the premium caviar of the Volga River–Caspian Sea region. DeSalle and Birstein (1996) surveyed 23 lots of premium black caviar purchased from reputable dealers in New York City, using mtDNA sequences. They found that five of the lots (22%) were mislabeled eggs from less desirable but imperiled species, including three species listed on the Internation Union for the Conservation of Nature (IUCN) Red List (http://www.iucnredlist.org/) as Vulnerable (Siberian Sturgeon, *Acipenser baerii*) or Endangered (Amur River Sturgeon, *A. schrenckii*, and Ship Sturgeon, *A. nudiventris*).

Red Snapper (*Lutjanus campechanus*) is an esteemed fish in the restaurants and markets of North America, and commands a premium price. Yet few consumers have the discriminating pallet needed to be sure they are consuming the right species, and the genus *Lutjanus* has many members that are widespread, abundant, and delicious. In 1996 the Gulf of Mexico Fisheries Management Council imposed fishing restrictions after finding that the Red Snapper was overfished, driving down supply and driving up prices. Marko et al. (2004) surveyed specimens of Red Snapper purchased in eight states in the USA. The mtDNA cytochrome *b* sequences were compared to reference sequences available in Genbank (see above, Fish genomics). Seventeen of 22 specimens (77%) were not Red Snapper. Among the fraudulently labelled specimens, five were identified as other Atlantic snappers, two were Pacific Crimson Snapper (*L. erythropterus*), and the remaining 10 could not be identified because sequences from the corresponding species have not been submitted to Genbank. Some of these may be rare or unknown to science, invoking the possibility of overfishing before these species can be identified for management purposes. The fact that over half of the putative Red Snapper came from international sources indicates that this problem is global in scale.

Shark fin is one of the most contentious items in international wildlife trade, a commerce that takes an estimated 10 to 100 million sharks annually, and generates revenues equivalent to over a billion US dollars. In response to sharp declines in abundance worldwide, many countries have banned the practice of **finning** (harvesting the shark fins and discarding the rest of the fish), and three sharks (Whale, Basking, and Great White) are banned from international trade by the Convention on International Trade in Endangered Species (see Chapter 26). In these circumstances it is useful to know what species are entering the marketplace, and whether prohibited species are present. In response to this conservation concern, Shivji et al. (2002) developed diagnostic species-specific markers based on a nuclear ribosomal DNA sequence. In preliminary trials, 10 out of 55 putative Silky Sharks (*Carcharhinus falciformis*) proved to be other species. Subsequently Clarke et al. (2006) surveyed markets in Hong Kong and found that Blue Shark (*Prionace glauca*) predominated among auctioned fins (17%). Other sharks in the auctions included Shortfin Mako (*Isurus oxyrinchus*), Silky (*C. falciformis*), Sandbar (*C. obscurus*), Bull (*C. leucas*), hammerhead (*Sphyrna* spp.), and thresher (*Alopias* spp.).

These genetic surveys provide two lessons about the wildlife trade:

1. Legal markets such as those for Red Snapper in the USA are often a cover for poaching, smuggling, and illicit products entering the marketplace. Some of these products are from endangered or overutilized species.
2. Esteemed species are replaced by fraudulent alternatives. The practice of species mislabelling, dubbed "mock turtle syndrome", is observed in 15–95% of luxury products surveyed to date, including caviar, fish fillets, shark fins, seal penises, whale meat, and turtle meat (Roman & Bowen 2000).

The response of wildlife management agencies to this illicit trade remains to be seen, but clearly the commerce in scarce fish products should be monitored. The readers of *The diversity of fishes* can help, using the easy tissue collection technique described in Box 17.1. If you find some suspicious fish (or other wildlife) products, take a fin clip, a small tab of tissue, or a skin swab, and consult your local conservation geneticist.

Summary

SUMMARY

1. Fish genetic studies encompass comparisons from siblings to the deepest branches in the vertebrate phylogeny. Microsatellite DNA is most commonly used for pedigrees, breeding studies, and shallow population structure. The mtDNA sequences are commonly used to resolve shallow population structure, deep population structure (and ESUs), phylogeography, and phylogenetic trees. Nuclear introns and exons are sequenced to resolve the ancient separations among genera, families, and orders of fishes. These genetic studies are greatly facilitated by automated DNA analysis.
2. Complete fish genomes have been sequenced for four fishes, and several more are in progress. These studies have revealed 30,000–40,000 genes in the fish nuclear genome. The lungfish have the largest fish genome (81.6 pg of DNA), the bichir have the largest actinopterygian genome (5.85 pg), and the tetraodontiforms have the smallest genomes (0.35 pg), compared to 3.4 pg in the human genome.
3. Microsatellite analyses have revealed much about the breeding biology of fishes. When males guard a nest, they father about 70–95% of offspring. Females will lay eggs in multiple nests, with 1–10 mothers contributing to a single nest. Among live-bearing fishes, multiple paternity is common and widespread, approaching 100% in some species. A few sharks have been surveyed to date, showing 19–86% multiple paternity within broods.
4. The sex role reversal of the syngnathids (seahorses) offers a rare opportunity to test sexual selection theories. Contrary to most species in which the males carry the conspicuous ornamentation, it is the female syngnathids that display sexual dimorphisms. Microsatellite surveys show a tendancy towards polyandry (multiple males mating with a single female), rather than the predominant polygyny (multiple females mating with a single male) observed in nesting fishes.
5. Population genetic structure, the level of isolation between populations of the same species, is highest in freshwater fishes and marine fishes that lack a pelagic larval stage. Among the fishes with a pelagic stage, there is no simple relationship between the length of the pelagic stage and the extent of dispersal. The ecosystem specialists, with highly restricted habitat or feeding, tend to have higher population structure than generalists. Comparisons of maternally inherited mtDNA, and biparentally inherited nDNA can reveal differences in dispersal between males and females, a common outcome in migratory marine fishes.
6. Phylogeography is the field bridging population genetics and phylogenetics, concerned with the geographic distribution of genetic lineages. Very often the biogeographic separations defined previously by species distributions (see Chapter 16) are supported by surveys of genetic diversity within species. Phylogeographic surveys can reveal rare dispersal events that are difficult to detect, but very important for understanding the diversity of fishes.
7. Molecular systematics has provided robust hypotheses about the relationships among fishes at all levels. Using a molecular phylogeny, evolutionary biologists can track the origin of innovations like the beak of the parrotfishes. These studies show extremely slow morphological evolution in some groups (bonefishes) and very rapid evolution in other groups (cichlids).
8. Conservation genetics is the application of DNA data to a variety of wildlife management issues. A key goal in this field is to preserve the genetic diversity that allows species to resist disease and adapt to changing conditions. Population genetic studies can delineate the boundaries of fishery stocks and management units within species. Molecular systematics can reveal unreconized species that may be subject to harvest or depletion. Molecular forensics can show which species are entering the marketplace, and demonstrate that some legal harvests can provide a cover for the exploitation of endangered species.

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SUPPLEMENTARY READING

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Chapter 18

Special habitats and special adaptations

Chapter contents

Given our themes of diversity and adaptation, it seems appropriate to explore habitats and geographic regions that have led to spectacular evolutionary events among fishes. Certain climatic regimes and regions appear unusually harsh for successful invasion by complex vertebrate life forms. But fishes have been able to occupy almost all naturally occurring aquatic ecosystems that have any degree of permanence or at least predictability. It is often quite easy to determine the major selective pressures impinging on fishes in these habitats, and it is also often obvious what physiological, anatomical, and ecological adaptations have evolved in response to specific environmental pressures. An axiom of evolutionary biology is that animals exposed to similar selection pressures are likely to evolve similar adaptations. This axiom, formalized as the **Principle of Convergence**, states that the stronger the selection pressures, the more similar unrelated animals will appear. In other words, where selection pressures are particularly extreme, animals will converge in morphology, physiology, behavior, and ecology, approaching an optimal design for that particular set of environmental forces. The special habitats discussed below – the deep sea, the open sea, polar regions, deserts, turbulent water habitats, and caves – show this principle in operation.

The deep sea

The most diverse deepsea fish assemblages occur between 40°N and 40°S latitudes, roughly between San Francisco and Melbourne, Australia in the Pacific Basin and between New York City and the Cape of Good Hope in the Atlantic Basin. Separation of deepsea fishes occurs more on a vertical than on a latitudinal basis (Fig. 18.1). The three major regions of open water are **mesopelagic** (200–1000 m), **bathypelagic** (1000–4000 m), and **abyssal** (4000–6000 m); deepsea regions below 6000 m are referred to as **hadal** depths. A second group of **benthal** or bottom-associated species swims just above the bottom (= **benthopelagic**) or lives in contact with it (= **benthic**), usually along the upper continental slope at depths of less than 1000 m; corresponding ecological zones of benthal species are referred to as bathyal, abyssal, and hadal. The upper 200 m of the open sea, termed the **epipelagic** or **euphotic zone**, has its own distinctive subset of fishes (see below). This is the region where the photosynthetic activity of phytoplankton exceeds the respiration of the plants and animals living there, i.e., where production/respiration >1. The euphotic zone is the energy source for the deeper waters (Marshall 1971; Wheeler 1975; Nelson 1994; Castro & Huber 1997, Neighbors & Wilson 2006).

The deepsea fishes of the mesopelagic and bathypelagic regions are readily recognized by just about anyone with a passing interest in fishes or marine biology. Deepsea fishes often have light-emitting organs, termed **photophores**;

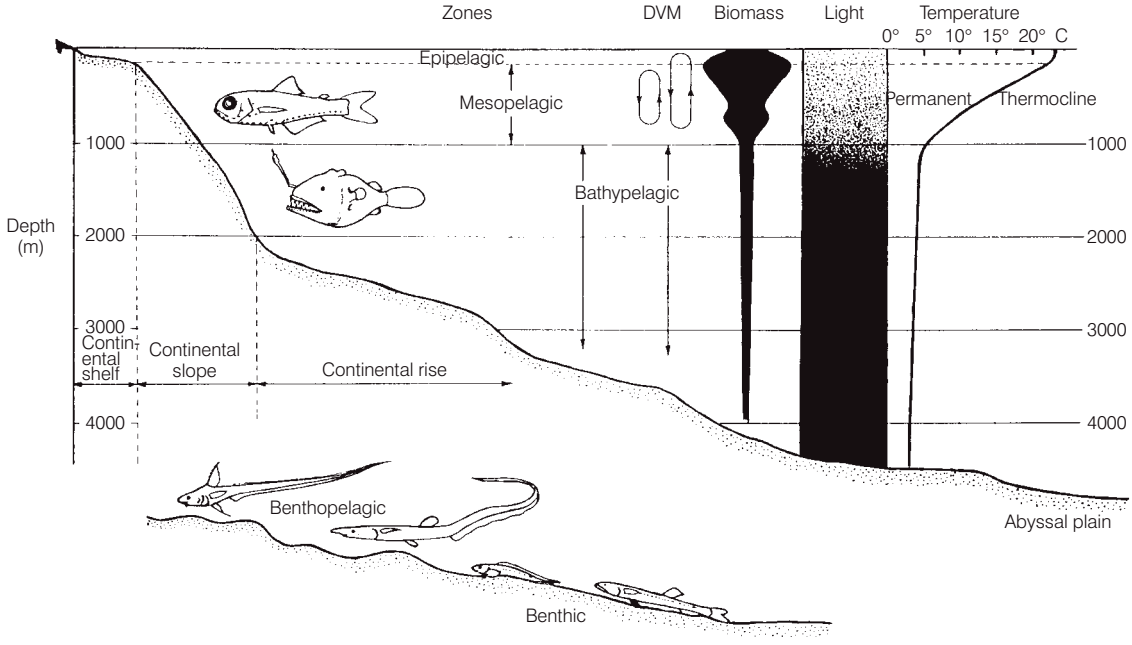


Figure 18.1

Regions and physical features of the deepsea environment relative to depth. Representative species are a mesopelagic lanternfish, bathypelagic ceratioid anglerfish, benthopelagic rattail and halosaur, and benthic snailfish and greeneye. Many mesopelagic species undergo a diurnal vertical migration (DVM) to shallower waters at dusk, returning to deeper water at dawn. Total biomass of living organisms, available light, and temperature all decline with depth in the deep sea. From Marshall (1971), used with permission.

large or long mouths studded with daggerlike teeth; chin barbels or dorsal fin rays modified as lures; long, thin bones; and greatly enlarged, tubular eyes or greatly reduced eyes (Marshall 1954, 1971). Such familiar appearances could result from a relative scarcity of forms. For example, widespread familiarity with deepsea fishes could occur if we were exposed to many illustrations of the same strange animals. As the taxonomic listing in Table 18.1 reveals, the recognizability of deepsea fishes is not a function of scarcity or a depauperate fauna. More than 1000 species of fishes inhabit the open waters of the deep sea and another 1000 species are benthal, with good representation across orders of cartilaginous fishes and superorders of bony fishes. Similarities among unrelated fishes are therefore not due to phylogenetic relations but to convergent adaptations.

Deepsea fishes look alike because different ancestors invaded the deep sea from shallow regions and evolved similar anatomical and physiological solutions to an extreme environment. Understanding the convergent adaptations of deepsea fishes requires that we first understand the physical environment of the deep sea and its influences on biota. Five physical factors contrast markedly between the surface and the deep sea and appear to have been strong selective forces on fishes (Marshall 1971; Hochachka & Somero 1984).

Physical factors affecting the deep sea

Pressure

The weight of the overlying column of water, measured in atmospheres, increases constantly with depth at a rate of l atm/10 m of descent (1 atm = 1.03 kg/cm^2 or 14.7 lbs/in^2). Thus between the top of the mesopelagic region at 200 m and the lower bathypelagic region at 4000 m, pressure increases 20-fold, from 20 to 400 atm. The deepest living fishes, the neobythitine cusk-eels, *Bassogigas profundissimus* and *Abyssobrotula galatheae*, have been collected at 7160 and 8370 m, respectively, where they would experience pressures of 700–800 atm, or *c*. 12,000 lbs/in^2 (Nielsen & Munk 1964; Nielsen 1977). Below the surface, pressure at any given depth is constant and predictable, whereas at the surface it can change rapidly and significantly with each passing wave.

The tremendous pressures of the deep sea do not create problems for most biological structures because fishes are made up primarily of water and dissolved minerals, which are relatively incompressible. However, pressure has an influence on the volume of water molecules, water-containing compounds, and proteins, which affects the rates of chemical reactions. Several deep mesopelagic and bathypelagic species have evolved proteins that are much less sensi-

Table 18.1

Representative teleostean taxa from the three major deepsea habitat types. The approximate number of deepsea families is given in parentheses the first time a group is listed. Based on Marshall (1971, 1980); Wheeler (1975); Gage and Tyler (1991); Nelson (2006). Figures from Marshall (1971), used with permission.

Mesopelagic (750 spp.)
Superorder Elopomorpha
- Albuliformes (3): Notacanthidae – spiny eels
- Anguilliformes (6): Nemichthyidae – snipe eels; Synaphobranchidae – cutthroat eels

Superorder Protacanthopterygii
- Argentiniformes (5): Microstomatidae – deepsea smelts; Opisthoproctidae – barreleyes; Alepocephalidae – slickheads; Platytroctidae – tubeshoulders

Superorder Stenopterygii
- Stomiiformes (5): Gonostomatidae – bristlemouths; Sternoptychidae – hatchetfishes; Stomiidae – barbeled dragonfishes

Superorder Cyclosquamata
- Aulopiformes (11): Evermannellidae – sabertooth fishes; Alepisauridae – lancetfishes; Paralepididae – barracudinas; Giganturidae – telescopefishes

Superorder Scopelomorpha
- Myctophiformes (2): Neoscopelidae – blackchins; Myctophidae – lanternfishes

Superorder Lampriomorpha
- Lampriformes (4): Stylephoridae – tube-eyes

Superorder Acanthopterygii
- Stephanoberyciformes: Mirapinnidae – hairyfish
- Perciformes: Chiasmodontidae – swallowers; Gempylidae – snake mackerels


hachetfish


giganturid

Bathypelagic (200 spp.)
Superorder Elopomorpha
- Anguilliformes: Nemichthyidae – snipe eels; Serrivomeridae – sawtooth eels
- Saccopharyngiformes: Saccopharyngidae – swallower and gulpers; Eurypharyngidae – pelican eels

Superorder Protacanthopterygii
- Argentiniformes: Alepocephalidae – slickheads

Superorder Stenopterygii
- Stomiiformes: Gonostomatidae – bristlemouths

Superorder Paracanthopterygii
- Gadiformes: Melanonidae – pelagic cods; Macrouridae – grenadiers and rattails
- Ophidiiformes: Ophidiidae – cusk-eels; Bythitidae – viviparous brotulas
- Lophiiformes (12): Ceratioidei – deepsea anglerfishes, seadevils (11)

Superorder Acanthopterygii
- Stephanoberyciformes: Melamphaidae – bigscale fishes; Stephanoberycidae – pricklefishes; Cetomimoidea – whalefishes (3)
- Beryciformes (9): Anoplogastridae – fangtooths
- Perciformes: Chiasmodontidae – swallowers


gulper


whalefish

Benthal[a] (1000 benthopelagic and benthic spp.)
Superorder Elopomorpha
- Albuliformes: Halosauridae – halosaurs; Notacanthidae – spiny eels
- Anguilliformes: Synaphobranchidae – cutthroat eels

Superorder Cyclosquamata
- Aulopiformes: Synodontidae – lizardfishes; Chlorophthalmidae – greeneyes; Ipnopidae – spiderfishes and tripodfishes

Superorder Paracanthopterygii
- Gadiformes: Macrouridae – grenadiers; Moridae – morid cods; Merlucciidae – merlucciid hakes
- Ophidiiformes: Ophidiidae – cusk-eels; Bythitidae – viviparous brotulas; Aphyonidae – aphyonids
- Lophiiformes: Ogcocephalidae – batfishes

Superorder Acanthopterygii
- Scorpaeniformes: Liparidae – snailfishes
- Perciformes: Zoarcidae – eel-pouts; Bathydraconidae – Antarctic dragonfishes; Caproidae – boarfishes


brotula

[a] Chimaeras and many squaloid sharks are benthopelagic. Most benthal fishes live above 1000 m, although some grenadiers and rattails live between 1000 and 4000 m, macruronid southern hakes live somewhat deeper, tripodfish live to 6000 m, snailfishes to 7000 m, and neobythitine cusk-eels live down to 8000 m.

tive to the effects of pressure than are their shallow water relatives (Hochachka & Somero 1984; Somero et al. 1991). Gas-containing structures are particularly affected because both volume relationships and gas solubility are sensitive to pressure. The organ most affected is the gas bladder because it is difficult to secrete gas into a gas-filled bladder under high pressure. Three trends occur in the gas bladders of deepsea fishes that reflect the constraints of pressure:

1. The efficiency of gas secretion depends on the interchange surface of the capillaries of the **rete mirabile**, the main gas-secreting organ (see Chapter 5, Buoyancy regulation). Whereas the retes of epipelagic fishes are usually less than 1 mm long, retes of upper mesopelagic fishes are 1–2 mm long, those of lower mesopelagic fishes are 3–7 mm long, and those of some bathypelagic fishes are 15–20 mm long.
2. Although mesopelagic fishes have large gas-filled bladders, most bathypelagic fishes have lost their gas bladders. Flotation might therefore be a problem for these fishes, but their body musculature and skeletons are reduced as energy saving mechanisms and they consequently approach neutral buoyancy. As long as a fish remains at relatively constant depths, it has minimal need for buoyancy control. However, many mesopelagic fishes undergo **diurnal vertical migrations**, have a greater need to adjust their buoyancy, and have retained their gas bladders. Deep benthopelagic fishes are able to hover just above the bottom with minimal energy expenditure via a different mechanism. Instead of trying to secrete gases against incredible pressure gradients, they have evolved **lipid-filled** gas bladders. Lipids are relatively incompressible and are lighter than sea water and thus provide flotation. Interestingly, the larvae of these fishes have gas-filled bladders, but these larvae, and the larvae of nearly all deepsea fishes, are epipelagic, where the costs of gas secretion and buoyancy adjustment are much less. Benthopelagic squaloid sharks such as *Centroscymnus* and *Etmopterus* show parallel evolution. These deepsea sharks have exceptionally large livers that account for 25% of their total body mass. Their livers contain large quantities of the low-density lipid **squalene**. Deepwater holocephalans also achieve neutral buoyancy via squalene and by reduced calcification of their cartilaginous skeletons (Bone et al. 1995).
3. Most deepsea fishes belong to the relatively primitive teleostean superorders Protacanthopterygii, Stenopterygii, Cyclosquamata, and Scopelomorpha. These taxa typically have a direct, physostomous connection between the gas bladder and the gut. Deepsea fishes are, however, "secondarily" physoclistous, having closed the pneumatic duct, thus preventing gas from escaping out the mouth.

Temperature

At the surface, temperature is highly discontinuous, changing markedly both seasonally and daily. In the deep sea, temperature is a predictable function of depth. Surface waters are warmer than deeper waters. Water temperature declines with depth through the mesopelagic region across a **permanent thermocline** until one reaches the bathypelagic region, where temperature remains a relatively constant 2–5°C, depending on depth.

Temperature is a strong predictor of distribution for different taxa of deepsea fishes. Ceratioid anglerfishes and darkly colored species of the bristlemouths (*Cyclothone*) are restricted to the deeper region. Even within the mesopelagic zone, species sort out by temperature. Hatchetfishes, pale *Cyclothone*, and malacosteine loosejaws are restricted to the lower half at temperatures between 5 and 10°C, whereas lanternfishes and astronesthine and melanostomiatine stomiiforms occur in the upper half at 10–20°C. Latitudinal differences in temperature–depth relationships lead to distributional differences within species. Some species such as ceratioid anglers that are mesopelagic at high latitudes occur in bathypelagic waters at lower latitudes, a phenomenon known as **tropical submergence** that results from the warmer surface temperatures in the tropics.

Since temperature remains fairly constant at any given depth, absolute temperature is a minimal constraint on a fish that does not move vertically. But vertically migrating mesopelagic species must swim through and function across a temperature range of as much as 20°C (see Fig. 18.1). Lanternfish species that migrate vertically have larger amounts of DNA per cell than do species that are non-migratory. Increased DNA could potentially allow for multiple enzyme systems that function at the different temperatures encountered by the fishes (Ebeling et al. 1971).

Space

The volume occupied by the deep sea is immense. Approximately 70% of the earth's surface is covered by ocean, and 90% of the surface of the ocean overlies water deeper than 1000 m. The bathypelagic region, which makes up 75% of the ocean, is therefore the largest habitat type on earth. This large volume creates problems of finding food, conspecifics, and mates because bathypelagic fishes are never abundant. Life in the bathypelagos is extremely dilute. For example, female ceratioid anglerfishes are distributed at a density of about one per 800,000 m^3, which means a male anglerfish is searching for an object the size of a football in a space about the size of a large, totally darkened football stadium.

Deepsea fishes show numerous adaptations that reflect the difficulties of finding potential mates that are widely distributed in a dark expanse. Unlike most shallow water forms, many deepsea fishes are **sexually dimorphic** in ways directly associated with mate localization. Mesopelagic fishes, such as lanternfishes and stomiiforms, have species-specific and sex-specific patterns and sizes of light organs, structures that first assure that individuals associate with the right species and then that the sexes can tell one another apart. Among benthopelagic taxa, such as macrourids, brotulids, and morids, males often have larger muscles attached to their gas bladders that are likely used to vibrate the bladder and produce sounds that can attract females from a considerable distance.

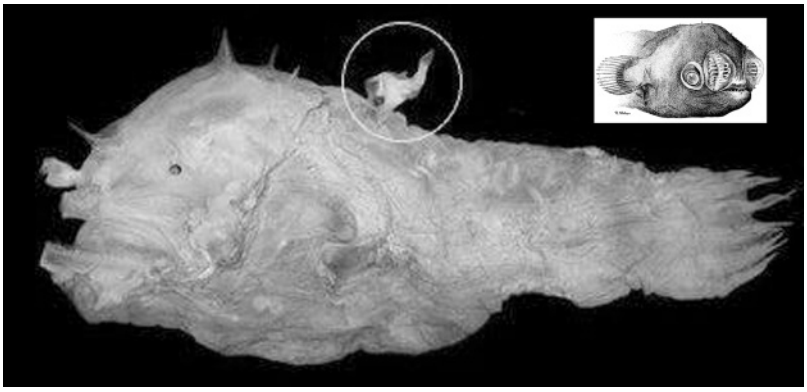


Figure 18.2
Size differences in male versus female anglerfishes. A 6.2 mm parasitic male *Photocorynus spiniceps* (Linophrynidae) (circled) attached to the dorsal area of a 46 mm female. Inset: a free-living, 18 mm male of *Linophryne arborifera* (Linophrynidae), showing the greatly enlarged eyes and olfactory lamellae apparently used in finding females. From Pietsch (2005), used with permission; photos courtesy of T. W. Pietsch.

Some of the most bizarre sexual dimorphisms occur among bathypelagic species, where problems of mate localization are acute. The most speciose group of bathypelagic fishes is the ceratioid anglerfishes, of which there are 11 families and about 162 species (Bertelsen 1951; Pietsch 1976, 2005; Nelson 2006; Pietsch & Orr 2007; see Fig. 14.28). In several families, the males are dwarfed, reaching only 20–40 mm long, whereas females attain lengths 10 or more times that size, up to 1.2 m in one species. In five families, males attach temporarily to females, spawning occurs, and the males swim free (Pietsch 2005). In five other families, the males are entirely and permanently **parasitic** on the females, and males in these taxa may be as small as 6.2 mm, making them the smallest known sexually mature vertebrate (Fig. 18.2). Males attach most frequently to the ventral midline of the belly of the female, but may be attached on the sides, backs, head, and even the fishing lure of a female; as many as eight males have been found attached to a single female (including some species mismatches). In parasitic species, males attach by the mouth, his mouth tissue fuses with her skin, and he becomes parasitically dependent on her for nutrition. Many of his internal organs degenerate, with the exception of his testes, which can take up more than half of his coelom. Females do not mature sexually until a male attaches to them (Pietsch 2005).

The premium placed on locating a female is reflected throughout the anatomy and physiology of searching males. During this phase, males have highly lamellated olfactory organs and well-developed olfactory tracts, bulbs, and forebrains, whereas females have almost entirely degenerate olfactory systems. Males also have extensive red muscle fibers, the kind used for sustained swimming. Females have predominantly white muscle fibers, which usually function for short bursts of swimming. Males of some species possess enlarged, tubular eyes that are extremely sensitive to light (see below), whereas females have small, relatively insensitive eyes. Males also have high lipid reserves in their livers, which they need because their jaw teeth become replaced by beaklike denticles that are useless for feeding but are apparently specialized for holding onto a female (the denticular jaws are derived embryologically from the same structures that in females develop into the fishing lure, discussed below; Munk 2000). All this comparative evidence indicates that males are adapted for swimming over large expanses of ocean, searching for the luminescent glow and some olfactory cue emitted by females. Females in contrast are floating relatively passively, using their bioluminescent lures to attract prey at which they make sudden lunges, and trailing pheromones through the still waters. The coevolved nature of these traits is evident from the dependence of both sexes on locating each other. Neither sex matures until the male attaches to the female.

Convergence occurs in the unrelated bathypelagic bristlemouths, which are probably the most abundant vertebrates on earth. Again, males are smaller than females, have a well-developed olfactory apparatus, extensive red muscle fibers, and larger livers and fat reserves. Although the males are not parasitic on the females, they are unusual in that they are **protandrous hermaphrodites**, meaning that an individual matures first as a male and then later switches sex and becomes a female. Sex change theory predicts just such a switch because relative fitness favors being a male when small and a female when large (see Chapter 10, Determination, differentiation, and maturation; Chapter 21, Gender roles in fishes). Cetomimid whalefishes – one of the few percomorph groups to occupy the bathypelagic region and second only to oneirodid anglerfishes in diversity there – have also converged on having dwarf males, although male whalefishes are not known to be parasitic on the larger females (Nelson 2006).

Light

Below the euphotic zone, light is insufficiently strong to promote significant plant growth. Visible light to the human eye is extinguished by 200–800 m depth, even in the uniformly clear water of the mesopelagic and bathypelagic regions. Deepsea fishes are 15–30 times more sensitive to light and can detect light down to between 700 and 1300 m,

depending on surface clarity. The mesopelagic region is often termed the **twilight zone**, whereas the bathypelagic region is continually dark. What little light that passes into the mesopelagic region has been differentially absorbed and scattered by water molecules and turbidity and is limited to relatively short, blue-green wavelengths centered on 470 nm.

The greatly reduced illumination of the mesopelagic region, and the missing light of the bathypelagic region, have produced obvious adaptations among both the eyes and photophores of fishes living there. Bathypelagic fishes live in permanent darkness and, with the exception of male ceratioid anglers, have greatly reduced eyes that probably function primarily for detecting nearby bioluminescence. Mesopelagic fishes have modifications to their eyes that generally increase their ability to capture what little ambient light is available, although different species appear to have emphasized capturing dim ambient spacelight versus brighter point sources from bioluminescence (Warrant & Locket 2004). Mesopelagic fishes have very large eyes, often measuring 50% of head length; most North American freshwater fishes have eye diameters that are only 10–20% of head length.

Mesopelagic fishes also have comparatively large pupils and lenses and lengthened eyes. Elongation results either from a space between the pupil and lens, termed the **aphakic** or **lensless space**, or from lengthening of the retina-containing portion of the eye posterior to the lens. Aphakic spaces have evolved convergently in protacanthopterygian platytroctids and bathylagine deepsea smelts, stenopterygian loosejaws (Malacosteinae), cyclosquamate waryfishes, and scopelomorph lanternfishes, most of which live in the upper region of the mesopelagic zone. Tubular eyes, more characteristic of deeper mesopelagic species, have evolved convergently in four superorders and five orders of mesopelagic fishes, including protacanthopterygian barreleyes, stenopterygian hatchetfishes, paracanthopterygian anglerfishes, and acanthopterygian whalefishes. Eye elongation provides two visual benefits, increasing the sensitivity of the eye to light by about 10% and also increasing binocular overlap, which aids depth perception (Marshall 1971; Lockett 1977).

Mesopelagic fishes have pure rod retinae with visual pigments that are maximally sensitive at about 470 nm, which is a good match to the light environment at mesopelagic depths and also matches the light output from photophores, structures that are much more common among mesopelagic than bathypelagic fishes. **Bioluminescence** has evolved independently in at least five superorders of deepsea teleosts – protacanthopterygians, stenopterygians, scopelomorphs, paracanthopterygians, and acanthopterygians – as well as in dogfish sharks, squids, crustaceans, and other invertebrates. Light organs, in addition to identifying the species and sex of the emitter, may also illuminate nearby prey. The structures that bioluminesce may be a simple luminescent gland backed by black skin that emits on its own or contains bioluminescent bacteria. More complex circular photophores may be backed by silvery reflective material with a lens through which light passes. In highly derived photophores, the lens may be pigmented and hence the light transmitted is of a different wavelength, as in the malacosteine loosejaws which have a red filter over the subocular photophores and also have retinal reflectors and receptors sensitive to red wavelengths (e.g., Herring & Cope 2005). This unique combination of luminescent emission and spectral sensitivity could give loosejaws a private channel over which they can communicate without being detected by potential predators or prey. It could also serve to maximize illumination of red mesopelagic crustaceans (Lockett 1977; Denton et al. 1985; Sutton 2005). Photophores tend to flash on for 0.2–4 s, depending on species. Different species of lanternfishes may have similar photophore patterns but different flash rates, suggesting a convergence in communication tactics between deepsea fishes and fireflies (Meinsinger & Case 1990).

Food

Limited light and huge volume mean that food is extremely scarce in the deep sea. All marine food chains, except at **thermal vents**, originate in the euphotic zone, which makes up only 3% of the ocean. Food for bathypelagic fishes must therefore first pass through the filter of vertebrates, invertebrates, and bacteria in the mesopelagic zone; much of this food rains down weakly, unpredictably, and patchily in the form of carcasses, sinking sargassum weed, detritus, and feces. All deepsea fishes are carnivorous, feeding either on zooplankton, larger invertebrates, or other fishes. Zooplankton biomass at the top of the bathypelagos is only about 1% of what it is at the surface, and densities of benthic invertebrates decrease with depth and distance from continental shores. High densities, diversities, and productivity of invertebrates at thermal vents on the deepsea floor do not support a similar abundance or diversity of fishes. Only three species – a bythitid brotula and two zoarcid eel-pouts – are endemic to and frequent vent areas (Grassle 1986; Cohen et al. 1990). A general scarcity of food in the deep sea puts a premium on both saving and obtaining energy. Convergent traits in both categories are readily apparent.

Foraging adaptations

Deepsea fishes show a number of convergent foraging traits (Gartner et al. 1997). In general, zooplanktivores have small mouths and numerous, relatively fine gill rakers, whereas predators on larger animals have larger mouths and fewer, coarser gill rakers. **Daggerlike teeth** or some other form of long, sharp dentition is so characteristic of deepsea forms that their family names often refer directly or indirectly to this trait, including such colorfully named groups as dragonfishes, daggertooths, bristlemouths, snag-

gletooths, viperfishes, sabretooths, and fangtooths. Large, expandable mouths, hinged jaws, or distensible stomachs are also reflected in such names as gulpers, swallowers, and loosejaws. Saccopharyngoid gulper and swallower eels have enormous mouths that can expand to > 10 times the volume of the animal's entire body, the largest mouth : body volume of any known vertebrate (Nielsen et al. 1989). Black dragonfishes, viperfishes, ceratioid anglerfishes, and sabertooth fishes can swallow prey larger than themselves (Fig. 18.3), as much as three times so in the case of the anglerfishes. Their swallowing abilities are increased because the pectoral girdle is disconnected from the skull, enlarging the intercleithral space of the throat (see Chapter 8, Pharyngeal jaws). All of these anatomical specializations point to a strategy of taking advantage of any feeding opportunity that may come along, despite the size of the prey.

A small number of shallow water paracanthopterygian species, notably the goosefishes, frogfishes, batfishes, and anglerfishes, possess modified dorsal spines that are waved in front of prey species to lure them within striking distance. Such lures reach their greatest and most diverse development among mesopelagic and bathypelagic fishes, where they occur on viperfishes, various dragonfishes, astronesthine snaggletooths, most ceratioid anglerfishes, and arguably as luminescent organs in the mouths of hatchetfishes, lanternfishes, and some anglerfishes and on the illuminated tail tip of the gulper eels. The typical anglerfish lure consists of an elongate dorsal spine, the **illicium**, tipped by an expanded structure called the **esca** (Fig. 18.4). Escae tend to have species specific shapes, can regenerate if damaged, and are moved in a variety of motions that imitate the swimming of a small fish or shrimp (see Pietsch 1974).

Most mesopelagic fishes undertake evening migrations from the relatively unproductive mesopelagic region to the richer epipelagic zone to feed; they then return to the mesopelagic region at dawn (see Fig. 18.1). The migration involves movements to near the surface from as deep as 700 m, can take an hour or more, and may entail considerable energy expenditure. This movement is so characteristic of mesopelagic fishes, crustaceans, and mollusks that the community of organisms that migrates is referred to as the **deep scattering layer**, whose presence is discernible on sonar screens because of reflection of sonar signals off the

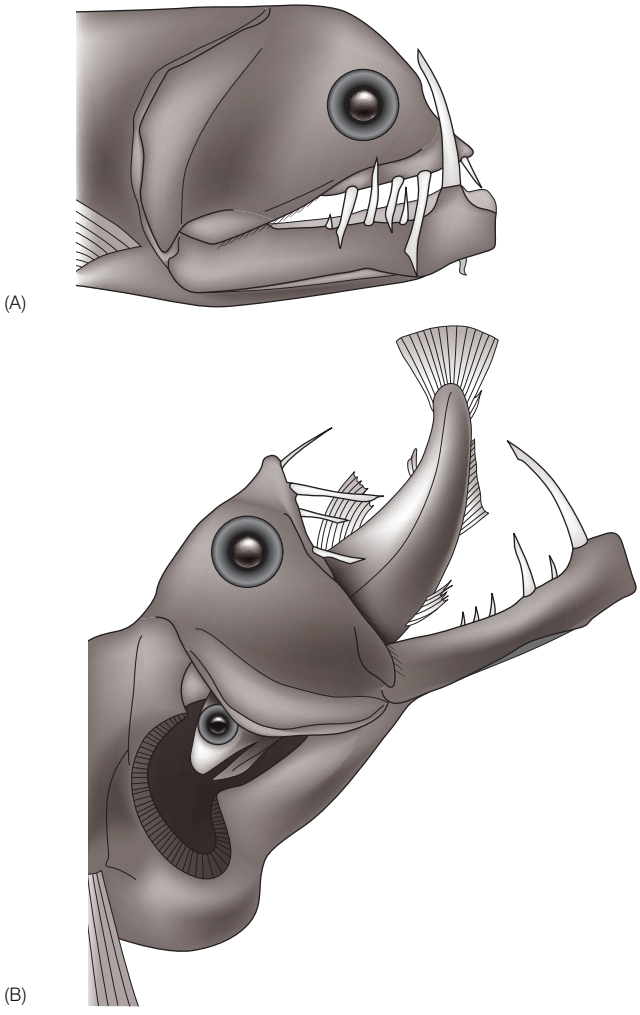


Figure 18.3
Extreme movements of the head and mouth during swallowing in the viperfish, *Chauliodus sloani*. (A) Mouth at rest, showing the premaxillary and mandibular teeth that sit outside the jaw when the mouth is closed. The maxillary and palatine teeth are small and slant backward. (B) Mouth opened maximally as prey is captured and impaled on the palatine teeth prior to swallowing. The anterior vertebrae and neurocranium are raised, the mandibuloquadrate joint at the back corner of the mouth is pushed forward, and the gill covers are pushed forward and separated from the gills and gill arches. The heart, ventral aorta, and branchial arteries are also displaced backward and downward. Such wide expansion of the mouth accommodates very large prey and is in part necessary for prey to pass between the large fangs. After Tchernavin (1953).

Figure 18.4
An adult female wolftrap angler, *Lasiognathus amphirhamphus* (Thaumatichthyidae), about 15 cm long. The rodlike structure pointing tailward is the skin-covered caudal end of the dorsal spine that forms the illicium. The spine slides in a groove on the head, allowing the anglerfish to move it forward when fishing but to retract it otherwise. Photo courtesy of T. W. Pietsch.

gas bladders of the fishes. Hypotheses about the adaptiveness of the migration include: (i) a net energy gain from feeding in warm water and metabolizing in cold water; and (ii) exploiting surface currents that bring new food into the water column above the migrator. It is apparent that the migration serves a foraging purpose, given the 100-fold difference in plankton biomass between the two regions and also given that stomachs of migrators are empty in the evening before migration and full in the morning after migration.

It is in the deeper region of the bathypelagos that we find the most extreme adaptations for opportunistic prey capture and energy conservation. Bathypelagic fishes remain in place, perhaps because external cues of changing daylight are lacking or the energetic costs of migrating are too high. They instead lure prey with bioluminescent lures. Observations from submersibles suggest that bathypelagic forms adapt a "float-and-wait" foraging mode, hovering relatively motionless in the water column and making quick lunges at prey. This motionless hovering and luring even occurs when purportedly bathypelagic anglerfish forage near the bottom, as evidenced by fortuitous observations of a Whipnose Anglerfish, *Gigantactis*, swimming slowly upside-down just off the bottom, its illicium held stiffly in front in a slight downward-pointing arc (Moore 2002) (Fig. 18.5).

Energy conservation

Deepsea fishes minimize their daily and long-term expenditure of calories in many ways. Biochemically, rates of enzymatic and metabolic activity and even levels of adenosine triphosphate (ATP) generating enzymes are lower in deepsea fishes than in shallow water relatives, which conserves energy used in locomotion, osmotic regulation, and protein synthesis (Somero et al. 1991). Energy savings are also accomplished via elimination or replacement of heavy components. Structurally, bathypelagic fishes are fragile compared with shallow water, mesopelagic, and even deepsea benthic fishes. Many of the heavy bony elements of shallow water relatives have been eliminated. Pelvic fins are often missing or reduced to rudiments, bones of the head are reduced to thin strands, and many species are scaleless. Spines are rare among deepsea fishes; even the few acanthopterygian groups that have managed to invade the deep sea, such as melamphaid bigscale fishes and chiasmodontid swallowers, have very feeble fin spines. Body musculature is also greatly reduced, by as much as 95% in the trunk and caudal regions compared with shallow water forms.

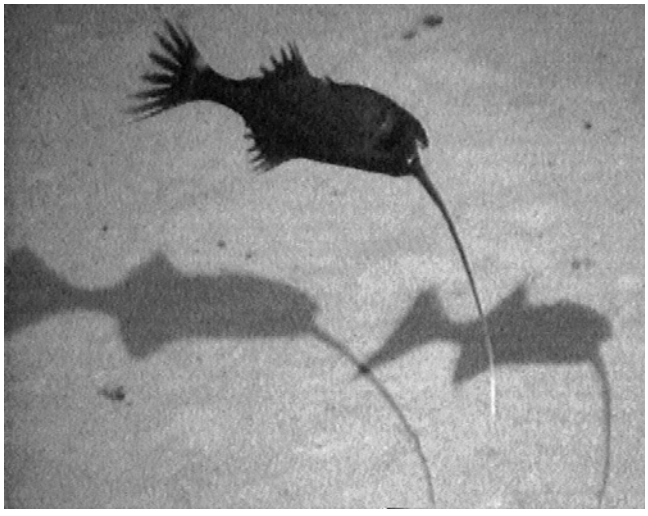


Figure 18.5

A 50 cm long Whipnose Anglerfish presumably foraging just above the bottom at 5000 m depth. Its illicial lure is extended down toward the bottom (lower two profiles are shadows cast by photographic lights). Interestingly, in gigantactinids, the teeth of the lower jaw are elongated and curved, much like the upper jaw teeth of other anglerfishes, implying that upside-down foraging may be common in Whipnose Anglerfishes. From Moore (2002), used with permission.

Lacking trunk musculature, predator evasion becomes a problem. Most deepsea fishes are colored in ways that should minimize their detection by potential predators. Mesopelagic fishes tend to be silvery or brown with ventral photophores that point downward. Silvery fishes disappear in open water (see Chapter 20, Invisible fishes). Ventral photophores may aid in breaking up the silhouette of the fish when viewed from below against the backdrop of weak downwelling light (Johnsen et al. 2004). Bathypelagic fishes are generally dark brown or black, as would be expected where the background is black. Additional energy savings are attained by replacing heavy structural components with less dense substances. Where glycerol lipids occur in shallow water fishes, deepsea forms have less dense waxy esters. These structural changes save energy because metabolic costs of both construction and maintenance are reduced. In addition, elimination and replacement of heavy elements reduces the mass of the fish, making it closer to neutral buoyancy and eliminating costs associated with fighting gravity.

Bathypelagic fishes as a group tend to have **free neuromasts** in their lateral lines, rather than having lateral line organs contained in canals, as in mesopelagic and benthic groups. Free neuromasts in shallow water fishes, such as goosefishes, cavefishes, and many gobies, are usually associated with a very sedentary life style, again suggesting a premium on energy-conserving tactics and an ability to detect minor water disturbances among bathypelagic species.

Convergence in the deep sea

The deep sea offers numerous striking examples of the Principle of Convergence. Benthopelagic fishes from at least 12 different families have evolved an eel-like body that tapers to a pointed tail, often involving fusion of elongated

dorsal and anal fins with the tail fin (Gage & Tyler 1991). Another aspect of convergence exemplified in the deep sea is that selection pressures can override phylogenetic patterns, producing closely related fishes that are biologically very different because they live in different habitats (Marshall 1971). *Gonostoma denudatum* and *G. bathyphilum* are Atlantic bristlemouths in the stenopterygian family Gonostomatidae. *G. denudatum* is a mesopelagic fish, whereas *G. bathyphilum*, as its name implies, is a bathypelagic species. *G. denudatum* is silvery in color and has prominent photophores, well-developed olfactory and optic organs and body musculature, a well-ossified skeleton, a large gas bladder, large gill surface per unit weight, large kidneys, and well-developed brain regions associated with these various structures. *G. bathyphilum*, in contrast, is black, has small photophores and small eyes, small olfactory organs (except in males), weak lateral muscles, a poorly ossified skeleton, no gas bladder, small gills and kidneys, and smaller brain regions. Only the jaws of *G. bathyphilum* are larger than its mesopelagic congener. Similar comparisons can be drawn between other mesopelagic and bathypelagic gonostomatids, and between mesopelagic and bathypelagic fishes in general. Even bathypelagic forms derived from benthopelagic lineages, such as the macrourids and brotulids, have converged on bathypelagic traits (Marshall 1971).

The extreme demands of the deepsea habitat have also led to convergence in non-teleostean lineages. The mesopelagic cookie cutter sharks, *Isistius* spp., have a high squalene content in their livers that increases buoyancy. They also possess photophores and migrate vertically with the biota of the deep scattering layer (the widespread nature of bioluminescence, some fish producing their own light and others using symbiotic bacteria, is in itself a remarkable convergence). Deepsea sharks and holocephalans also possess visual pigments that absorb light maximally at the wavelengths that penetrate to mesopelagic depths, as is also the case for another mesopelagic non-teleost, the Coelacanth, *Latimeria chalumnae*. Deepsea crustaceans and mollusks have also evolved anatomical and physiological traits similar to those of fishes, including the emission of luminous ink (e.g., platytroctids, ceratioids, squids) (Marshall 1980; Hochachka & Somero 1984).

The open sea

The epipelagic region is technically the upper 200 m of the ocean off the continental shelves (see Fig. 18.1), but the terms **epipelagic** and **pelagic** are often used synonymously to describe fishes that swim in the upper 100–200 m of coastal and open sea areas (pelagic fishes can be further divided into 12 subgroups based on constancy of occurrence, relative depth, ontogenetic shifts, diel migrations, and use of structure; see Allen & Cross 2006). Common pelagic groups include many species of elasmobranchs (mako, Whitetip, Silky, and Whale sharks), clupeoids (herrings, sardines, sprats, shads, pilchards, menhadens, anchovies), atherinomorphs (flying fishes, halfbeaks, needlefishes, sauries, silversides), opahs, oarfishes, Bluefish, carangids (scads, jacks, pilotfishes), dolphinfishes, remoras, pomfrets, barracudas, scombroids (cutlassfishes, mackerels, Spanish mackerels, tunas, swordfishes, billfishes), butterfishes, and tetraodontiforms (triggerfishes, molas). Diversity overall is estimated at around 325 species (Fig. 18.6).

The pelagic realm is unquestionably the most important and productive region of the sea as far as human consumption is concerned. Pelagic fishes constitute nearly half of the 70–80 million tons of fish captured annually worldwide. Coastal pelagics, particularly clupeoids, make up about one-third of the total, and offshore pelagics such as tunas and billfishes make up an additional 15% (Blaxter & Hunter 1982; Groombridge 1992; FAO 2004).

Characteristic of the pelagic region are high solar insolation, variable production that can be very high in regions of **upwelling** or convergence of major currents, large volume, and a lack of physical structure. The abundance and diversity of fishes in the open sea is made possible by the periodic high productivity that occurs as nutrient-rich cold water upwells to the surface, promoting the bloom of algal plankton species and creating a **trophic cascade**, at least until the nutrients are used up. The greatest concentrations of fishes in the sea, and the largest fisheries, occur in such areas of upwelling. Upwelling areas may account for 70% of the world fisheries catch (Cushing 1975). The anchovy fisheries of South America and Africa, and the sardine fisheries of North America and Japan have been direct results of pelagic fishes accumulating in areas of upwelling. Several of these fisheries have collapsed through a combination of overexploitation and shifts in oceanographic conditions that reduced the magnitude of the upwelling (see Chapter 26, Commercial exploitation). The boom and bust cycles of temperate pelagics result from a patchy distribution of food in both time and space interacting with life history patterns of high-latitude pelagic species, which puts a premium on an ability to travel long distances and locate blooms.

Adaptations to the open sea

Many common threads run through the biology of pelagic fishes, suggesting convergent adaptation to pronounced and predictable selection pressures. In general, pelagic fishes are countershaded and silvery, round or slightly compressed, streamlined with forked or lunate tails, schooling, have efficient respiration and food conversion capabilities and a high percentage of red muscle and lipids, are migratory, and account for all fish examples of **endothermy**. Differences in most of these characters correspond to how pelagic a species is; extreme examples are found amongst

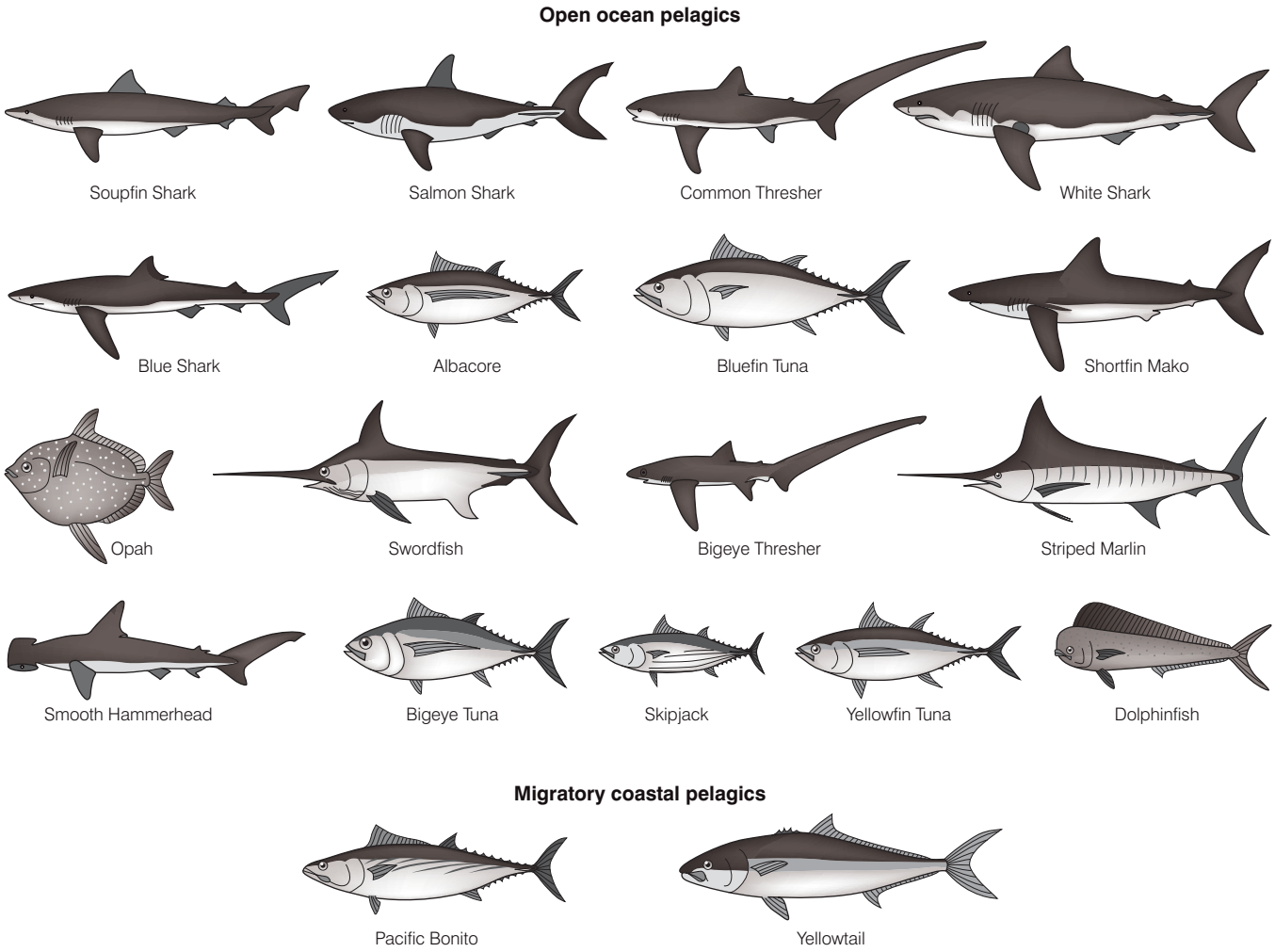


Figure 18.6
Open ocean and migratory coastal pelagic species of the California coast. Many of the open ocean species occur worldwide in temperate and especially tropical oceans. After Allen and Pondella (2006).

the open water, migratory tunas, which have the fastest digestion rates, the highest metabolic rates, and the most extreme specializations for sustained levels of rapid locomotion of any fishes (Magnuson 1978) and are among the most advanced of the teleost fishes.

Several superlatives apply to pelagic fishes and reflect adaptations to life in open water and an emphasis on continual swimming, often associated with long-distance migrations. Large sharks, salmons, tunas, and billfishes move thousands of kilometers annually (see Chapter 23, Annual and supra-annual patterns: migrations), but even smaller coastal pelagics can make annual migrations of 150 km (sprats) and even 2000 km (herring) (Cushing 1975). To sustain continual swimming, pelagics have the highest proportion of red muscle among ecological groups of fishes. Within the mackerels and tunas, the amount of red muscle increases in the more advanced groups, which are also increasingly pelagic and inhabit colder water during their seasonal migrations. In more primitive mackerels, the red muscle is limited to a peripheral, lateral band of the body, whereas in advanced tunas the red muscle is more extensive, occurs deeper in the body musculature, and is kept warm by the countercurrent heat exchangers that are also more developed in advanced scombrids (Sharp & Pirages 1978; see Chapter 7, Heterothermic fishes). Countercurrent exchangers have evolved convergently in tunas and mackerel sharks – both pelagic fishes that range into cold temperate and deep waters. This convergence suggests that endothermy and heat conservation arose independently in these groups and allowed otherwise tropical fishes to expand their ranges into colder regions (Block et al. 1993).

Body shapes and composition in pelagics reflect the demands of continual swimming. Unlike benthic fishes with depressed bodies and littoral zone fishes with deep, circular, compressed bodies, pelagic fishes tend to have **fusiform** shapes that minimize drag. This is accomplished with a

rounder cross-section and by placing the maximum circumference of the body one-third of the way back from the head, an ideal **streamlined** shape also evolved convergently by pelagic sharks, whales, dolphins, and extinct ichthyosaurs (see Chapter 8, Locomotion: movement and shape). Streamlining is enhanced by having relatively small fins or having depressions or grooves on the body surface into which the fins can fit during swimming (e.g., tunas, billfishes). In high-speed fishes such as sauries, mackerels, and tunas, a series of small finlets occur both dorsally and ventrally anterior to the tail. These finlets may prevent vortices from developing in water moving from the median fins and body surfaces towards the tail, which would allow the tail to push against less turbulence. The extremely small second dorsal and anal fins of mackerel sharks, swordfishes, and billfishes could function analogously.

Tunas add a corselet of large scales around the anterior region of maximum girth that may reduce drag and thus create more favorable water flow conditions posteriorly, where actual propulsion occurs. In the region of the caudal peduncle and tail, sharks, jacks, tunas, Swordfish, and billfishes have a single or multiple **keels** that extend laterally. In the tunas, a single peduncular keel is supplemented by a pair of smaller caudal keels that angle towards each other posteriorly (Fig. 18.7). Peduncular keels reduce drag as the narrow peduncle is swept through the water, whereas caudal keels may act as a nozzle that accelerates water moving across the tail, adding to its propulsive force (Collette 1978). Peduncular keels have evolved convergently in cetaceans, but the keels are oriented vertically, as would be expected from their mode of swimming.

Many pelagic fishes swim continuously. In the Bluefish, jacks, tunas, Swordfish, and billfishes, this constant activity is linked to a respiratory mode known as **ram gill ventilation** (see Chapter 5, Water as a respiratory environment). Instead of pumping water via a muscular buccal pump, pelagic fishes swim with their mouths open while water flows across the gill surfaces. Ram gill ventilation requires that a fish swim continually at speeds of at least 65 cm/s, which is easily attained by any but the smallest tunas at their cruising speed of 1 body length/s. The more common buccal pump mechanism accounts for 15% of the total

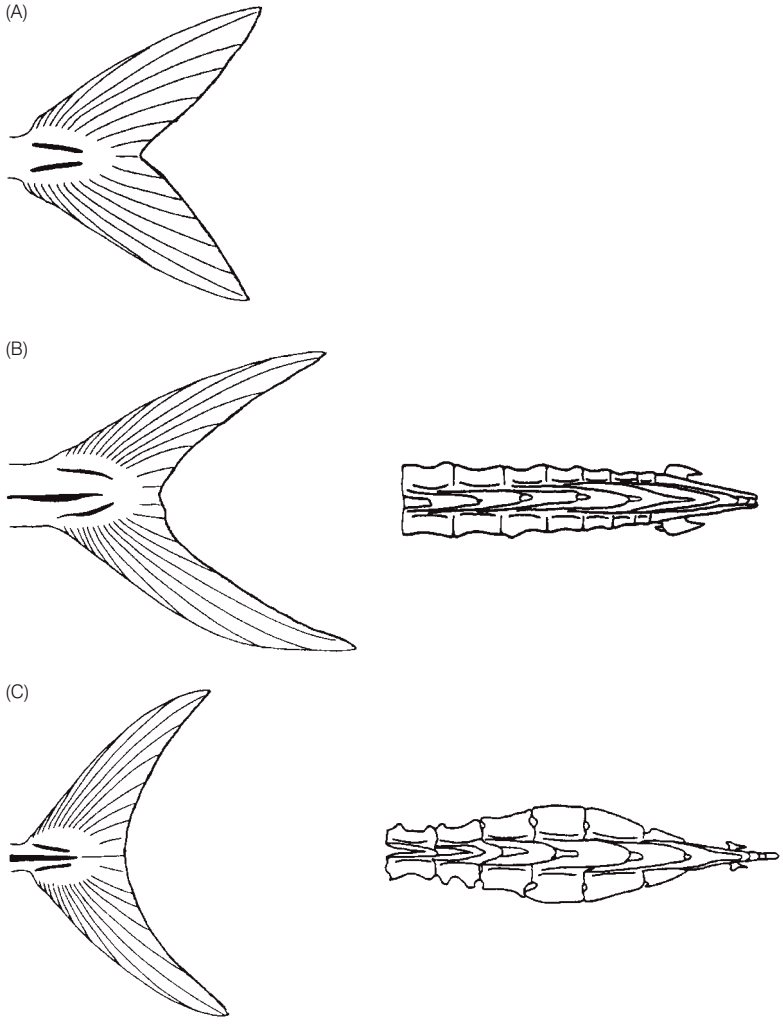


Figure 18.7

Keels and tails in scombrid fishes. The evolution of mackerels and tunas has involved increasing degrees of pelagic activity. The more primitive mackerels and Spanish mackerels live inshore and swim more slowly and less continuously. More advanced high seas tunas swim continuously and faster and are more migratory. These ecological differences are reflected in tail shape and accessories, with more efficient, high aspect ratio tails and more elaborate keels characterizing the more pelagic tunas. (A) Mackerels have forked tails with one pair of fleshy caudal keels. (B) Spanish mackerels have a semilunate tail, caudal keels, and a median peduncular keel, but the peduncular keel is external only, lacking internal bony supports (right: dorsal view of peduncle skeleton). (C) Tunas have lunate tails and multiple keels, with lateral extensions of the peduncular vertebrae supporting the keels (shown on the right). Lunate tails and peduncular keels have also evolved in mackerel sharks, jacks, and billfishes. From Collette and Chao (1975) and Collette (1978), used with permission.

energy expended by a fish, suggesting that ram ventilation conserves energy. A trade-off arises because tunas and billfishes have minimal branchiostegal development and have lost the ability to pump water across their gills. They must therefore move continually to breathe. However, these fishes are negatively buoyant and must move to keep from sinking anyway (Roberts 1978).

The high levels of activity of pelagics are fueled by an efficient circulatory system. Pelagics have an enhanced capacity for supplying oxygen to their muscles. For example, menhadens, bluefish, and tunas have two to three times the hemoglobin concentration of typical inshore, sedentary forms; hemoglobin concentration in tunas is more like that of a homeothermic mammal than like a fish. Tunas have large hearts that account for 2% of body mass and have concomitantly large blood volumes. The uptake of oxygen and release of carbon dioxide at the gills in herrings and mackerels is facilitated by exceedingly thin lamellar walls (5–7 μm thick) and numerous lamellae (> 30/mm); comparable values for less active, inshore species are 10–25 μm and 15–25 lamellae/mm. The surface area of the gill lamellae relative to body weight is very high in mackerel sharks, menhadens, Bluefish, dolphinfishes, and tunas. The efficiency of the lamellae is enhanced by the fusion of adjacent lamellae and elaboration of the leading and trailing edges of the gill filaments. These modifications have occurred convergently in tunas, Swordfish, and billfishes but not in the less pelagic mackerels. Tunas remove more oxygen from the water as it passes over their gills than any other fish. This highly efficient oxygen uptake system is necessary to fuel their extremely high metabolic rates (Steen & Berg 1966; Collette 1978; Blaxter & Hunter 1982).

Foraging

An open water existence limits the foraging options available to pelagic fishes. As a result, the fishes feed on phytoplankton, zooplankton, or each other. Many clupeoids utilize phytoplankton directly by swimming through plankton concentrations with an open mouth, thereby filtering the particles out of the water in a **pharyngeal basket** that has densely packed gill rakers (100–300/cm) and includes an **epibranchial organ** that releases digestive enzymes while the food is still in the oral region. The digestive tract is long and has numerous pyloric caeca. Food passes very rapidly through this system, often taking less than an hour, but these fish can utilize a broad array of food types and are very efficient at converting food into protein.

The foraging and migratory patterns of such pelagics as tunas and billfishes become clearer when the nature of food availability in open tropical seas is considered. Estimates of zooplankton resources in the central Pacific indicate average densities on the order of 25 parts per *billion*. Large pelagic predators are feeding at even higher trophic levels, so their food is scarcer by one or two orders of magnitude. Since no animal is going to survive on food distributed evenly at such low densities, the success and rapid growth rates of many tunas attest to the extreme patchiness of food on the high seas. A nomadic life style, driven by high metabolism and rapid swimming, makes sense when vast expanses must be covered in search of such patchily distributed resources (Kitchell et al. 1978).

Life history patterns in pelagic fishes

Pelagics are by definition open ocean fishes throughout their lives. Two general patterns characterize the overall life histories of pelagic fishes, brought on by the relationship of parental versus larval food requirements, life span, spawning frequency, oceanic currents, and fish mobility. These patterns are referred to as cyclonic or anticyclonic.

Cyclonic patterns characterize higher latitude species such as Atlantic Herring, in which the adults and larvae live in different parts of the ocean. Adults have a seasonal feeding area and tend to spawn once per year. Before they spawn, they migrate upcurrent to a region where food for larvae and juveniles will be particularly abundant. Larvae and, later, juveniles drift with the currents to the adult feeding region. These fish invest considerable energy into each spawning episode, both in terms of the costs of the migration and also in egg production. Because of the spatial separation of adult and larval habitats, adults may not have reliable cues for predicting conditions at the spawning grounds, which leads to highly variable spawning success and large fluctuations in year class strength (see Chapter 24, Population dynamics and regulation).

Anticyclonic patterns are more characteristic of low-latitude species such as tropical tunas and scads. The comparative aseasonality of tropical waters leads to less temporal fluctuation but extreme spatial variation in productivity. Adults move in a roughly **annual loop** through a major ocean basin, during which time they spawn repeatedly (with the exception of Bluefin Tuna) rather than only in particular locales. Larvae and juveniles develop and feed along with adults, carried by the same current system in their relatively nomadic existence. The energy put into reproduction is spread out amongst several spawning episodes. Adults can use local environmental cues to determine the appropriateness of conditions for larvae, which is critical given the low productivity and patchiness of tropical open oceans. Hence anticyclonic species often show weaker fluctuations in year class strength. Within families, tropical species mature more quickly and live shorter lives.

Interestingly, tunas evolved in the tropics but some species such as the Giant Bluefin spend a large part of the year feeding in productive temperate locales (see Block & Stevens 2001). Bluefin show the phylogenetic constraint of their tropical history by returning to the tropical waters of the Gulf of Mexico or Mediterranean Sea to spawn, forcing

them into what is more of a cyclonic than an anticyclonic pattern (Rivas 1978). The same historical factors constrain anguillid eels such as the American, European, and Japanese species, which also return from temperate feeding locales to tropical breeding locales, but several years pass between the two life history stages (see Chapter 23, Representative life histories of migratory fishes).

The high but periodic productivity of small planktonic animals in the open sea and the presence of major ocean currents have been contributing factors in the evolution of dispersive, planktonic larvae in most marine fishes, regardless of whether the adults are planktonic, pelagic, demersal, deep sea, or inshore (see Chapter 9).

Flotsam

A special open ocean fauna occurs around what little structure is found in the open sea. Floating bits of seaweed (usually sargassum), jellyfishes, siphonophores, and driftwood almost always have fishes associated with them. Many **flotsam-associated** fishes such as filefishes and jacks are the juveniles of inshore or pelagic species; others such as sargassumfishes and driftfishes are found nowhere else, attesting to the reliability of occurrence of such objects. Flotsam also serves as an attractor for large predators, such as sharks, dolphinfishes, tunas, and billfishes (Gooding & Magnuson 1967); a single log will commonly have more than 400 tuna of 5 kg each associated with it, often involving several species (Sharp 1978). It has been suggested that concentrations of flotsam are indicators of regions of high productivity in the open sea because the flotsam accumulates at the top of vertical circulation patterns (Langmuir cells) that also concentrate nutrients and zooplankton (Maser & Sedell 1994). The mechanisms by which pelagics locate floating objects and their importance to fishes that do not feed around them remain a matter of conjecture (see Fig. 20.6).

Evolution and convergence

The greatest development of a pelagic fish fauna is in the ocean. However, most major lakes have an open water fauna that consists partly of members typically associated with open waters as well as species whose ancestors were obviously inhabitants of nearshore regions. These **limnetic** fishes include osteoglossomorphs (Goldeye, Mooneye), clupeids (shads), characins, cyprinids (Golden Shiner, Rudd), salmonids (whitefishes, trouts, chars), smelts, silversides, moronid temperate basses, and cichlids. Many of these fishes live at the air–water interface and show specializations that are apparently influenced by this habitat, including upturned mouths, ventrally positioned lateral lines, and convergent fin placement and body proportions. These surface-dwelling traits occur in both marine and freshwater families, including characins, minnows, silversides, marine and freshwater flyingfishes (exocoetids and gasteropelicids), halfbeaks, and killifishes (Marshall 1971). Regardless of ancestry, the same anatomical and behavioral themes that are seen in the ocean recur in freshwater limnetic species, including silvery color, compressed bodies, forked tails, schooling, high lipid content, and planktivorous feeding adaptations. Analogously, *Pleuragramma antarcticum*, a pelagic nototheniid in Antarctic waters, shows many traits characteristic of epipelagic fishes worldwide. Although derived from stocky, dark-colored, benthic ancestors, *Pleuragramma* has deciduous scales, a silvery body, forked tail, high lipid contents for buoyancy, and is compressed in cross-section. The pelagic larvae of many benthic Antarctic fishes are also silvery, compressed, and have forked tails (Eastman 1993; see below, Antarctic fishes). These examples of convergence suggest that fairly uniform and continuous selection pressures characterize the open water habitat.

With the exception of the clupeoids, most successful taxa of adult marine pelagic fishes are acanthopterygians. Missing among otherwise successful marine groups are elopiforms and paracanthopterygians, although both groups have done well in deepsea mesopelagic and bathypelagic regions. These two groups may be phylogenetically constrained from inhabiting shallow open water regions, not the least because of their tendency to be nocturnal in habit. Other strongly nocturnal taxa are also missing from pelagic and limnetic habitats, including the otherwise successful catfishes, seabasses, croakers, grunts, and snappers, to name a few. Which is not to say that pelagic waters are devoid of life at night. The diel vertical migrations of many mesopelagic fishes bring them near the surface after sunset, where they can forage comfortably in the dark.

Polar regions

The far north (**Arctic**) and south (**Antarctic**) polar regions are roughly the areas above 60° latitude. They have much in common, primarily related to cold water temperatures and short growing seasons, but they differ geologically and environmentally and support very different biotas, including fishes. The Arctic is a frozen oceanic region surrounded almost entirely by land, whereas the Antarctic is a frozen continent surrounded by ocean (Fig. 18.8). Freshwater fishes are lacking from the Antarctic because most water bodies have permanent ice cover and many freeze to the bottom during the winter. High Arctic lakes and rivers have a limited fish fauna; 55 species occur in the Canadian Arctic, but most of these are primarily temperate species at the northern edge of their range (Scott & Crossman 1973). Freshwater fishes at high latitudes show interesting behavioral adjustments to the strong effects that seasonality has on light levels, day length, and growing season (Box 18.1). Polar oceans are in a liquid state below the first few meters

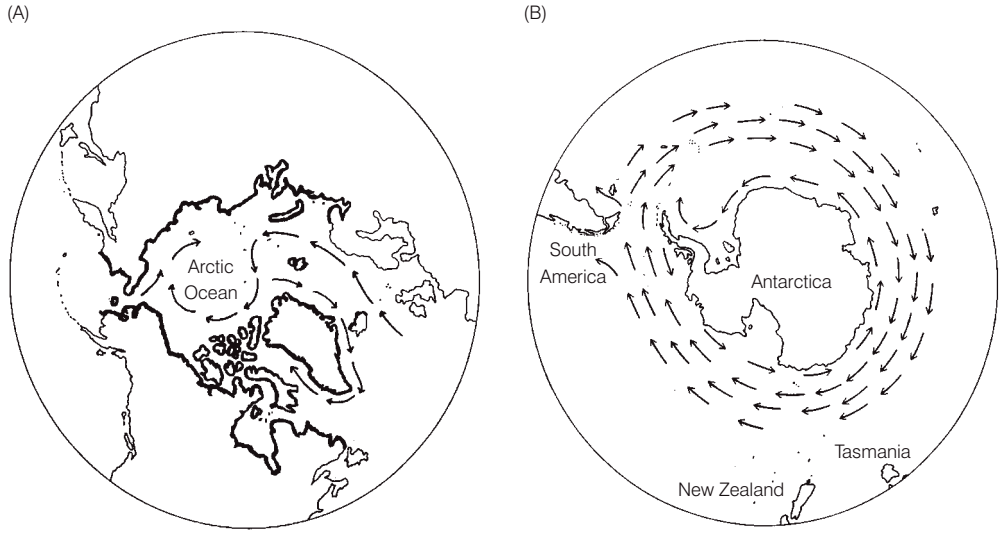
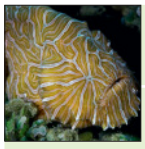


Figure 18.8
North and south polar regions. General oceanic circulation patterns are shown by arrows. (A) The Arctic Ocean centers on the North Pole; the southern limits of the region are indicated by the dark continental borders. (B) The Southern Ocean surrounds Antarctica. Some of the islands on the periphery of the south polar region are indicated.



Box 18.1

BOX 18.1

The effects of high latitude on activity cycles and predator–prey interactions

As discussed in Chapter 23 (Diel patterns), most fishes have particular periods of activity, feeding either during daylight or darkness, with a small number primarily active during crepuscular periods of dawn and dusk. These cycles of activity have a strong endogenous basis and are maintained for some time under laboratory conditions of constant light or darkness. However, in nature, the activity cycles are cued by the rising and setting of the sun.

The situation at high latitudes presents a very different set of environmental influences and selective pressures. Above the Arctic Circle, light levels never reach "nighttime" values during mid-summer, and growing seasons are short and intense. Winter brings a time of continual relative darkness and low food availability. Summer and winter therefore present extreme and opposite light conditions. Do fishes maintain strict diurnality or nocturnality under such variable and extreme conditions, or do they adjust their activity patterns to the changing seasons?

Laboratory studies with European species whose natural ranges extend beyond the Arctic Circle have produced some striking and seemingly adaptive departures from the standard picture developed at lower latitudes. The Burbot, *Lota lota*, belongs to a family of strongly nocturnal fishes, the cods (Gadidae). At intermediate latitudes below the Arctic Circle, burbot are nocturnal throughout the year. However, at higher latitudes, a peculiar pattern occurs. During the summer the fish are continually active, whereas during the winter they shift to diurnal behavior. During spring and fall they are primarily nocturnal. Similar activity cycles have been observed in other nocturnal or crepuscular species, including sculpins and Brown Trout, and can be induced experimentally in Brown Bullheads.

Interpreting these patterns is not immediately easy. The best explanation, however, is that the change to arrhythmic, continual behavior in summer is a means of taking advantage of high, continuous, and aperiodic levels of algal and aquatic insect production during the short growing season of summer. Limiting activity to the short nighttime period each day during summer would severely restrict an animal's intake. Nocturnality during spring and fall may represent a return to the normal, evolved response of the species as day length and twilight length closely approximate the more usual and widespread conditions at lower latitudes. The switch to diurnality during winter in an animal well adapted to function in the dark remains puzzling. Regardless, changes in the length of, and light intensity during, twilight provide the apparent cues that lead to the phase shifts observed in these fishes (Muller 1978a, 1978b).

The influence of **twilight length** at high latitudes is also shown in the predator–prey relations of marine fishes. Dawn and dusk at low latitudes are the times when fish switch between feeding and resting and are often times of maximal predator activity. If twilight is a dangerous time for prey fishes at low latitudes where twilight lasts for a relatively

short time, we might expect the prolonged twilight that occurs at higher latitudes to be even more dangerous.

Conducting extensive underwater observations at high latitudes can be uncomfortable and few such studies have been attempted. In the one instance where the question of twilight interactions was addressed, observers found that extended twilight meant extended periods of predation. Hobson (1986) watched sculpins, greenlings, and flatfishes preying on Pacific Sand Lances, *Ammodytes hexapterus*, in Alaska. Sand lances school and feed on zooplankton during the day and bury in the sand at night. Schools of sand lances are relatively immune to these benthic predators during daylight, and the predators do not occur at night in the limited resting areas that the sand lances use. However, during twilight, the predators aggregate in the resting area under the schools as they break up. The predators are particularly effective at capturing Sand Lances that have just entered the sand or that re-emerge shortly after burying because of apparent dissatisfaction with their initial choice of resting site. The twilight transition from schooling to resting appears to be the most dangerous time for the Sand Lances.

Twilight conditions at the date and latitude of observation (May, 57°N) were very long, lasting about 2 h. This is about twice as long as at tropical latitudes where similar observations have been made with different predators and prey. The period of intense predation in Alaska is also about twice as long as that observed at tropical locales. The longer days of spring and summer at high latitudes mean that diurnal fishes experience a much longer foraging period, but this increase is bought at the high price of increased predation during the lengthened twilight periods.

and have more fishes, but the superabundance of ice at the surface, plus scouring by ice or ice anchored to shallow bottoms limit the distribution and behavior of polar fishes, which have developed remarkable adaptations to avoid freezing to death.

Antarctic fishes

Antarctica is surrounded by at least 900 km of the open, deep Southern Ocean that flows around and away from the Antarctic continent. Strong **circumpolar currents** and distinct temperature differences occur between the polar and subpolar regions, delimited by a region known as the **Antarctic Convergence** at 50–60°S. This region creates a distance, depth, and thermal barrier to interchange between the cold-adapted species of the Antarctic region and warm-adapted species to the north. Antarctic fishes have also had sufficient time to adapt and speciate; the Antarctic region has been at its present locale with its present climate for about 20–25 million years, having separated from Australia during the Early Cenozoic (Hubold 1991; Eastman 1993). Spatial and temporal seclusion and climatic extremes have resulted in a diverse fish fauna dominated by endemic notothenioid thornfishes, cod icefishes, channichthyid crocodile icefishes, plunderfishes, and dragonfishes, as well as several non-notothenioid groups (Farrell & Steffensen 2005; Fukuchi et al. 2006; see Chapter 16, Marine zoogeographic regions).

Notothenioids as a group are benthic fishes and fully half of all species still live on the bottom in less than 1000 m of water (Fig. 18.9). As is general among benthic fishes, they lack gas bladders, are dark in coloration, and are

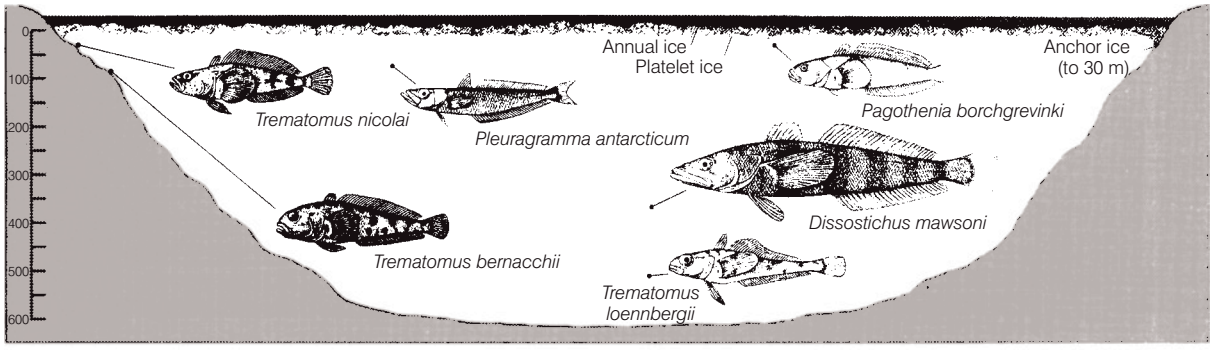


Figure 18.9

Body form and habitat types of common Antarctic nototheniid fishes. The dots show the preferred depths and habitats. From Eastman (1993), after Eastman and DeVries (1986), used with permission of Scientific American, Inc., all rights reserved.

round or depressed in cross-section with a square or rounded tail. Benthic forms often seek cover inside sponges, either as a refuge from predatory mammals or as a spawning substrate. Eggs placed inside hard sponges such as hexactinellid glass sponges are probably protected from most predators (Dayton et al. 1974; Konecki & Targett 1989). Larvae are pelagic and show adaptations specific to shallow, open water existence, including silvery coloration, relatively compressed bodies, and forked tails (see above, The open sea). Notothenioids have also radiated into most non-benthic niches and consequently show substantial variation in body form and behavioral tactics, starting with a common body plan.

A few species, including the abundant Cod Icefish, *Pleuragramma antarcticum*, are pelagic zooplanktivores. So-called **cryopelagic fishes** live in open water just below the ice. The food chain for these fishes starts with ice algae, which is eaten by amphipods and euphausiids, which are in turn eaten by the fishes. Cryopelagic fishes have a uniform light coloration that may help them blend in with the icy background against which they would be viewed. They also possess better chemical defenses against freezing and have greater buoyancy than benthic relatives.

Notothenioids are interesting reproductively because they produce a small number of relatively large, 2–5 mm eggs during a short, 1–2-month spawning season. The unhatched larvae have developmental periods of 2–6 months, followed by a long, slow-growing pelagic stage that lasts a few months to 1 year. Many benthic species exhibit parental and biparental guarding (Daniels 1979; Kellerman & North 1994).

Notothenioids are opportunistic feeders, taking a wide range of prey types, with many pelagic and mesopelagic juveniles and adults feeding on the ubiquitous krill, *Euphausia superba*, that is also the major prey of whales, penguins, and other seabirds. Although the annual temperature variation in Antarctica is seldom more than 4°C (–2° to +2°C), and in some locales as little as 0.1°C, fishes show marked variation in summer versus winter feeding rates. Rates are still relatively high during winter (e.g., 65% of summertime intake in *Harpagifer antarcticus*; Targett et al. 1987), unlike temperate locales where many fishes cease feeding in **winter**.

Mesopelagic fishes are particularly abundant throughout the water column of the Southern Ocean. Lanternfishes are the most diverse group of mesopelagic fishes at lower latitudes, but are epipelagic in the Antarctic. The lanternfish *Electrona antarctica* is the most common fish above 200 m. It feeds heavily during the day, in contrast with the typical mesopelagic pattern of nocturnal foraging that characterizes lanternfishes at lower latitudes. "Mesopelagic" species are also an important component of the community living near the ice edges or "oceanic marginal ice zone". Large numbers of myctophid lanternfishes are eaten in the open sea and at the edge of the pack ice by seabirds, whales, and seals. A commercial midwater trawl fishery even exists for mesopelagic species, with annual catches of the lanternfish *Electrona carlsbergi* exceeding 78,000 tons (>70 × 10^6 kg) from the South Georgia Island region. As with their more northerly, low-latitude relatives, deep-living mesopelagic fishes in the Antarctic show lower enzyme activity and slower metabolic rates than shallow water forms, which is interpreted as an adaptation to low food availability at depth (Kellerman & North 1994; see above, The deep sea).

Harpagiferid plunderfishes, which are advanced perciform fishes, are remarkably similar in morphology and behavior to the relatively primitive scorpaeniform sculpins of northern temperate waters. Similarities may represent adaptations to a predominantly benthic existence, including a relatively depressed, elongate, tapering body; large, spiny head with large eyes and a large, terminal mouth; long dorsal and anal fins; large pectoral fins; rounded caudal fin; and a dorsally located lateral line. Both groups show ecological and behavioral similarities as well, feeding by a sit-and-wait mode on relatively large, mobile benthic invertebrates. In essence, plunderfishes and sculpins have converged to fill similar niches in their respective communities (Wyanski & Targett 1981).

Adaptations and constraints of Antarctic fishes

Notothenioids are best known for two adaptations related to existence in the cold, often energy-limited waters of the area, where water temperatures average –1.87°C and total darkness prevails for 4 months each year. First, their blood contains remarkably effective **antifreeze compounds** that depress the freezing point of their body fluids and make it possible for them to live in water that is colder than the freezing point of most fish blood including, remarkably, their own. Second, some have evolved **neutral buoyancy**, which has permitted these species to move off the crowded bottom where most notothenioids live and into the water column.

No known species of fish can actually tolerate having its tissue freeze. The major threat to fishes in the Antarctic is ice, which floats at the surface in the form of bergs, sheets, and platelet ice, but also attaches to the bottom in water less than 30 m deep in a form called anchor ice. The greatest danger comes from ice crystals penetrating or propagating across the body and seeding the formation of ice inside the fish, which would cause cell rupture. Many Antarctic fishes live in water that is colder than their blood's freezing point. Fishes from lower latitudes typically freeze when placed in water colder than –0.8°C, whereas Antarctic fishes can live in water as cold as –2.19°C. They accomplish this because their blood contains the salts normally found in fish blood and also as many as eight different glycopeptide antifreeze compounds. The glycopeptides apparently function by keeping the ice from propagating across the

fish's skin. A notothenioid can be cooled as low as –6°C without freezing, as long as free ice is not in the water.

Several other adaptations accompany the production of antifreeze compounds. Notothenioids are relatively unusual among teleosts in that their kidneys lack glomeruli, which are the structures that remove small molecules from body fluids and transfer them to the urine for excretion. Glomeruli would remove the antifreeze glycopeptides, which would be energetically expensive to continually replace (see Chapter 7, Coping with temperature extremes). A fairly strong correlation exists between antifreeze effectiveness and the frequency with which a species encounters free ice. For example, the shallow water bathydraconid dragonfishes frequently come in contact with ice and have the highest levels of antifreeze compounds. Within the cod icefish genus *Trematomus*, shallow water species that live in the coldest water and rest in ice holes or on anchor ice have freezing points of –1.98 to –2.07°C, whereas deeper living species that seldom encounter ice crystals freeze at –1.83 to –1.92°C. Even within species, shallow water populations have significantly more freezing resistance than deeper water populations (DeVries 1970). The primitive bovichtid thornfishes of New Zealand live in temperate waters and do not produce antifreeze. Bovichtids possess glomeruli, indicating that the aglomerular condition of Antarctic species evolved along with other adaptations to the colder Antarctic environment (Eastman 1993).

Neutral buoyancy has developed in at least two water column dwelling members of the family Nototheniidae, the Cod Icefish, *Pleuragramma antarcticum*, and its giant predator, the Antarctic Toothfish, *Dissostichus mawsoni*. Whereas most Antarctic fishes are 15–30 cm long, toothfish reach lengths of 1.6 m and weights of over 70 kg. Neutral buoyancy allows these fishes to occupy the comparatively underutilized water column zone, thus taking them away from threatening anchor ice crystals and into a region of seasonally abundant food sources such as fish larvae and krill. Both species have evolved from benthic ancestors and have retained what can only be viewed as a phylogenetic constraint on living in open water: they are similar to benthic notothenioids in that they lack a gas bladder. As fish muscle and bone are relatively dense, a gas bladderless fish would constantly have to fight gravity to stay in the water column. Neutral buoyancy in these two nototheniids is achieved via several mechanisms. Toothfish have cartilaginous skulls, caudal skeletons, and pectoral girdles, which reduces their mass because cartilage is less dense than bone. The skeleton itself is less mineralized than in benthic relatives, by a factor of six in the toothfish and 12 in *Pleuragramma*. Bone is also reduced in the vertebral column, which is essentially hollow except for the notochord. Additional buoyancy is achieved by lipid deposits dispersed around the body, including a blubber layer under the skin, and fat cells or sacs located between muscle fibers or muscle bundles (Eastman & DeVries 1986; Eastman 1993). Weightlessness via analogous routes of weight reduction and replacement is also seen convergently in bathypelagic fishes, another water column dwelling group where evolution has placed a strong premium on energy-saving tactics.

A unique trait of channichthyid icefishes may represent an evolutionary adjustment to polar conditions. These fishes are sometimes referred to as "white blooded" or "bloodless" because their blood contains no hemoglobin and their muscles contain no myoglobin, giving them a very pale appearance. The highly oxygenated, cold waters of Antarctica may have been responsible for the evolutionary loss of respiratory pigments, perhaps via a "regressive" evolutionary process similar to the one that led to pigmentless, eyeless cave fishes (see below, Caves). Channichthyids possess a number of other characteristics that have evolved in conjunction with a lack of hemoglobin, including relatively low metabolic requirements (reduced protein synthesis, reduced activity, slow growth), increased vascularization of skin and fins to increase gas exchange, and an increase in cardiac size, output, and blood volume (Hemmingsen 1991). Some nototheniids have increased blood volumes and reduced hemoglobin concentrations, perhaps reflecting an intermediate stage in the response to respiratory conditions in the Antarctic that have led to the hemoglobin-free condition of the channichthyid icefishes (Wells et al. 1980).

Arctic fishes

The Arctic has fewer endemic fishes due to the combined effects of less geographic isolation and younger age. The oceanic environment between **subarctic** or **boreal** and Arctic areas is fairly continuous. On the western, Pacific side, the Bering Sea flows into the Arctic Ocean and has done so since the Bering Strait opened up 3.5 million years ago. Similarly, on the eastern, Atlantic side, the Arctic Ocean is directly connected to the Greenland Sea. Hence, Arctic fishes are either species that evolved there since the current climate developed or are cold-tolerant Pacific or Atlantic species that experience gene flow from source areas rather than being endemic to the Arctic itself. The Arctic has undergone repeated warming and cooling until about 3 million years ago when the present cold conditions stabilized, leaving less time for organisms to adapt to current conditions (Briggs 1995). Consequently, fishes in the northern polar region have had less time to speciate.

Adaptations to cold are evident in Arctic fishes, where species have converged with Antarctic fishes in the production of antifreeze compounds (Farrell & Steffensen 2005). Glycoprotein antifreeze occurs in Arctic and Greenland Cod, whereas Warty Sculpin, Canadian Eel-pout, and Alaska Plaice possess peptide antifreezes (Clarke 1983). Arctic Cod are frequently observed resting in contact with ice and taking refuge inside holes in ice, so their potential for encountering seed crystals is very high. In some of these fishes, kidney glomeruli are convergently reduced to help

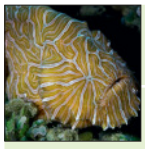
retain antifreeze compounds in the body (Eastman 1993). Several boreal cods, sculpins, eel-pouts, and flatfishes whose ranges extend into Arctic water also have antifreeze compounds in their blood.

Water temperatures show greater annual and latitudinal variation in the Arctic than in the Antarctic, which means that fishes are likely to encounter extreme winter cold but also relatively high summer temperatures. Winter temperatures do commonly drop to –1.8°C as in the Antarctic, but water can reach 7 or 8°C during the summer. The greater seasonal range is reflected in the tolerance of different species to warm temperatures, as well as differences in seasonal production of antifreeze. Few Antarctic fishes can tolerate water temperatures above 7 or 8°C regardless of acclimation temperature, whereas Arctic species have upper lethal temperatures of 10–20°C depending on species and acclimation temperature (DeVries 1977). Several north polar species produce less antifreeze during the summer, particularly among boreal fishes that may encounter temperatures well above freezing. Winter Flounder, *Pleuronectes americanus*, have a blood volume of 3% antifreeze in winter and 0% in summer. Reduced antifreeze production during warmer months probably saves energy and may also increase the blood's capacity to carry oxygen or nutrients.

Deserts and other seasonally arid habitats

Deserts appear inhospitable for fishes. However, algae and many invertebrates capitalize on the periodic availability of water in arid regions. It is not surprising then to find a small number of fishes capable of surviving under conditions of periodic **dewatering** in desert regions around the world, presenting dramatic examples of adaptation and convergent evolution.

Deserts are difficult to define because they differ in altitude, temperature range, amount of rainfall, and seasonality of water availability, among other traits. Many treatments define a desert as an area that receives less than 30 cm of rainfall annually. A more general definition is that a desert is an area where "biological potentialities are severely limited by lack of water" (Goodall 1976), a definition that stresses the common thread of water scarcity as the significant selection factor and can therefore apply to areas with seasonal droughts, such as swamplands that dry up periodically. For fishes, the disappearance of water is only the most extreme stage in a continuum of conditions that occur during dewatering. As water evaporates, temperatures generally rise, dissolved substances such as salts become more concentrated, oxygen tension drops, carbon dioxide increases, and competition and predation intensify. Desert fishes must therefore be tolerant of widely varying and extreme salinity, alkalinity, temperature, and depleted oxygen (Box 18.2). They may also have to be able to outcompete other fishes and avoid predators despite physiological stress. Desert stream fishes also have to withstand periodic flash flooding. Desert-adapted fishes, not counting species that migrate to more permanent habitats when waters recede, often show three general adaptations: (i) an annual life history involving egg deposition in mud during the wet season, an egg resting period (**diapause**) during the dry season, death of the adults, and egg hatching when habitats are reinundated the next year; (ii) **accessory respiratory structures** for using atmospheric oxygen (lungs, gill and mouth chambers, cutaneous respiration); and (iii) in



Box 18.2

BOX 18.2

Acidity, alkalinity, and salinity

The acidity or alkalinity of a water body strongly determines the existence and types of fishes that occur there. Sea water is naturally buffered against abnormal shifts in hydrogen ion content (**pH**) and hence pH is seldom a concern for marine fishes; sea water usually has a pH of about 8.0–8.3. Fresh water, in contrast, is easily affected by substances that alter pH. Changes in acidity in turn affect the activity of metals and other potential toxins in the water. Freshwater fishes normally live in water with a pH range between 6 and 8, a pH of 7 being neutral. **Acidic** conditions (pH $\ll$ 7) often result from the decay of organic matter that is not filtered through soil or further broken down. The black or tea-stained coloration of many swamps, and the black water rivers of the southeastern USA and of major tributaries of the Amazon such as the Rio Negro and of many African rivers, are examples of naturally occurring low pH water (pH 3.8–4.9). Such "soft" waters are also low in dissolved substances and inorganic ions, but high in organic acids such as humic and fovic acids (Lowe-McConnell 1987). Some fishes have evolved under conditions of low

pH and do best in slightly acidic waters (e.g., many tetras), whereas other groups are intolerant of acidic waters. Minnows, which are so widespread throughout North America, are often missing from river systems where the pH falls below 4.5 (Laerm & Freeman 1986), although cyprinids do well in Southeast Asian waters with low pH. **Acid rain**, a lowering of pH that results from industrial pollution, causes reproductive failure in many fishes and has eliminated fishes from the poorly buffered lakes of the Adirondack Mountains in New York and in many lakes throughout Scandinavia (Baker & Schofield 1985; Helfman 2007).

High pH is caused by an abundance of hydroxyl (OH) groups, producing **alkaline** conditions. High alkalinity occurs naturally in waters that run through or over limestone rocks, or where extensive evaporation occurs. Some fish have adapted to alkaline conditions that are lethal to most other animals. A small (< 8 cm) African cichlid, *Oreochromis grahami*, is the only fish that can live in Lake Magadi in Kenya under conditions of extreme alkalinity, salinity, and temperature. Water flows into the lake from hot springs at a pH of 10.5, a salinity of 40 ppt, and a temperature of 45°C. The water has a high load of sodium bicarbonate, sodium chloride, sodium sulphate, and sodium fluoride and has a conductivity of 160,000 μmho/cm (most African lakes have a pH of 7–9 and a conductivity of 100–1000 μmho/cm). The fish occupy pools and graze on algae at temperatures below 41°C. Their upper temperature limit creates a distinctive browse line where inflowing spring water has cooled sufficiently to allow fish activity. Algae in regions above 40°C are safe from fish grazing (Coe 1966; Fryer & Iles 1972).

Salinity determines the distribution of many if not most fish families. Biogeographic categories of freshwater fishes focus on whether taxa can tolerate salinities greater than a few parts per thousand (ppt). In one approach (see Briggs 1995; Berra 2001), freshwater fishes are classified as **primary** (those that cannot cross saltwater boundaries, such as minnows, characins, most catfishes, pike), **secondary** (those that can cross at least short saltwater regions, e.g., cyprinodontoids, cichlids), and **peripheral** (those derived from marine families or that spend part of their lives in the ocean, e.g., salmons, sculpins) (see Table 16.2).

The actual barriers to free movement between regions of high and low salt concentration are physiological in nature. At the simplest, freshwater fishes have a need to conserve salts and eliminate water, whereas saltwater fishes must conserve water and stem the influx of salts (see Chapter 7, Osmoregulation, ion and pH balance, and excretion). Extremes of and rapid changes in ionic concentration can cause **osmotic stress**. Although pure distilled water is stressful, it is also unusual in nature and hence an uncommon limitation. Hypersalinity occurs in many areas, either as a result of heated water flowing through easily soluble rocks, or due to daily or seasonal evaporation and concentration of salts as water courses dry up during low tides or droughts.

Some of the most widely distributed families in fresh water turn out to be those that show a high tolerance to both rapid fluctuations and extreme conditions of salinity. Many cyprinodontoid killifishes and pupfishes can tolerate ranges of salinity from 0% to 100% of sea water (100% is about 35 ppt) and appear to tolerate rapid shifts in salinity from high to low concentration, such as those brought on by rainstorms. Some, such as the Mediterranean *Aphanius* and several North American *Cyprinodon*, live in water two to three times saltier than sea water. These capabilities have preadapted them for life in isolated habitats such as desert springs and pools (Roberts 1975b). Similar abilities characterize cichlids and gobies, two of the world's largest families of fishes. *Tilapia amphimelas*, a cichlid, inhabits Lake Manyara in Africa, where the sodium content is twice that of sea water and is increased ionically by abundant potassium salts (Fryer & Iles 1972). Certain large inland water bodies are too saline to support even the most osmotically tolerant species, including the Dead Sea of the Middle East and the Great Salt Lake in Utah, where salinities exceed 200 ppt. Water withdrawal due to human activities can cause salinization of a lake and threaten the fishes there, as has occurred in the Aral Sea of the former Soviet Union (see Chapter 26).

perennial species, **estivation**, where adults pass the dry season in some sort of resting state.

Deserts occur on all major continents and many of these deserts contain fishes. Africa has many habitats that dry up seasonally and that contain fishes with desert adaptations. Among the most successful groups in Africa are cyprinodontiform killifishes and rivulines, which are popular aquarium species. Many of these fishes (e.g., *Fundulosoma*, *Notobranchius*, *Aphyosemion* spp.) are **annual**, living for 8 months in mud holes, swamps, and puddles (Fig. 18.10). They mature after only 4–8 weeks, spawning daily and burying eggs as much as 15 cm deep in muddy bottoms, a remarkable feat for fishes that seldom exceed 5 cm long. The adults die and the eggs spend the dry season in a state of arrested development until the next rains come. Some eggs can remain in such a state of diapause for up to 5.5 years. An annual life history effectively maintains a permanent population in a temporary habitat (Wourms 1972; Simpson 1979).

African and Asian clariid or walking catfishes are capable of leaving drying water bodies and moving across up to 200 m of moist grass in search of water. They will also bury

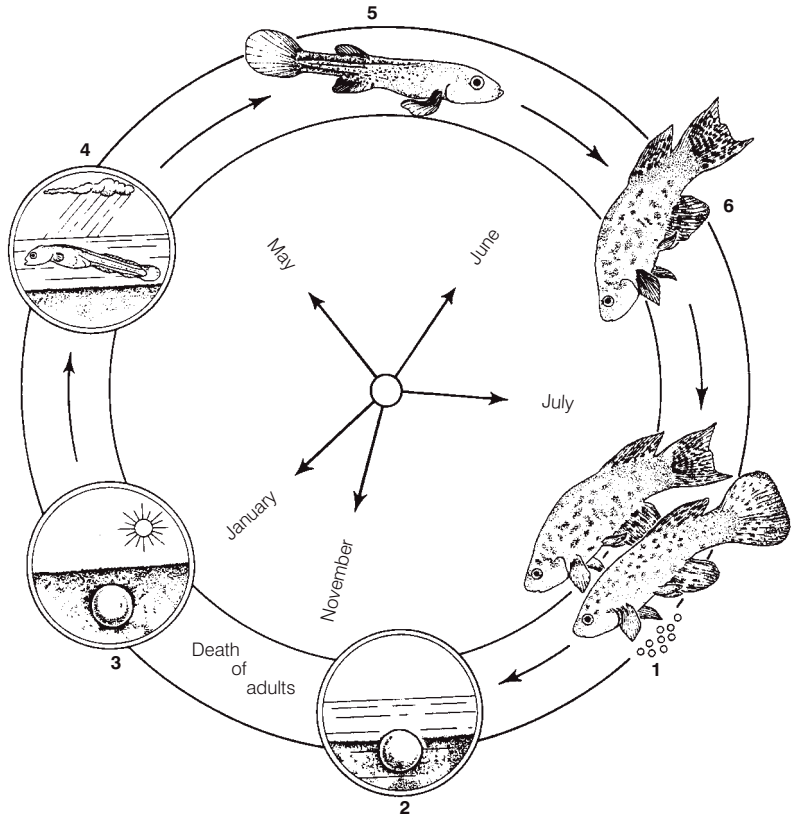


Figure 18.10

Life cycle of annual cyprinodontoids, as shown by the Venezuelan *Austrofundulus myersi*: 1, spawning occurs over a protracted period; 2, shelled eggs are deposited in the mud; 3, as water dries up, adults die but eggs remain viable in an arrested developmental stage; 4, with the return of the rains, eggs hatch; 5, larvae and juveniles grow rapidly; 6, maturation occurs after only a month or two, followed by spawning. From Wourms (1972), used with permission.

themselves as deep as 3 m in sandy sediments as water levels drop. They can survive by employing aerial respiration via treelike **suprabranchial organs** over the second and fourth gill arches, although they cannot survive if the sand dries up (Bruton 1979).

The African lungfishes (Protopteridae) are true estivators. During a drought, they burrow into mud, secrete a cocoon, and enter a torpid condition in dry mud until the next rains, an event for which they can wait 4 years (see Chapter 13, Subclass Dipnoi, Order Ceratodontiformes: the lungfishes). Many other fishes in African swamps are adapted to the deoxygenation that accompanies seasonal dry periods, using a variety of air-breathing mechanisms (see Table 5.1). Mochokid catfishes, killifishes, and *Hepsetus odoe*, the Pike Characin, are surface dwellers, taking advantage of higher oxygen tensions near the air–water interface. Lungfishes and bichirs use lungs, clariid catfishes have gill chamber organs, anabantids have labyrinth organs, snakeheads have pharyngeal diverticula, and featherfin knifefishes and phractolaemids have alveolar gas bladders.

In South America, drought resistance has evolved in parallel to the African examples. Many fishes of the Amazon region have evolved means of using atmospheric oxygen when drought or vegetative decay lower oxygen levels (Kramer et al. 1978). Surface swimmers, such as arawanas and some characids (pacus, *Brycon*), have vascularized lips. Modifications of the alimentary tract to absorb oxygen are common, including the mouth region of Electric Eels and swamp eels, air-filled stomachs in loricariid catfishes, a vascularized hindgut in callichthyid armored catfishes, and a vascularized gas bladder in lungfish, Arapaima, and erythrinid trahiras. As with the walking catfishes, South American species are reported to abandon drying pools and cross small stretches of wet vegetation or mud in an apparent search for new and wetter habitats (e.g., erythrinids such as *Hoplias* and *Hoplerythrinus*, callichthyid catfishes, some rivulines) (Lowe-McConnell 1987).

Conventional desert areas also exist in South America. The Chaco region of northwestern Paraguay receives less than 30 cm of water annually, with a normal 3-month winter drought period that can last as long as a year (Smith 1981b). During the annual drought, aquatic habitats become isolated and dry up. During the rainy season, these habitats are often repopulated by fishes from overflowing portions of the Paraguay River. The ichthyofauna of the Chaco consists of both drought-adapted and nonadapted species. Adaptations to drought include estivation in mud by juvenile and adult lungfish (*Lepidosiren*), accessory respiratory structures for using atmospheric oxygen (lungfishes; catfishes, *Hoplosternum*, *Pterygoplicthys*; characiforms, *Hoplias*), and annual life histories and diapausing eggs among cyprinodontiforms, which are also successful throughout much of tropical South America (e.g., *Cynolebias*, *Rivulus*, *Austrofundulus*). Localized extirpation

occurs annually in species that invade the Chaco region during the wet season but that lack the abilities to overcome drought conditions.

Australia is largely a desert continent. Its freshwater fish fauna is dominated by **marine derivatives**, such as river eels, plotosid catfishes, rainbowfishes, barramundi, temperate basses, grunters, pygmy perches, gobies, and sleepers. Several Australian fishes show distinct adaptations to periodic drought. The endemic, monotypic Salamanderfish *Lepidogalaxias salamandroides* occurs commonly in southwestern Australian habitats that dry up during the annual summer drought. As waters recede, the fish burrows into bottom sediments and surrounds itself with a thick mucus coat (Berra & Allen 1989; Pusey 1990). Two major problems faced by estivating fishes are water loss and a concomitant build-up of toxic nitrogenous wastes such as urea, which normally must be transported away with water-wasting urine. Salamanderfish conserve water by absorbing it from the surrounding soil until soil moisture content approaches zero. They avoid the production of nitrogenous wastes in part by metabolizing lipids rather than proteins; the endpoint of lipid metabolism is carbon dioxide, not nitrogen compounds (Pusey 1989).

Several species in the related family Galaxiidae in Australia and New Zealand occur in similar temporary habitats and may also estivate during dry periods. Some gobies and hardyhead silversides that live in desert springs in central Australia are exceptionally tolerant to high temperatures, high salinities, and low dissolved oxygen. The Desert Goby, *Chlamydogobius eremius*, typifies desert-adapted species in its ability to survive an extreme range of conditions, including ionic concentrations ranging from distilled water to water more saline than sea water, temperatures between 5 and 40°C, and oxygen concentrations below 1 ppm. To avoid lethal conditions in thermal springs or high summer temperatures, it seeks cooler vertical or lateral portions of springs, buries itself in cooler silt, and even emerges from the water to capitalize on evaporative cooling and aerial respiration (Glover 1982).

North American deserts

Additional examples of desert adaptations could be presented from almost any continent (except Antarctica), but some of the best studied desert fishes occur in the southwestern United States. The Basin and Range Province of North America contains four different deserts, the Great Basin, Mojave, Sonoran, and Chihuahuan deserts (Naiman & Soltz 1981). The province, which includes such seemingly inhospitable areas for fishes as Death Valley, Ash Meadows, Salt Creek, and Devil's Hole, constitutes < 10% of the total land area of North America. Although desert conditions have existed periodically in the region for approximately 70 million years, the southwestern deserts as they exist today are relatively young, no more than 12,000 years having passed since the last wetter, "pluvial" period when the area contained abundant, interconnected standing and running water. Despite their relative youth and small size, the southwestern deserts contain 182 native species, 149 of which are endemic to the basin and many of which are endemic to single locales (the area includes both US and Mexican endemics). Endemicity in the fishes of the desert southwest is the highest of any place in North America.

Two major types of desert habitat are occupied by fishes: (i) isolated pools and basins supplied by underground springs that have fairly regular flow; and (ii) intermittent marsh and arroyo habitats along flowing water courses that originate in wetter areas such as mountainous highlands and that flow into arid regions. The native fishes that occur there belong to five principal families and segregate according to fish size, habitat size, and environmental extremes. Small livebearers (Poeciliidae) and even smaller desert pupfishes of the family Cyprinodontidae live in the most extreme or isolated habitats such as intermittent streams and spring basins; these fishes include 20 desert-adapted species in the genus *Cyprinodon*. Small streams contain small minnows (Cyprinidae) that are < 6 cm long; larger streams and small rivers support medium-sized suckers (Catostomidae) and trout (Salmonidae). The largest fishes, such as large suckers and the Colorado Pikeminnow (*Ptychocheilus lucius*, up to 2 m), live in large rivers. Body size is intimately tied to habitat size (Smith 1981b). The smallest pupfish, the Endangered 2 cm **Devil's Hole Pupfish**, *Cyprinodon diabolis*, lives on an 18 m^2 shelf in a spring basin in the smallest habitat of any known vertebrate (Fig. 18.11). In contrast, the Colorado Pikeminnow is the largest minnow in North America and lives in the area's largest habitat, the Colorado River.

The fishes in marshes and small streams experience the harshest conditions and show the strongest adaptations to desert existence. Desert pupfishes show extraordinary tolerances to environmental extremes. They can live in water with as little as 0.13 mg O_2/L (0.13 ppm dissolved oxygen), which is a record for fishes that do not supplement gill respiration with some accessory breathing apparatus. Most fishes show stress at < 5 ppm, depending on water temperature. Although these are freshwater fishes, some desert pupfishes can tolerate salinities over 100 ppt and as high as 140 ppt, three to four times that of sea water. Pupfishes experience water temperatures that vary from freezing in winter to 44°C in summer, the highest recorded for a habitat containing live fishes; the Cottonball Marsh Pupfish tolerates higher temperatures than any other known teleost (Feldmeth 1981). Many of the spring-dwelling pupfishes have lost their lateral lines and pelvic fins, which may be energy-saving responses in isolated habitats that lack predators.

Other taxa show physiological and behavioral adjustments to drought conditions, such as the Longfin Dace,

Figure 18.11

Devil's Hole, Nevada, natural home of the Devil's Hole Pupfish, the first fish listed under the US Endangered Species Act. Visible are water-level monitoring equipment and a platform for people to walk on while doing fish counts. Photo by J. Barkstedt, used with permission.

Agosia chrysogaster, of the Sonoran Desert, adults of which move into moist algae during hot days and emerge during cooler nights to forage in only a few millimeters of water (Minckley & Barber 1971).

Although most emphasis is given to periods of low water in deserts, a major influence on stream- and river-dwelling fishes is the periodic occurrence of flash floods, when waters can change from low-flow, nearly stagnant conditions to raging torrents in a matter of seconds (Naiman 1981). Colorado River endemics (see Fig. 26.3), such as the Humpback Chub (*Gila cypha*), Bonytail Chub (*G. elegans*), and Razorback Sucker (*Xyrauchen texanus*), have anterior humps, flattened heads, keeled napes, cylindrical bodies, small scales, and elongate, narrow caudal peduncles that have been postulated to provide hydrodynamic stability during periods of high or turbulent flow, although the large humps could also be a convergent response to gape-limited predation by another endemic, the Colorado Pikeminnow (e.g., Portz & Tyus 2004).

High-flow adaptations are not restricted to large fishes. The Threatened 5 cm Gila Topminnow, *Poeciliopsis occidentalis*, has been extirpated through much of its range due to predation by introduced Mosquitofish, *Gambusia affinis*. However, Topminnows are able to coexist with Mosquitofish in streams that experience periodic flash floods because the Topminnows show instinctive behavioral adaptations to high discharge, including rapid movement to shoreline areas as waters rise, and proper orientation to strong currents. Mosquitofish, which evolved in southeastern regions that lack flash floods, behave inappropriately and are flushed out of rivers when floods occur (Meffe 1984).

Although the desert pupfishes and other fishes survive and reproduce in the extreme conditions of the desert southwest, these fishes do not exhibit several other traits common to many desert forms, such as estivation, air breathing, or diapausing eggs. Adaptations of the desert pupfishes are most likely extensions of capabilities possessed by ancestral lineages rather than being newly evolved. Cyprinodontids are small fishes that frequently inhabit estuaries where temperature, salinity, and oxygen availability vary widely. Adaptation to such estuarine conditions would constitute **preadaptation** for desert conditions. Given the superlatives accompanying the above descriptions of thermal, salinity, and oxygen tolerance in pupfishes, additional adaptation may have been unnecessary. Working against the evolution of desert-specific adaptations are the comparative youth of the region, as well as the periodic connection of desert water courses and pools with each other and with estuarine and riverine areas that serve as sources of new immigrants. Selection for desert adaptations would be relaxed during wetter periods, and dilution of such adaptations would also occur due to gene flow from source areas.

Given the limited extent, isolation, and small populations characteristic of desert habitats, it is not surprising that southwestern fishes are very sensitive to environmental degradation (Miller 1981; Soltz & Naiman 1981; Contreras-Balderas et al. 2002). A variety of activities have led to declines and extinctions, including pumping of springs and groundwater, pollution by humans and livestock, draining of marshes, damming of streams, introductions of exotic competitors and predators, and hybridization (see Chapter 26). Approximately 15 species and numerous localized populations of southwestern fishes are extinct. Desert species account for nearly two-thirds of the federally listed Endangered and Threatened fishes in North America. The International Union for the Conservation of Nature (IUCN 2004) lists 14 desert cyprinodontiform species as Critically Endangered. Some species have been described after they were exterminated (e.g., the aptly named La Trinidad Pupfish, *C. inmemoriam*, described on the basis of a single specimen collected before its single habitat dried up due to water extraction; Lozano-Vilano & Contreras-Balderas 1993). The fishes of this region have adapted well to the environmental challenges of extreme desert conditions, but nothing in their history allows them to handle the kinds of

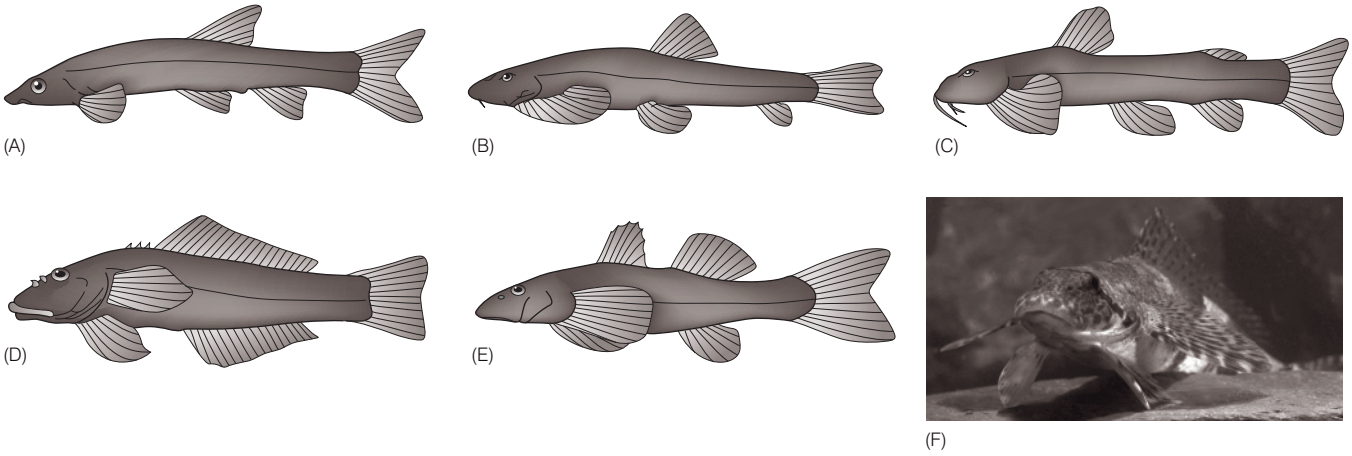


Figure 18.12

Convergence in body form among unrelated fishes that occupy swiftwater habitats in streams and rivers. (A) *Kneria*, an African kneriid (Gonorynchiformes). (B) *Gastromyzon*, an Asian balitorid hillstream loach (Cypriniformes). (C) *Amphilius*, an African amphiliid loach catfish (Siluriformes). (D) *Cheimarrichthys*, a New Zealand cheimarrichthyid Torrentfish (Perciformes, Trachinoidei). (E) *Rhyacichthys*, an Indo-Australian rhyacichthyid loach goby (Perciformes, Gobioidei). (F) Head-on photo of a Torrentfish, showing body profile and fin shape and placement characteristic of swiftwater fishes (*c*. 10 cm). (A–E) after Nelson (2006); (F) from McDowall (2000), used with permission.

insults that often result from careless or callous humans (Pister 1981; Minckley & Deacon 1991; Rinne & Minckley 1991; Contreras-Balderas et al. 2002).

Strong currents and turbulent water

High-energy zones in both marine and fresh waters – wave-swept rocky shores in the ocean and rapids in rivers and streams – appear unsuitable for fishes because of the difficulties of remaining in place, let alone feeding and breeding under such conditions. Invertebrates successfully occupy such locales but, except for the groups that hide behind or under rocks, tend to be rather sessile or essentially glued in place (e.g., chitons, limpets, barnacles, and sea anemones in the ocean; caddis fly larvae, black fly larvae, and water penny beetle larvae in streams). With the exception of parasitic male anglerfishes, fishes have not evolved immobile forms and yet some species are exposed to the force of the waves and currents in the same habitats as these stay-at-home invertebrates.

Fishes have converged on a general body shape, fin shape and distribution, and special devices for living in high-energy zones. Good examples in marine habitats are inhabitants of wave-swept, **intertidal surge regions**. Groups include various scorpaeniform cottid sculpins, perciform blennioids (blenniid combtooth blennies, tripterygiid triplefins, clinid kelp blennies, labrisomid blennies), sicydiine gobies, and especially the aptly named clingfishes (Gobiesocidae). All tend to have bodies that are depressed dorsoventrally and somewhat tapered (= terete) or teardrop-shaped when viewed from above, often with enlarged pectoral fins placed low on the body (e.g., Horn 1999; Boyle & Horn 2006). In the extremes, the pelvic fins are fused to form a suction disk (e.g., in clingfishes and gobies). *Sicyases sanguineus*, a large (30 cm) Chilean gobiesocid, lives in and above the intertidal zone in locales exposed directly to waves (Paine & Palmer 1978; Cancino & Castilla 1988).

High-energy freshwater habitats have produced the most striking convergences, exemplified by fishes that live in **torrent zones** and share a body form clearly appropriate to maintaining position in strong, unidirectional currents (Fig. 18.12). The suite of anatomical traits on which these fishes have converged include:

- A dorsoventrally depressed, small (<15 cm) body, sometimes triangular or square in cross-section with a flattened ventral surface.
- Large, horizontally oriented pectoral fins positioned low on the body; pelvic fins are also sometimes enlarged.
- A suction device, such as the mouth (e.g., suckermouth catfishes, algae eaters), or formed either by joined paired fins (hillstream loaches, gobies, clingfishes) or fins in combination with the ventral body surface (loach catfishes, loach gobies), sometimes with adhesive pads (sisorid catfishes and perhaps kneriids).
- Subterminal or inferior mouths in just about all species.
- A missing swim bladder (psilorhynchids, amblycipitid loach catfishes).
- Modifications to respiratory behavior (rapid inhalations followed by a quiescent period of several

minutes; Berra 2001) or respiratory structures, such as the incurrent opening at the top of the gill cover in gyrinocheilids, an analogous arrangement in astroblepid climbing catfishes, and a special fold of skin on which gill membranes rest in loach catfishes.

The common habitat indicated for many of these fishes is "mountain streams". Some are algae scrapers (gyrinocheilds, loricariid catfishes, parodontids, loach gobies), others are well known for ascending waterfalls (kneriids, astroblepid climbing catfishes, *Lentipes* gobies). Many have scientific or common names that reflect specialized morphologies or suggest habitat preferences. The list includes species from perhaps 16 families and at least five different orders of teleosts (Table 18.2); other taxa in North American streams that use similar habitats and show some of the modifications include catostomid hognose suckers (*Hypentelium*), scorpaeniform sculpins (*Cottus*), and several percid darters (*Etheostoma*, *Percina*).

The relationship between form and function in many of these is fairly obvious. The depressed-flattened shape of the body as well as the large, horizontally oriented paired fins would help push the fish down against the substrate. An adhesive or suction device similarly prevents being dislodged. Subterminal mouths allow for algae scraping or benthic feeding, whereas opening a terminal mouth creates drag. Many have reduced or lost the gas bladder, a broadly convergent trend among benthic fishes in general but an obvious necessity in swift flowing water.

Undoubtedly, some anatomical characteristics reflect phylogeny as much as adaptation to habitat, although phylogeny can preadapt organisms to particular habitats as well as constrain them from occupying others (see below, Preadaptation, evolution, and convergence). Preadaptation may help explain the abundance of catfish families in Table

Table 18.2

A sampling of freshwater fishes that inhabit torrent and rapid zones of streams and rivers. Most if not all have converged on body shapes and proportions, fin arrangements and shapes, and other traits that reflect the need to hold position on the bottom in swift flowing water.

Order	Family	Scientific name[a]	Common name
Gonorynchiformes	Kneriidae	*Kneria*	Knerias
Cypriniformes	Cyprinidae	*Rhinichthys cataractae*	Longnose Dace
Cypriniformes	Psilorhynchidae	*Psilorhynchus*	Mountain carps
Cypriniformes	Gyrinocheilidae	*Gyrinocheilus*	Algae eaters
Cypriniformes	Balitoridae	*Balitora*, *Gastromyzon*	Hillstream loaches
Characiformes	Parodontidae	*Parodon*	Parodontids
Siluriformes	Amphiliidae	*Amphilius*	Loach catfishes
Siluriformes	Nematogenyidae	*Nematogenys inermis*	Mountain Catfish
Siluriformes	Astroblepidae	*Astroblepus*	Climbing catfishes
Siluriformes	Loricariidae	*Otocinclus*, *Farlowella*	Suckermouth armored catfishes
Siluriformes	Amblycipitidae	*Amblyceps*	Torrent catfishes
Siluriformes	Sisoridae	*Sisor rheophilus*	Sisorid catfishes
Perciformes	Cheimarrhichthyidae	*Cheimarrichthys fosteri*	New Zealand Torrentfish
Perciformes	Gobiesocidae	*Gobiesox fluviatilis*	Mountain Clingfish
Perciformes	Rhyacichthyidae	*Rhyacichthys*	Loach goby
Perciformes	Gobiidae	*Lentipes concolor*	O'opu Alamo'o

[a] The specific name is given for representative or monotypic species, and the generic name is given when several species exist.

18.2; catfishes as a group are freshwater benthic dwellers and somewhat depressed in body shape. Existing adaptations probably facilitated the invasion of high-energy, freshwater habitats by marine gobiesocid clingfishes, given their flattened, teardrop-shaped bodies, benthic habits, absent swim bladder, and pelvic fins fused into a suction disk. Most of the seven clingfishes that inhabit fresh water (of a total of 140 species in the family) live in high-velocity stream zones at moderate to high elevations of Central and northern South America, regions where few of the other fishes listed in Table 18.2 occur. These clingfishes likely encountered an available, relatively unoccupied **adaptive zone** for which they already possessed appropriate traits (e.g., Guzman et al. 2001). Similar circumstances may help explain the successful invasion of insular fresh waters by the other perciforms in Table 18.2, such as the cheimarrhichthyidae Torrentfish (New Zealand), rhyacichthyid loach gobies (New Guinea, New Caledonia), and the gobiid O'opu Alamo'o (Hawaii).

Caves

Among the more extreme aquatic environments imaginable are underground water systems where no light penetrates and where food availability depends on infrequent replenishment from surface regions. However, **cave living** has advantages, including a scarcity of competitors and predators and a constant, relatively moderate climate. Fishes have evolved independently in caves around the world and, not surprisingly, similar adaptations to cave life have evolved repeatedly despite phylogenetic differences. The darkness, low productivity, and even high atmospheric pressure of cave environments have also led to some surprisingly strong convergences between cave and deepsea fishes.

Caves usually develop in limestone formations (**karst**) because of the solubility of carbonaceous rock, although caves exist in other rock types such as lava tubes on volcanic slopes. Caves include places where water dives underground and resurfaces after a short distance, or where springs upwell near the surface and are illuminated by dim but daily fluctuating daylight (technically a **cavern**). The classic cave environment is a continually dark, subterranean system where fluctuations in temperature, oxygen, and energy availability are minimal and where little interchange occurs with other areas. The biota of caves are especially interesting because a continuum of habitats exists between the surface, caverns, and deep caves. We can consequently often identify closely related and even ancestral organisms from which cave populations and species evolved. This allows comparison of cave and surface forms and analysis of the processes and selection pressures that have produced cave adaptations.

Approximately 136 species and 19 families in 10 different orders of teleostean fishes have colonized caves. These unusual fishes – termed variously **hypogean**, **troglobitic**, **phreatic**, and **stygobitic** – occur in scattered locales at tropical and warm temperate latitudes on all continents except Antarctica and Europe (Proudlove 1997a, 2006; Weber et al. 1998). With the exception of some bythitid cusk-eels and gobies, the families are restricted to fresh water. Most cave fishes are ostariophysans (characins, loaches, minnows, and eight catfish families), which is not surprising given the overwhelming success of this superorder in freshwater habitats. The remaining four families are either paracanthopterygian (ambloypsid cavefishes) or acanthopterygian (poeciliid livebearers, synbranchid swamp eels, and cottid sculpins). Only one family, the amblyopsid cavefishes, consists primarily (four of six species) of cave-dwelling forms. Many are known from only one or a few locations, although sampling difficulties make accurate population estimations difficult. But isolation seems to be commonplace: at least 48 species are known from only their type locality.

Adaptations to cave living

Typical cave-adapted fishes are characterized by a lack of pigmentation, reduced squamation, a reduction or loss of light receptors (involving eyes and the pineal gland) (Fig. 18.13), greatly expanded lateral line and external chemo-

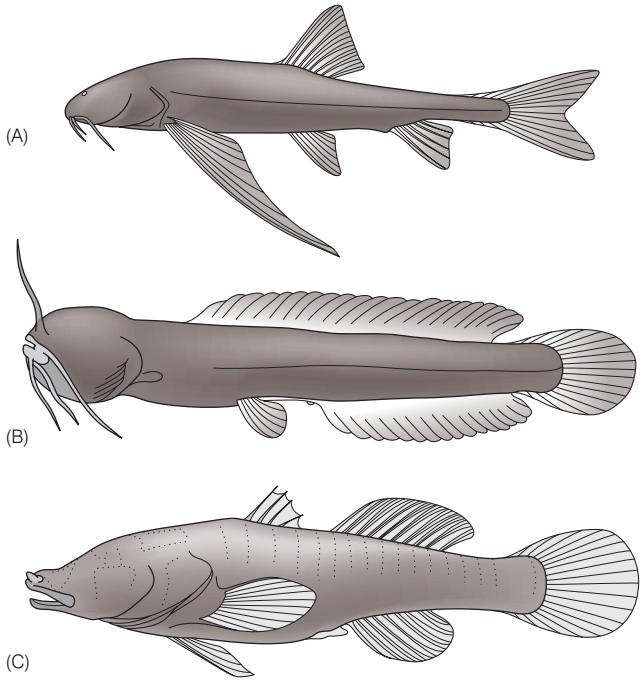


Figure 18.13
Cave fishes from three different orders, showing convergent loss of eyes, among other oddities. (A) A balitorid river loach, *Triplophysa xiangxiensis* (Cypriniformes), from China. (B) A clariid catfish, *Horaglanis krishnai* (Siluriformes), from India. (C) An eleotrid sleeper, *Typhleotris madagascariensis* (Perciformes), from Madagascar. After Weber et al. (1998).

sensory receptors, and relative decreases versus increases in brain areas associated with vision versus hearing and chemoreception, respectively. Behaviors typically mediated by vision are lost, such as schooling, the dorsal light reaction, and circadian rhythms (Wilkens 1988; see Chapters 6, 23). Taste buds in surface-dwelling *Astyanax fasciatus*, a characin, are generally restricted to the mouth region, whereas in cave-adapted populations of the same species they cover the lower jaw and ventral areas of the head. Chemosensory capabilities are better in cave forms; cave-adapted *A. fasciatus* are about four times more effective in finding meat on the bottom of a darkened aquarium than are the surface forms.

Adaptations to unpredictable or irregularly occurring food supplies also exist. When fed *ad libitum* (as much as they can consume), cave *Astyanax* build up larger fat reserves than surface forms, again by a factor of four (37% of body mass vs. 9%). Parallel comparisons can be made within the family of cavefishes (Amblyopsidae). The cave genera (*Amblyopsis*, *Typhlichthys*, *Speoplatyrhinus*) swim more efficiently, have lower metabolic rates, and find prey quicker and at greater distances in the dark than surface forms (*Chologaster*). The cave forms are also better at avoiding obstacles and at memorizing the locations of objects than are the surface fish. Cave catfishes (blindcats) in the North American family Ictaluridae show parallel changes with respect to eye loss, absence of pigmentation, pineal reduction, enlarged lateral line pores and canals, and brain modifications. Many analogous adaptations have also been observed in other cave-adapted taxa, including beetles, amphipods, crickets, crayfishes, shrimps, and salamanders (Poulson 1963; Poulson & White 1969; Culver 1982; Langecker & Longley 1993; Parzefall 1993).

Adjustments to cave existence also occur in the reproductive biology and life history traits of cave-dwelling fishes. Not surprisingly, visual displays are generally lacking during courtship of cave species, even in taxa such as livebearers and characins where they occur commonly in surface forms (Parzefall 1993). With respect to life history traits, cave-adapted amblyopsids produce fewer but larger eggs with greater yolk supplies, have larvae that spend more time before hatching, and have a later age at maturation and longer life spans (Bechler 1983). Reproductive rates of cave populations are surprisingly low. Only about 10% of the mature fish in a population of cavefishes may breed in any one year, each female producing 40–60 large eggs. These eggs are incubated in the mother's gill cavity for 4–5 months, long after the young are free-swimming. This may be the longest period of parental care for an externally fertilized fish species. Many of these characteristics are what one would expect in a habitat where adult mortality and interspecific competition are low, environmental conditions stable, and food scarce (Culver 1982; see Chapter 24).

The degree of anatomical and behavioral change in a cave population is often correlated with the length of time available since the cave was colonized. Eye loss, characteristic of cave-adapted forms, shows some responsiveness to light availability. When young *Astyanax fasciatus* from caves of different presumed ages are raised in the presence of light, individuals from old cave populations do not develop eyes, surface populations develop eyes, and populations thought to have invaded caves more recently vary in eye size (Parzefall 1993).

Food sources in caves are rather limited. Since no photosynthesis can occur in the sunless cave environment, food can only arrive if brought in by other animals or carried in by percolation through the rock or by water currents, such as during occasional floods. Common food types differ among families, but bat and cricket guano, bacteria, algae, small invertebrates (isopods, amphipods, copepods), and conspecifics are the common food types of most groups (Parzefall 1993). In Mexican caves containing the livebearer *Poecilia mexicana*, bat guano is supplemented by bacteria associated with sulfur springs in the cave, an interesting analog to deepsea vent communities (see above, The deep sea). Cave fishes respond to chemical or mechanical cues given off by the food; a clay ball dropped into the water containing cave fishes will induce active swimming and searching by fish within 1 m of the ball.

Cave fishes usually live at low densities, particularly those in isolated deep caves; most populations involve hundreds or at most thousands of individuals. Population density is strongly correlated with food availability, which again correlates with degree of isolation. Typical population densities of such fishes as the amblyopsid cavefishes are low, ranging from 0.005 to 0.15 fish/m^2. The Blind Cavefish, *Astyanax fasciatus*, can reach densities of 15/m^2 and *Poecilia mexicana* can reach densities of 200/m^2 where sulfur springs occur, and near-surface caves that contain bats as an energy source host even higher densities of cave-dwelling fishes.

Not surprisingly, small populations living in isolated habitats with few competitors or predators and evolving life histories that include slow growth and reproduction, make cave fishes exceedingly vulnerable to environmental disturbance, a convergent trend that cave fishes share with desert spring forms for many of the same reasons. Pollutants, water withdrawal, and competition, predation, and disease brought in by introduced species are major threats. As an ecological grouping, caves must be the habitat type with the proportionately highest rate of imperilment among fishes (and other organisms). The IUCN (2004) listed 52 cave fish species as at high risk, and experts consider at least another eight species to be in need of protection (Proudlove 1997b). The Congo Blind Barb, *Caecobarbus geertsii*, is threatened by the aquarium trade and is consequently listed in Appendix II of the Convention on International Trade in Endangered Species (CITES). In the USA, the Alabama Cavefish, *Speoplatyrhinus poulsoni*, is federally protected as Endangered and the Ozark Cavefish, *Amblyopsis rosae*,

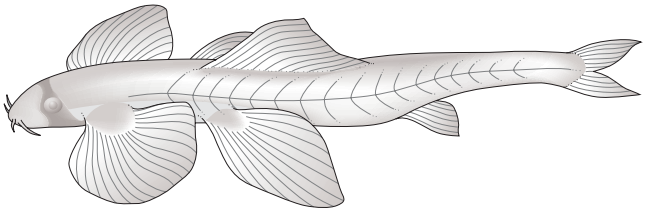


Figure 18.14

Cryptotora thamicola, a cave-dwelling torrentfish from Thailand. Known only from two locales and designated Vulnerable by IUCN because of small populations and limited distribution, this remarkable 30 mm fish shows classic specializations for both cave and swift water. Illustration by S. Madsden. See also the BBC Planet Earth video on Caves for live footage.

is Threatened. Two other cavefishes that occur in the USA – the Northern Cavefish, *Amblyopsis spelaea*, of Kentucky and Indiana and the Southern Cavefish, *Typhlichthys subterraneus*, found in five southeastern states, Indiana, and Missouri – are both designated as Vulnerable by the IUCN (2004) (see Romero 1998; Romero & Bennis 1998).

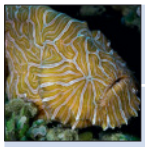
At the pinnacle of this discussion of evolution in special habitats is a specialized freshwater fish that truly exemplifies the Principle of Convergence. *Cryptotora thamicola* is a balitorid from Thailand, a member of the hillstream loach family along with several torrent-dwelling fishes. Its morphology conforms with other torrent dwellers: greatly enlarged pectoral and pelvic fins with adhesive pads, and a short, blunt, sloping forehead. It occurs in fast-flowing, cascading water where it has been observed to climb waterfalls (Kottelat 1988; Trajano et al. 2002; Proudlove 2006). Except the waterfalls are in caves, and *Cryptotora* is a classic cave dweller: naked, eyeless, and colorless (Fig. 18.14). Strong selection pressures produce predictable adaptations, and adaptation to one selective regime does not preclude simultaneous adaptation to other, strong selection factors.

Preadaptation, evolution, and convergence in cave fishes

Adaptation to the cave environment often involves two contrasting trends in the development of structures. Organs that may have been useful to surface ancestors but are of limited use in the cave, such as eyes and pigment, are gradually lost, a process known as **regressive evolution**. They are replaced by **hypertrophied** ("overdeveloped") structures, such as widely distributed and enlarged lateral line and chemosensory receptors and their neural correlates. The mechanisms and agents of selection leading to regressive evolution – namely the relative importance of neutral or directional selection, pleiotropy, energy economy, population size, time since isolation, and gene flow – remain a matter of active debate (Culver 1982).

Some groups possess preadaptations that may have made the transition to cave life quicker. Surface-dwelling Mexican characins show reduced eye development when raised in the dark, and blinded surface fish are as effective at avoiding obstacles as are cave-adapted fish. At least 10 cave families commonly contain nocturnal species; nocturnality and its attendant emphasis on non-visual sensory modes would be an important preadapation for cave living. Some cave-dwelling characins develop taste buds outside the mouth. This pattern also exists in surface-dwelling ictalurid catfishes; in fact, taste buds are more numerous on the barbels and general body surface than in the mouth of ictalurids, which could make transition to a cave environment easier. An elongate body and other eel-like features occur in nearly one-third of cave forms, such as the synbranchid swamp eels, cusk-eels, clariid catfishes, loaches, trichomycterid catfishes, and arguably the amblyopsid cavefishes themselves. Seven acanthopterygian species (i.e., non-anguilliforms) are eel-like. Anguilliform swimming may be advantageous in the narrow confines of many caves (see Chapter 8, Locomotory types). Evolution of eel-like bodies has occurred in several dozen non-anguilliform fishes, another case of convergent evolution worth studying in its own right (see Chapter 24, Habitat use and choice).

Several authors have noted the similarities in traits between cave fishes and bathypelagic deepsea forms, referring to the similarities as the **deepsea syndrome**. Similar adaptations in the two habitat types include losses of pigmentation, squamation, and light receptors, expanded lateral line and chemosensory receptors, and attendant modifications in the brain. In the blind catfishes, which live deeper than most other cave fishes (400–500 m), additional convergences occur in terms of reduced body size, gas bladder regression, large lipid deposits, and reduction of body musculature and skeletal ossification. These changes can be viewed as adaptations to overcome problems associated with energy conservation in an environment with limited food availability (Langecker & Longley 1993). These parallels underscore once again the descriptive power of the Principle of Convergence: if selection pressures and processes are strong and analogous, convergence can occur not just among species within a habitat but also between habitats.



Summary

SUMMARY

1. The Principle of Convergence states that strong selection pressures tend to produce strong similarities in unrelated animals. Several aquatic habitats offer examples. Mesopelagic ocean depths between 200 and 1000 m contain 750 species of fishes that are typically dark in color, with photophores, large mouths, slender teeth, reduced skeletons and squamation, long rete mirabiles, low enzyme activity, and daily vertical migrations. Bathypelagic fishes (1000–4000 m, 200 species) show stronger and more bizarre convergences, including sex reversal, extreme skeletal and musculature reduction, eye loss, longer retes, marked sexual dimorphism, and behavioral energy conservation. These characteristics are apparent adaptations to low energy availability.
2. Oceanic, pelagic fishes swim in the upper 100–200 m of water. This is the primary region for commercial fish production and is the habitat of herringlike fishes, sauries, carangoids, dolphinfishes, mackerels, tunas, and billfishes. Pelagic fishes are typically streamlined, silvery, and migratory, with a high proportion of red muscle for sustained swimming. They respire efficiently and save energy by using ram-gill ventilation. Life history differences between temperate and tropical species are influenced by seasonal and spatial food availability, and lead to dramatic differences in year class fluctuations. Freshwater pelagics have converged on many traits with oceanic species.
3. The polar Arctic and Antarctic regions lie above 60° latitude. The Antarctic has more endemic, specialized fishes, half of which are in the icefish suborder Notothenioidei. Antarctic fishes avoid freezing because their blood contains antifreeze compounds. Channichthyids are unusually pale because they lack hemoglobin and myoglobin. Some notothenioids have evolved neutral buoyancy via reduced skeletal mineralization and increased lipid deposition. Arctic fishes have converged on similar traits.
4. Desert freshwater fishes live on almost all continents in regions where water scarcity creates extreme conditions. Desert fishes often possess accessory respiratory structures for using atmospheric oxygen, and have a life cycle that includes a resting stage during droughts, either involving a diapausing egg or an estivating adult. In addition to low oxygen, desert fishes often encounter extremes of salinity and alkalinity. The deserts of the southwestern USA and western Mexico have a surprising diversity of endemic fishes, many of which are threatened.
5. Fishes that inhabit high-energy zones such as the wave-swept intertidal zone or steep stream beds have converged upon a body shape that is depressed, paired fins that are expanded, a suction device, subterminal mouths, and small body size. All these traits appear to facilitate the holding of position on the bottom despite strong water flow.
6. Cave fishes live in lightless, freshwater environments where food is scarce. Cave-adapted forms typically have reduced eyes, pigmentation, and squamation; low metabolic activity and reproductive rates; low population densities; and increased chemosensory and lateral line development. Their biology makes them especially vulnerable to habitat disturbances. Cave-dwelling fishes have converged on many of the traits evolved by deepsea fishes, probably in response to food and light scarcity.

Supplementary reading

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Figure V *(opposite)*

A mating pair of Mandarinfish, *Synchiropus splendidus* (Perciformes: Callionymidae), Indonesia. These small (6 cm), secretive dragonets live among coral branches or rubble, and usually emerge just after sunset to mate. Recently extruded eggs can be seen just below the pair. Photo by D. Hall, www.seaphotos.com.

PART V

Behavior and ecology

Chapter 19

Fishes as predators

Chapter contents

CHAPTER CONTENTS

Predation has an overriding influence on the morphology, behavior, and ecology of fishes. The selection forces in operation are obvious and strong: fish with a relative feeding advantage may grow faster, but fish that get eaten are eliminated from the gene pool. The next two chapters explore the behavior and ecology of feeding in fishes, with emphasis on the evolutionary interplay between predatory and escape tactics, the so-called "predator–prey arms race". For organizational purposes, adaptations are classified by where they appear to fit in the predation cycle, which is the sequence of events involving **searching/detecting**, **pursuing**, **attacking**, **capturing**, and **handling** prey (Curio 1976). Often the distinction between phases is blurred; for example, pursuit and attack may occur simultaneously, as can attack and capture. Structures employed in feeding and their functions are detailed in Chapter 8 (Feeding: biting, sucking, chewing, and swallowing). An oft-cited adaptation in foraging contexts is the formation of groups, termed **shoaling** when swimming is unorganized, but referred to as **schooling** when individuals are polarized, swimming parallel and in the same direction (Pitcher & Parrish 1993). Groups function to both increase feeding success and deter predators, and function also changes at different phases of the predation cycle (see next section; Chapter 20, Shoaling and search; Chapter 22, Aggregations).

Search and detect

Predators can search for prey actively or passively. **Active search** implies locomotion while the predator scans the environment with any of the six sensory modes discussed in Chapter 6. Water column searchers, such as herrings, anchovies, minnows, tunas, and billfishes rely heavily on vision, as do nocturnal plankton feeders. Olfaction, gustation, and hearing are also important for some water column searchers, particularly sharks. Low-frequency sounds of 20–300 Hz are especially attractive to sharks, whereas amino acids elicit feeding responses in many predatory fishes. Smell, taste, touch, or electrolocalization (passive or active) are employed extensively by benthic and nocturnal foragers such as eels, catfishes, gymnotid knifefishes, sea robins (triglids), goatfishes (mullids), and threadfins (polynemids), with polyodontid paddlefishes apparently using electrical cues to find plankton swarms. Chemoreception and touch are used by other groups that possess barbels, such as sturgeons, minnows, cods, and croakers. Some fishes search by speculation, much as chickens scratch where buried prey are likely to occur. Goatfishes move along the bottom probing into sediments with their muscular barbels that are equipped with abundant taste receptors; some goatfishes flush prey by inserting their mobile barbels into refuge holes where prey have sought shelter (Hobson 1974). Boxfishes (Ostraciidae) and triggerfishes (Balistidae) expel jets of water from their mouths to blast sand away from potential buried prey. Logperch (Percidae) roll stones with their snouts in search of hidden insect larvae. These speculating foragers frequently have attendant species that follow them and snap up prey disturbed by the forager's activity.

The energy expended in active search can be saved by camouflaged predators that lie in wait on the bottom or in other structure. Such camouflage is often termed **protective resemblance** when hiding from predators, or **aggressive resemblance** when lying in wait (the latter usage is inaccu-

rate behaviorally since "aggression" should be reserved for combat situations between animals, not for predatory activities). Benthic, camouflaged predators lie on rocks or soft bottoms or can be slightly (or greatly) buried by sediment. Their skin is colored to resemble algae-covered rocks, tunicates, sponges, and other bottom types. Wartlike and other fleshy outgrowths of skin and fins are common. These fish rush explosively from the bottom to capture prey or open their typically large mouths rapidly and inhale prey. Many scorpionfishes (Scorpaenidae), flatheads (Platycephalidae), seabasses (Serranidae), and hawkfishes (Cirrhitidae) rest exposed on the bottom, whereas lizardfishes (Synodontidae), stonefishes (synanceine scorpaenids), stargazers (Uranoscopidae), and flatfishes (Pleuronectiformes) lie with only their eyes exposed above the sediment. For such lie-in-wait predators, vision is the primary sense mode by which prey are detected, except for the elasmobranchs which may also use electrical cues. Many benthic, immobile ambushers appear surprisingly conspicuous, at least to a human observer. They may rely on prey **habituating** to their presence and thus growing careless.

Some water column predators, including countershaded or silvery-sided fishes such as gars (Lepisosteidae), pikes (Esocidae), and barracuda (Sphyraenidae), also lie in wait, floating motionless near or below the surface and darting at prey that fail to recognize them. This group also includes substrate- and leaf-mimicking species such as trumpetfishes (Aulostomidae) and leaffishes (Nandidae). Many predators shift among search patterns. Trumpetfish lie in wait among gorgonian corals to ambush roving prey, hide behind swimming herbivores such as parrotfishes, or swim actively in the water column and attack relatively stationary schools of zooplanktivores. By day, torpedo rays erupt from the sand at prey that have wandered over them, whereas at night they swim actively above the bottom in search of swimming prey. Prey behavior and density often determine which search mode will be employed. For example, young lumpfish (Cyclopteridae) cling to rocks with their modified pelvic fins and make short excursions to feed on nearby zooplankton when prey densities are high. At low prey densities, the larvae swim through the water column searching for and feeding on plankters, thereby incurring the greater costs of active search but avoiding starvation (Brown 1986; Helfman 1990).

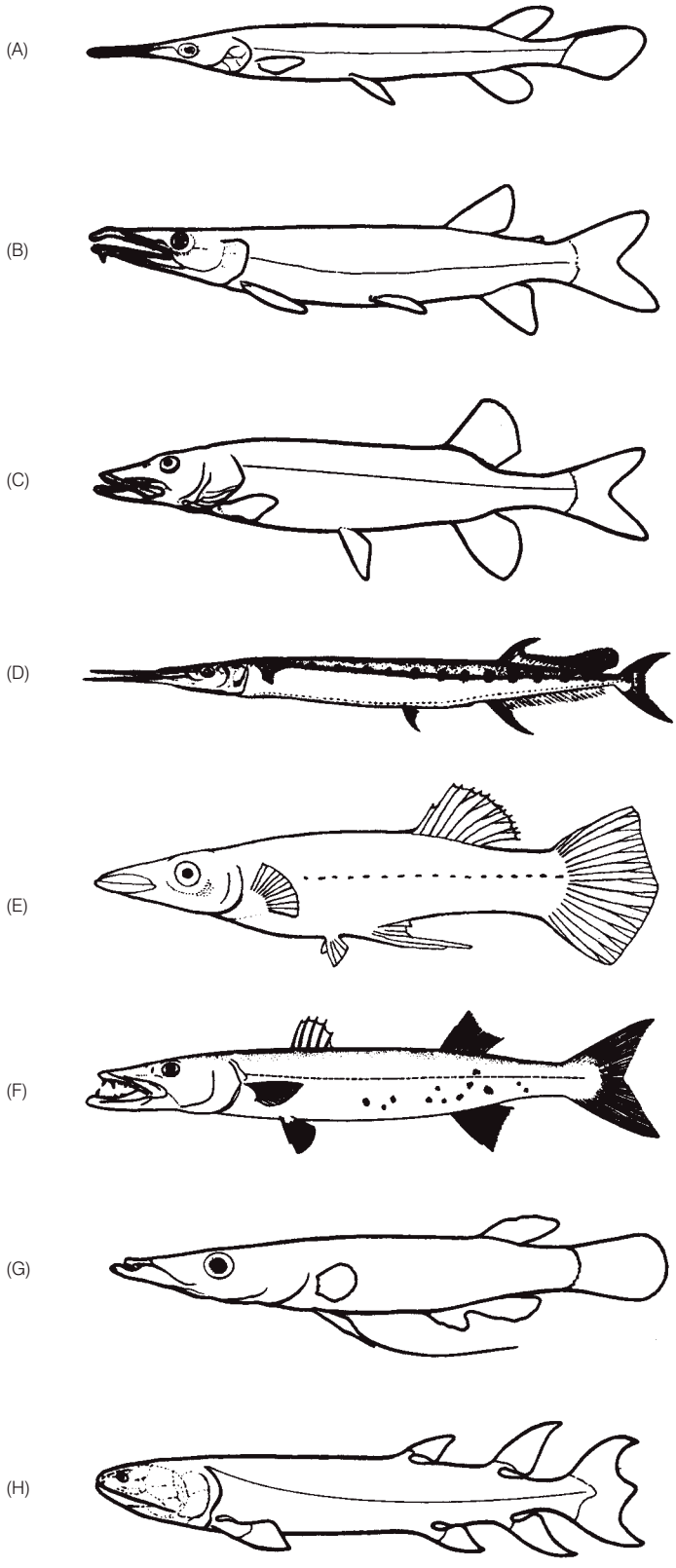
Considerable attention has been paid to the search tactics and detection capabilities of zooplanktivorous fishes. Fish swim through the water column scanning an area ahead of them that is shaped approximately like a hemisphere, the widest part being closest to the fish. The volume of this search space, the distance from objects at which fish react, and the size object that a fish is capable of detecting change with fish size, water clarity, illumination level, and current speed. Large juveniles can detect smaller objects than can small juveniles, and most fishes react further away in clearer water or after light levels exceed some threshold value (Hairston et al. 1982). Zooplanktivores that feed in currents employ searching tactics that vary as a function of current speed. Fish remain in place and wait for food objects to approach them; upon detection, fish then swim toward prey at low current velocities (10–14 cm/s) but fall back with the current at higher speeds (McFarland & Levin 2002).

Reaction distance is heavily dependent on prey size, to the extent that most zooplanktivores will react to and pursue the largest appearing prey in their visual field. This means that a small zooplankter near a fish may be taken preferentially to a larger plankter farther away because the smaller prey appears larger (the **apparent size hypothesis**). However, prey immobility and location also affect selection, smaller prey being preferred if they are mobile or are more directly in front of the forager (O'Brien et al. 1985; O'Brien 1987). The speeds at which fish search appear to approach the optimal in terms of maximizing intake relative to energy expense. For example, the actual sustained search speed of a 40 cm salmonid is 3 body lengths per second (BL/s), which is close to the calculated optimum sustained speed of 2.9 BL/s (Ware 1978; Hart 1993). Speeds vary as a function of fish size (= metabolic rate) and food concentration.

Although group formation is most commonly viewed as an antipredator response (see Chapter 20), grouped fishes may search more successfully than individuals. Foragers in groups may locate food sooner, ingest food faster, have more time available for foraging, and grow faster than solitary foragers. For example, in minnows (*Phoxinus phoxinus*, Cyprinidae), Goldfish (*Carassius auratus*, Cyprinidae), and Stone Loaches (*Noemacheilus barbatulus*, Cobitidae), shoal members spend less time before finding food than do solitary individuals, and the benefit increases with increasing shoal size (Pitcher & Parrish 1993). Accelerated rates arise because a fish in a shoal can search for food while simultaneously watching for signs of successful feeding in shoal mates, thus increasing the area over which it effectively searches. Also, the time each individual spends scanning for predators may decrease, leaving more time for feeding. These benefits are countered by **intragroup competition** for food, competition increasing as the group size increases.

Pursuit

Pursuit places a predator close enough to attack prey. Two dramatically different categories of predators have developed. One evolutionary course has favored species that maximize their speed while overtaking fleeing prey; the other course requires minimal aerobic output but a proliferation of deceptive tactics.



Cursorial, chasing predators are capable of high-speed sustained chases of rapidly swimming prey. Such fishes include the apex pelagic predators (lamnid sharks, tunas, billfishes). Morphologically, these are the most streamlined fishes, having bodies that are round in cross-section and taper to a thin, laterally keeled caudal peduncle, with the greatest body depth one-third of the way back from the head. The tail is narrow with a high aspect ratio (height : depth, see Chapter 8, Locomotion: movement and shape), and the median and paired fins typically fit into grooves or depressions during high-speed swimming. Nearer to shore, where prey can escape into structure, streamlining is sacrificed to allow for rapid braking and small radius turns. Bodies are more oval in cross-section, fins are larger, and tails broader. Predators such as salmons, snook (Centropomidae), Striped Bass (Moronidae), black basses (Centrarchidae), and large-bodied cichlids (e.g., Peacock Bass) are included here.

In **lurking** or lie-in-wait predators that swim above the bottom, pursuit is synonymous with attack. These fishes, which rely on **fast start** performance, have converged on a general body morphology that permits fast starts at a sacrifice in sustained speed and maneuverability. The group contains pikelike predators, including gars, pikes, pickerels, needlefishes, barracudas, and specialized fishes in such diverse families as the characins and cichlids (Fig. 19.1). These fishes have elongate, flexible bodies; long ("produced") snouts with many sharp, often thin teeth; broad, symmetrical median fins placed far back on the body opposite one another; and relatively large caudal fins with low aspect ratios. The low body profile of these fishes serves additionally in that it evokes a slower response by prey than do predators with deeper body profiles (see Dominici & Blake 1997). These fishes typically hover high in the water column or lurk motionless on the edges of vegetation beds, relying on their camouflage to gain access to prey. Additional piscivores that have converged on this morphology include the Australian endemic Long-finned Pike, *Dinolestes lewini* (Perciformes, Dinolestidae), and some of the world's

Figure 19.1

Variations on a theme: convergence in morphology among fast start predators. Lurking predators that swim in the water column tend to be elongate with long mouths, sharp teeth, and fins set far back on the body. Examples from six different orders and eight families are shown, including one extinct form. (A) Lepisosteiformes, *Lepisosteus* (Lepisosteidae), gar, 1 m. (B) Characiformes, *Ctenolucius* (Ctenoluciidae), Pike Characid, 1 m. (C) Esociformes, *Esox* (Esocidae), pike, 1 m. (D) Beloniformes, *Ablennes* (Belonidae), needlefish, 1 m. (E) Cyprinodontiformes, *Belonesox* (Poeciliidae), Pike Killifish, 20 cm. (F) Perciformes, *Sphyraena* (Sphyraenidae), barracuda, 1 m. (G) Perciformes, *Luciocephalus* (Osphronemidae), Pikehead, 15 cm. (H) †Osteolepiformes, *Eusthenopteron* (Eusthenopteridae), a Devonian tetrapodomorph, 75 cm. (A–C, G, H) from Nelson (1994); (D) from Collette (1995); (F) from Jordan (1905), used with permission.

largest "minnows" (Cyprinidae), such as the Colorado Pikeminnow, *Ptychocheilus lucius*, of North America, and the Kanyu or Yellowcheek, *Elopichthys bambusa*, of Asia – both of which can exceed 2 m and 40 kg.

A class of predators has developed around the energy savings that can be gained if prey can be lured within range of attack. The success of this ploy depends on the prey not recognizing the predator until it is too late to flee, or on a willingness of the prey to approach the predator. Predators can induce prey to approach if the predator looks like something the prey might want to eat. This sort of deception, misnamed **aggressive mimicry**, can involve all or part of the predator's body (e.g., Randall 2005). In goosefishes, anglerfishes, and frogfishes (Lophiiformes; see Chapter 18, The deep sea), the first dorsal spine is elongated and its end is highly modified into a species-typical **esca** or lure that resembles a small fish, shrimp, or worm (Fig. 19.2). The lure is wriggled in a lifelike manner, adding to the deception; in some species, the lure secretes a chemical attractant. The body of the predator is camouflaged to resemble the bottom or, in the case of deepsea anglers with bioluminescent lures, the dark surrounding waters. Small fishes approach the lure and are quickly inhaled by the large mouth, and their escape is often prevented by long, backward facing teeth (Pietsch & Grobecker 1978, 1987).

Luring has evolved independently in other groups. A scorpionfish (Scorpaenidae) also uses a modified dorsal spine for a lure; hatchetfishes (Sternoptychidae), lanternfishes (Myctophidae), some anglerfishes (Ceratioidei), and stargazers (Uranoscopidae) have lures in their mouths; barbeled plunderfishes (Artedidraconidae) use chin barbels, chacid catfishes use maxillary barbels, and snake eels (Ophichthidae) have a lingual (tongue) lure; and in gulper eels (Eurypharyngidae) the tail tip is illuminated (Randall & Kuiter 1989).

Nimbochromis livingstonii, a large predatory cichlid from Lake Malawi, Africa (see Box 15.2) lures prey in a unique manner. *N. livingstonii* capitalizes on the tendency of many small cichlids to scavenge on recently dead fishes. The predator lies on its side on the bottom and assumes a blotchy coloration typical of dead fish. When scavengers come to investigate and even pick at its body, the predator erupts from the bottom and engulfs them. This is the only known example of thanatosis or **death feigning** in fishes (McKaye 1981a). As a final twist, stonefish lie buried on the bottom and strike at prey fishes in a narrow zone directly above their mouths. If a potential prey fish swims between the mouth and the dorsal fin, the stonefish will raise its dorsal fin, chasing the fish back into the strike zone (Grobecker 1983).

Approach to a prey fish is facilitated by camouflage. Although most predators and their prey are countershaded or silvery, such coloration disguises a fish only when it is seen from the side. This is not the view that a prey fish has of an approaching predator. A convergent coloration trait shared by slow-stalking predators is the **split-head color pattern** (Barlow 1967). A dark or light line that contrasts with general body coloration runs from the tip of the snout along the midline between the eyes to the top of head or dorsal fin (see Fig. 20.2). This coloration is evident in pickerel (Esocidae), some soapfishes and seabasses (Serranidae), the tigerperch *Datnioides* (Lobotidae), the Leaffish, *Polycentrus schomburgkii* (Polycentridae), and some hawkfishes (Cirrhitidae), piscivores which are otherwise protectively colored and which approach their prey slowly and head-on. The split head pattern operates on the principle of **disruptive coloration**, dividing the head into halves and disrupting its outline. Prey may consequently require a moment to recognize the pattern as a whole, threatening head. Because

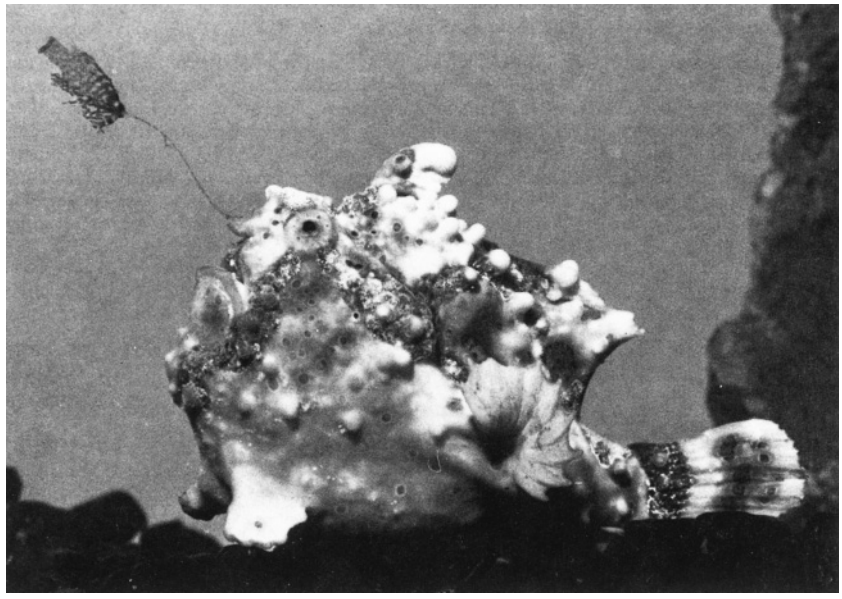


Figure 19.2

"Aggressive" mimicry in the frogfish *Antennarius maculatus*. The fishlike lure, or esca, sits at the end of the elongate first dorsal spine, termed the illicium. The resemblance of the lure to a real fish is increased by an anterior eyespot, vertical bars and mottling on the body, and finlike appendages. The lure is waved by movements of the illicium, thereby attracting potential prey fishes. From Pietsch and Grobecker (1978), used with permission.

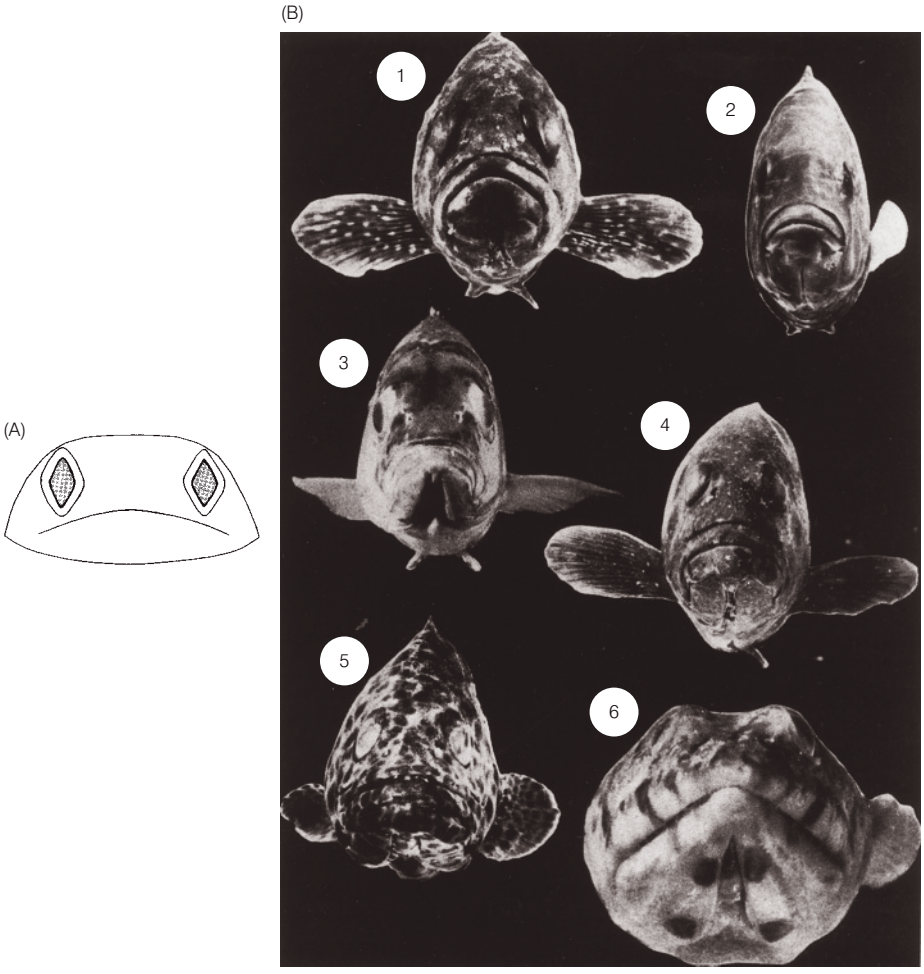


Figure 19.3
Is this the face of death? (A) The general features of a predatory face that elicit fright responses in prey fishes are a broad head; a wide, downturned mouth; and ringed, broadly elliptical eyes, as shown in drawing on the left. (B) Head-on views of piscivorous reef fishes: 1, *Epinephelus summana*, a seabass; 2, *Cheilinus trilobates*, a wrasse; 3, *Lutjanus kasmira*, a snapper; 4, *Cephalopholis argus*, a seabass; 5, *Epinephelus fario*, a seabass; 6, *Synodus variegatus*, a lizardfish. (A) from Karplus et al. (1982); (B) from Karplus and Algom (1981), used with permission.

predator–prey interactions occur on a timescale of tens of milliseconds, a moment's delay in recognition may be all that a predator requires to attack successfully. Prey fishes are often frightened by general, head-on, facial characteristics of predators (e.g., Dill 1974; Karplus et al. 1982), hence disguising the face would eliminate critical cues used in predator recognition (Fig. 19.3).

Group hunting is comparatively rare in fishes. Apparent **cooperative feeding**, involving some form of coordinated herding or driving of prey by circling or advancing predators, has been observed in several shark species, including the Blacktip Reef, Lemon, and Oceanic Whitetip sharks (Carcharhinidae), sand tiger sharks (Odontaspididae), and thresher sharks (Alopiidae), the latter using their long caudal lobe for both herding and stunning prey (Motta & Wilga 2001; Motta 2004). Detailed observations of apparent cooperative feeding have been made on Sevengill Sharks, *Notorynchus cepedianus*, surrounding and then attacking seals off South Africa (Ebert 1991). Sevengills form a loose circle around the prey, and the circle gradually tightens until one and then the group of sharks attacks the seal. Other fishes suspected of engaging in cooperative feeding include piranhas, jacks, Yellowtail, Black Skipjack Tuna, Bluefin Tuna, and Sailfish (Bigelow & Schroeder 1948b; Hiatt & Brock 1948; Voss 1956; Potts 1980; Partridge 1982; Sazima & Machado 1990; Steele & Anderson 2006). None of these fishes cooperate to the extent observed in pack hunting mammals such as hyenas, wolves, lions, or killer whales.

Attack and capture

An actual attack takes place as the predator launches itself at the prey and engulfs the prey in its mouth. The evolutionary advance of fishes is synonymous with the development of jaws (see below and Chapters 8, 11), which function to surround, impale, or inhale prey and then pass the prey posteriorly for processing (= handling or subduing; see below). Active prey are brought into the mouth by overtaking, extending the mouth, and suction, often in combination. Fast start predators overtake or intercept their prey and impale them on sharp teeth. Overtaking may involve rapid swimming via body musculature, but many fishes also

shoot the mouth out to surround the prey, as in Largemouth Bass (Nyberg 1971). The much-heralded evolution of protrusible jaws and pipette mouth, which reach their greatest development in acanthopterygian fishes, is arguably as much for overtaking prey as for suctioning.

Many benthic, lie-in-wait predators have particularly large mouths that can be opened and closed rapidly. Frogfishes, *Antennarius* (Antennariidae) can expand their oral cavity up to 14-fold, engulfing prey in less than 6 ms. Stonefish, *Synanceia*, engulf prey in 15 ms. Speed is not solely characteristic of large fish feeding on large prey. Zooplanktivorous damselfishes (*Chromis*, Pomacentridae) project their mouths to capture individual plankters in 6–10 ms; jaw protrusion followed by suction is used during capture (Coughlin & Strickler 1990). Slower movements suffice for nonevasive planktonic prey. Whale Sharks, Basking Sharks, manta rays, herrings, anchovies, and mackerels swim through plankton concentrations with their mouths open, passively filtering prey out of the water with their fine gill rakers. Some cyprinids and cichlids filter concentrated plankton by remaining in one place and pumping water in and out of the mouth, again using the gill rakers as a sieve (Drenner et al. 1987; Ehlinger 1989).

A few specialized predators **immobilize** prey before engulfing them. These specialists include torpedo rays and Electric Eels, thresher sharks, sawsharks, sawfishes, Swordfish, and billfishes (Box 19.1). In these predators, the attack involves a high degree of energy output, followed by a relatively leisurely capture. Electricity-generating predators stun individual prey with a powerful discharge; the process

Box 19.1

Of spears and hammers

Specialized structures in large predatory fishes suggest a foraging adaptation. However, verifying this suggested function is difficult because such predators are relatively rare, are difficult or dangerous to observe, and predation is an infrequent event. Two such structures are the spears of billfishes and the hammers of hammerhead sharks.

Billfishes belong to two related families in the suborder Xiphioidei. The bills in both families develop as forward growths of the upper (premaxillary) jaw bone. In the Swordfish (Xiphiidae), the sword is flattened and smooth, whereas in the marlins, spearfishes, and Sailfish (Istiophoridae), the bill is rough and round in cross-section. Much debate has centered around whether billfish spear their prey or strike laterally to stun the prey. The occurrence of healthy billfishes with greatly reduced or even missing bills led some workers to suggest that the bill serves no feeding role. However, good observational evidence indicates that the bill can serve both purposes. Sportfishers frequently observe marlin knocking prey such as small tuna into the air, or find their lures with characteristic scratch marks indicative of strong sideways blows of the rough spear. Tuna and dolphinfish perforated with spear holes have been found in marlin stomachs and observers have watched marlin spear hooked tuna prior to swallowing them. Marlin will also use the spear defensively, as an unlucky researcher discovered in April 2003, when he entered the water off Maui to videotape false killer whales attacking a 3 m + marlin. The marlin speared the diver through the right shoulder, causing considerable tissue damage (*Honolulu Advertiser*, 17 April 2003).

A fortuitous, if not unsettling, observation was made by two spearfishers off Durban, South Africa. Free-diving in about 20 m of water, one diver speared a *c*. 15 kg Amberjack, *Seriola lalandi* (Carangidae):

> The fish pulled off the spear and dashed straight for Roxburgh [at the surface] who simultaneously observed a 3–4 m marlin [probably a Black Marlin, *Makaira indica*] making a direct charge for the amberjack which was now hiding behind him. At the last moment the marlin halted and Roxburgh was able to push the bill aside after which the marlin circled diver and amberjack several times. Seconds later the amberjack dashed off at great speed to the bottom, closely followed by the highly agitated marlin. Within an estimated 5 s the marlin had reached its prey and impaled it on its bill. The marlin then shook the amberjack free and swallowed it. Duration of the entire incident was an estimated 30–50 s. (van der Elst & Roxburgh 1981, p. 215)

The Swordfish, *Xiphias gladius*, evidently uses its smooth, flat bill primarily to decapitate cephalopod prey and slash them into swallowable pieces. Slashing also occurs as a swordfish enters a shoal of prey; maimed fish are picked up on subsequent passes. Spearing may occur defensively or during territorial encounters: broken Swordfish (and billfish) bills have been found embedded in boat hulls and other objects. The deep submersible *Alvin* was attacked and skewered by a 60 kg Swordfish at a depth of 600 m; the fish was still stuck when the

sub was brought to the surface (Wisner 1958; Ellis 1985).

A greater mystery surrounds the expanded **cephalic lobes** of hammerhead sharks (Sphyrnidae). The anterior and lateral margins of the chondrocranium, particularly the olfactory and optic regions, are slightly to greatly expanded and flattened among members of this family. The eyes and nostrils sit at the ends of these cephalic lobes. It has been variously suggested that this highly modified head functions (i) as a bowplane to increase maneuverability; (ii) to increase stereoscopic or binocular vision in the forward direction; (iii) to increase stereolfaction, which would allow localization of odors; and/or (iv) to expand the sensory area for pressure and electromagnetic detection (Compagno 1984). None of these explanations is necessarily exclusive and all could operate to some degree, although experimental tests have failed to demonstrate exceptional capabilities with respect to hydrodynamic efficiency, electrolocalization ability, or olfactory localization (Johnsen & Teeter 1985; Parsons 1990; Kajiura et al. 2003, 2005). However, underwater observations suggest an additional if not primary use of the hammer during prey capture.

Stingrays figure commonly in the diets of many sphyrnids. The Great Hammerhead, *Sphyrna mokarran*, appears to be something of a stingray specialist: individuals have been found with as many as 96 stingray barbs embedded in the mouth, throat, and tongue. Researchers in the Bahamas observed an incident suggesting that the hammer can function specifically to facilitate feeding by sphyrnids on stingrays (Fig. 19.4). Snorkeling in 6 m of water over a seagrass bed, the divers witnessed a 3 m long Great Hammerhead pursuing a 93 cm wide Southern Stingray (*Dasyatis americana*, Dasyatidae). The shark thrust its head down against the mid-dorsal region of the ray, knocking the ray to the bottom. The shark then pinned the ray against the bottom using its head and pivoted around on the back of the ray, taking a bite from the left front margin of the ray's disk. The ray limped off and the shark pinned it to the bottom again, pivoted, and took a bite from the right anterior margin of the disk. This incapacitated the ray, which was then consumed by the shark. In this incident, the shark used its expanded head to both knock the stingray to the bottom and disrupt its flight, and also to hold the stingray on the bottom while the shark pivoted around to the anterior portion of the ray's disk to take bites. "It is doubtful that a shark with a conical snout could have been as effective in restricting the ray's movements (i.e., applying pressure to both pectoral fins simultaneously)" (Strong et al. 1990, p. 839). The researchers concluded that, while possibly serving improved sensory functions, the size and orientation of the expanded cephalic lobes of hammerhead sharks can be directly responsible for making sphyrnids efficient predators on large batoids.

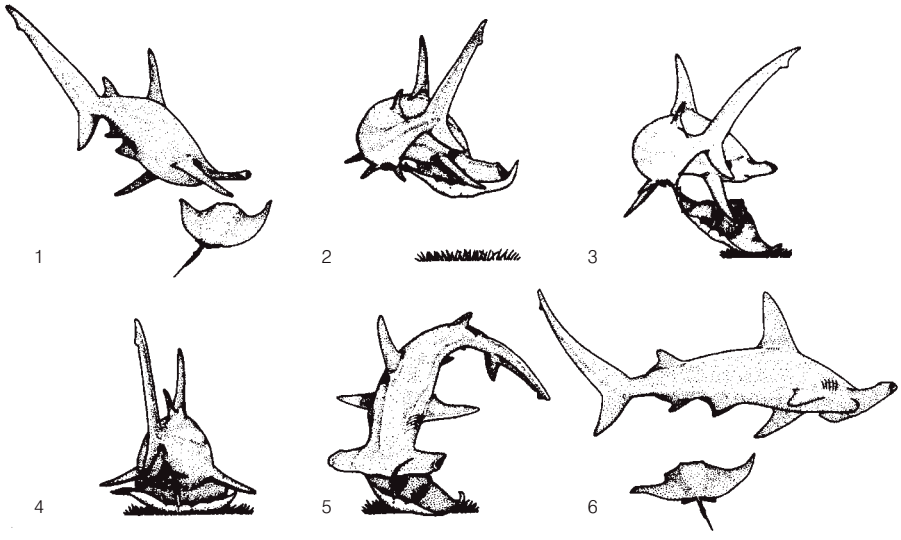


Figure 19.4

The use of the hammer during feeding by a Great Hammerhead Shark. A 3 m long hammerhead captured and consumed a l m wide Southern Stingray by knocking it to the bottom with its hammer and then using the hammer to hold the ray against the bottom while the shark pivoted around and fed on the front margins of the pectoral fins. The following sequence is shown: 1, shark chases the ray; 2, shark strikes downward across the back of the ray with the flat underside of its hammer; 3, ray bounces off the bottom from the force of the blow while the shark brakes with its pectoral fins; 4, shark delivers a second downward blow across the back of the ray; 5, shark pivots while holding the ray against the bottom and takes a bite from the front of the left pectoral fin; 6, injured ray attempts to swim off followed by the shark. From Strong et al. (1990); used with permission.

is well studied for torpedo rays but more poorly understood for Electric Eels (Bray & Hixon 1977; Lowe et al. 1994). In torpedo rays, the predator encompasses the prey with its pectoral fins and discharges its electric organ. The immobilized prey is then grasped in the mouth. Thresher sharks, sawfishes, Swordfish, and billfishes are among the few predators that are minimally bothered by the confusion created by a large group of prey fishes (see Chapter 20, Responses of aggregated prey). These predators enter a school and slash laterally with their bill (or tail in the thresher shark), and then pick up incapacitated or decapitated prey. The actual pattern is poorly understood.

Another fish that incapacitates its prey prior to capture is the archerfish (Toxotidae), which feeds on terrestrial insects. Archerfishes have a groove in the top of the mouth along which the tongue fits. The fish propels droplets of water directionally along the groove at its aerial prey. The insects fall into the water and are snapped up by the waiting archer. Laboratory trials have demonstrated that archerfishes can learn to hit targets 30–50 cm above the water, moving as fast as 20 cm/s, with up to 50% accuracy. This task requires correcting not only for refraction at the water's surface and the arc and decelerating velocity of the fired droplet but also the change in the three dimensional location of the target (Dill 1977a; Schuster et al. 2006). What makes this behavior even more astounding is that individuals can learn to adjust their shots by observing the efforts of shoalmates (Fig. 19.5). Osphronemid fishes in the genus *Colisa* also spit water at insects.

The actual strike of pikelike predators is short and fast, involving a prestrike S-shaped bending of the body and maximal forward propulsion driven by the combined surface area of the median and caudal fins; pike acceleration in this phase has been measured at more than 150 m/s (Webb 1986; Dominici & Blake 1997). Prey are impaled on the sharp jaw teeth, manipulated into a head-first position, and swallowed; in barracuda, large prey can be cut into smaller pieces for swallowing. In most predators, the attack is focused on the **center of mass** of the prey's body, because the escape response involves a pivoting on the center of mass and hence the center moves least relative to other prey body parts (see Chapter 20).

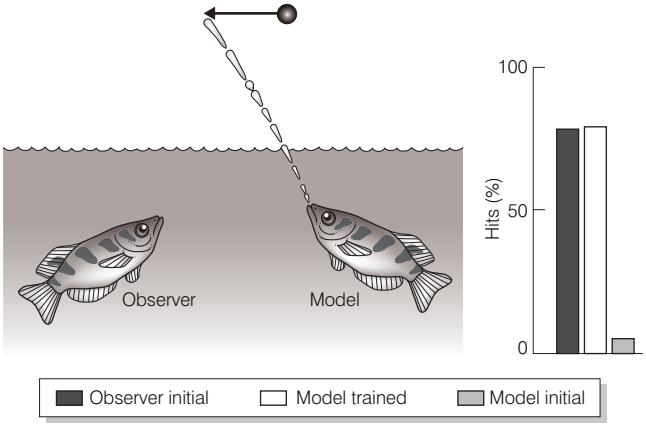


Figure 19.5

Archerfish learn to hit rapidly moving targets by observing other archerfish. Observer archerfish allowed to watch a school member (model) improving its accuracy are almost as accurate on their first shot as the model fish was after more than 1000 shots. Crosshatched bar, initial success of model; open bar, success of model after training; solid bar, average success of observer on its first shot having watched the model. The target was 54 cm above the water and was moving at 5 cm/s. After Schuster et al. (2006).

When attacking prey in shoals, the major obstacle to successful prey capture is the presence of other shoal members; a direct relationship exists between likelihood of escape and numbers of individuals in the shoal. Hence many predators engage in tactics that separate prey individuals from the group. For example, when Pike (*Esox lucius*, Esocidae) attack minnow (*Phoxinus phoxinus*) schools, the predator's strike often leaves individual prey separated from the school. The predator then preferentially chases these individuals, which may account for 89% of the predator's success (Magurran & Pitcher 1987). Similar **group-separating tactics** are employed by other predators, such as Blue Jack, *Caranx melampygus* (Carangidae), when attacking mixed species schools of snappers, and piranha, *Serrasalmus spilopleura* (Characidae), attacking cichlid shoals (Potts 1980; Sazima & Machado 1990). Stragglers are up to 50 times more likely to be attacked than fish within a group, and success rates for attacks on stragglers can be four times higher than for attacks on the main shoal (Parrish 1989a, 1989b).

Aggressive mimicry also occurs in a group context, the victims either being fish and invertebrates exterior to the shoal or even unsuspecting members of the shoal itself. In both cases, shoal membership by the mimic allows the predator to get close enough to attack. Juveniles of the Indo-Pacific grouper, *Anyperodon leucogrammicus* (Serranidae), swim with and resemble adult females of four similar species of wrasses (Labridae). Small fishes have no reason to fear the wrasses, which feed on a variety of small benthic invertebrates. However, the grouper is a piscivore and has been observed snaring small damselfishes while swimming among the shoaling wrasses. Similarly, hamlets of the West Indian genus *Hypoplectrus* (Serranidae) resemble damselfishes and angelfishes, the models here being zooplanktivores or herbivores. The hamlets are carnivores and their presumed mimicry could allow them to sneak up on invertebrate prey that do not distinguish them from the otherwise harmless, and usually more numerous, model species (Moland et al. 2005; Randall 2005). Some scale-eating fishes attack from within shoals, their primary prey being shoalmates that they resemble. These predators include a characid, *Probolodus heterostomus*, which feeds on schooling characids in the genus *Astyanax*, and a cichlid, *Corematodus shiranus*, which resembles and schools with

its prey, a tilapiine cichlid, *Oreochromis squamipinnis* (Sazima 1977; Thresher 1978).

Prey choice is also affected by relative numbers of different kinds of individuals in the prey shoal. **Oddity** in appearance or behavior often stimulates attack. In mixed schools, the minority species is often attacked disproportionately, as happens when Gafftopsail Pompano (Carangidae) feed on anchovetas (Engraulidae) that are schooling with more numerous Flatiron Herring (Clupeidae) (Hobson 1968). In experimental trials, Largemouth Bass are much more successful predators when one or two blue-dyed minnows are added to small minnow shoals; the odd individuals are taken preferentially (Landeau & Terborgh 1986). Predation on odd individuals within a school may result from them standing out against the background of the more common type or, as suggested by Landeau and Terborgh (1986), because oddity alleviates the confusion effect created by a mass of similar-appearing prey animals. Whether predatory fishes are more likely to attack injured individuals within a group remains unclear. Certainly sharks and barracudas are attracted to injured or erratically swimming prey, and the literature on mammalian predators (e.g., lions, wolves, hyenas) suggests that fishes would also feed preferentially on injured individuals. However, the only quantitative study of the subject indicates, if anything, an avoidance of injured prey (Major 1979). Regardless, predation on odd individuals indicates the strong selection that occurs for uniformity of appearance and behavior within a shoaling species.

Handling

Handling includes any **postcapture manipulation** required to subdue prey and make it ingestible and digestible. Fishes that feed on hard-bodied prey or on prey with primary external defenses such as spines, shells, bony scales, or toxic skins must usually spend time and energy in handling, as do scavengers that feed on prey too large to be swallowed whole (Box 19.2).

Assuming prey are small enough to be swallowed and possess no exceptional defenses such as bony armor, poisonous spines, or toxic skin secretions, piscivores face one major handling task. The prey must be manipulated into a **head-first** orientation for swallowing (Reimchen 1991). Such manipulation is less important with nonspiny fishes such as clupeiforms, most ostariophysans, and salmoniforms, but even soft-rayed fishes can become lodged in the throat if they are large and swallowed tail-first. Head-first swallowing facilitates depression of the dorsal, anal, and pelvic fins, all of which can anchor themselves in the predator's mouth or throat. Additionally, head-first swallowing reduces the likelihood of escape from the mouth since few non-eel-like fishes can swim backwards effectively. Positioning is accomplished by jaw and head movements. As many predators will attack fishes as long as themselves (or even longer in the case of many deepsea species), it is not unusual to observe a piscivore swimming with the tail or more of a prey fish protruding from its mouth. Such a large meal obviously represents an energetic bonanza, but is obtained at a potential cost if it hampers the predator's ability to escape its predators. On occasion, one finds a dead predator floating with a large, dead prey fish protruding from its mouth, testimony to the importance of gape limitation and the evolution of an ability to accurately estimate the size of potential prey.

Preparation for swallowing is accomplished by teeth. Dentition type is a reliable indicator of both prey type and foraging tactics (see Chapter 8, Dentition). Piscivores either hold their prey with large, sharp-pointed teeth or numerous needlelike teeth, or they chop prey up with flat, bladelike teeth (Fig. 19.7). These teeth may be in the marginal jaws or on the palate and tongue. Insect feeders generally have moderately stout, conical, recurved teeth, again marginally or as part of the pharyngeal apparatus (see Chapters 8, 14). Most fishes that feed on mollusks or echinoderms crush the shell in the mouth, using molarlike teeth. Fishes with parrotlike beaks (parrotfishes, puffers) feed on tough sponges, algae, or coral, with supplemental crushing in a pharyngeal mill in parrotfishes. Gill rakers also characterize different foraging types, functioning either for retention of prey or as mechanical barriers to escape. Numerous, long, thin, gill rakers filter out small plankters as water passes through the mouth and out the opercular openings; gill raker spacing is usually directly related to prey size. Fish eaters have harder, stouter, more widely spaced rakers that prevent escape through the gill opening (e.g., seabasses, Largemouth Bass).

Some armored and otherwise defended prey require special handling tactics. Sea urchins are abundant and their internal organs are edible. However, the defensive spines must first be removed. Special methods for despining urchins include plucking individual spines off to expose the outer test (triggerfishes, Balistidae), blowing water jets to roll the urchin over, exposing the relatively spineless ventral surface (triggerfishes), or picking the urchin up by a spine and bashing it open on a rock (wrasses, Labridae). Wrasses also smash crabs against rocks to remove a leg or claw, which they then crush in their pharyngeal jaws (Wainwright 1988a). Some predators apparently wash distasteful substances off the surface of prey by manipulating them in the mouth. For example, a Largemouth Bass fed whirligig beetles that secrete noxious chemicals or meal worms dipped in distasteful chemicals will repeatedly slosh the worm in its mouth and spit it out several times before finally swallowing it. Undipped worms are simply swallowed (T. Eisner, pers. comm.).

Final handling occurs in the stomach and intestines. Chemical breakdown via acids and enzymes is the rule,

Box 19.2

BOX 19.2

Overcoming gape limitation: spinning and knotting in eels

With few exceptions, fishes are **gape-limited**. This means their diets are constrained to include only items that can be swallowed whole. Swallowing entails movement of prey down the throat, which cannot expand to a width greater than the space between the cleithral bones. Feeders on hard-bodied prey can be limited by the relatively small gape of their pharyngeal jaws (Wainwright 1988a). Therefore, large, energetically valuable, even if easily obtained, food items must be passed up by most fishes.

The exceptions to this rule constitute some rather spectacularly endowed predators that are capable of chopping large items into smaller, swallowable pieces. Sharks as a group can take bites out of prey or cut prey items into pieces, undoubtably a trait that has contributed substantially to their 400-million-year success story. Among bony fishes, a few species have such sharklike capabilities, notably piranhas and African Tigerfish (Alestiidae), Bluefish (Pomatomidae), and barracuda (Sphyraenidae) – all fishes with specialized cutting or chopping dentition and powerful jaw muscles. Some advanced coral reef species use powerful jaws and teeth to tear pieces out of sponges, such as various pufferfishes (Tetraodontidae, Diodontidae). Others can take small pieces of fins or flesh from prey, including some characins and cichlids, sabre-toothed blennies (Blenniidae), and at least one species of *Forcipiger* butterflyfish (Chaetodontidae).

Probably the most common tactic for overcoming gape limitation is **nibbling**. Many small-mouthed shallow water marine and freshwater fishes can nibble small pieces from large prey, including centrarchid sunfishes, cichlids, damselfishes, wrasses, and surgeonfishes. But the great majority of fishes, those that utilize suction regularly during feeding, lack both the dentition and the jaw strength to nibble effectively. However, one body form among otherwise suction feeders has allowed the development of an alternative solution to gape limitation. Eel-like fishes and other elongate, aquatic vertebrates can spin rapidly around their long body axis while holding on to food and thus tear chunks from the larger mass of a prey item.

Eels as a group are predators and scavengers. The American Eel, *Anguilla rostrata*, and other members of the family Anguillidae feed by cruising close to the bottom and poking their snouts into sediment and crevices. Typical stomach contents after a night's foraging include a variety of small invertebrates and fishes, most of which are inhaled via the standard teleostean process of inertial suction. Occasionally, an eel will be fortunate enough to encounter a dead or dying fish, or a crab that has just molted and has a soft carapace, or a clam with its siphon sticking above the surface. Anguillids lack both the dentition and jaw musculature necessary for chopping up or nibbling at such items. What they do instead is grasp the item in their mouth and try to suction it. If this does not work, they give it a few shakes and tugs. If the item still does not yield, the eel will hold onto the food and rotate rapidly, up to 14 rotations per second (Fig. 19.6). This action twists the food and shears off a smaller piece. If the piece is small enough to swallow, it is suctioned. Otherwise the eel will shake the food some more, or wedge it against the bottom or in a crevice and start spinning again until a small enough piece is removed.

Rotational feeding has been documented for more than 20 fish species, including other anguillids, moray eels (Muraenidae), snake eels (Ophichthidae), conger eels (Congridae), clariid catfishes, rocklings (Phycidae), a rattail (Macrouridae), rice eels (Synbranchidae), a Sablefish (Anoplopomatidae), greenlings (Hexagrammidae), sculpins (Cottidae), pricklebacks (Stichaeidae), gunnels (Pholidae), cod icefishes (Nototheniidae), and dabs (Pleuronectidae). Amphibians that spin include tadpoles, sirens, and caecilians, most of which are eel-like in body form. Even a crocodile engaged in its infamous "death roll" while feeding folds its legs alongside its body when spinning, making it more eel-like. All these species are primarily aquatic.

Moray eels add another option to their food-handling modes. Although capable of shaking and spinning, morays also tie themselves in **knots**. A moray will grab a live prey fish, tie an overhand knot in its tail, quickly run the knot up to its head and lever the knot against the prey. The combined force of the strong jaws, sharp teeth, and pressure from the knot can decapitate a prey fish, disabling it and also making it small enough to swallow. Hagfishes also use knots when tearing chunks from dead fish, although the process is considerably slower. Hagfishes have not been observed spinning.

Both rotational feeding and knotting are closely linked to an elongate body form. Having evolved an eel-like form, species apparently reap the additional benefit of being able

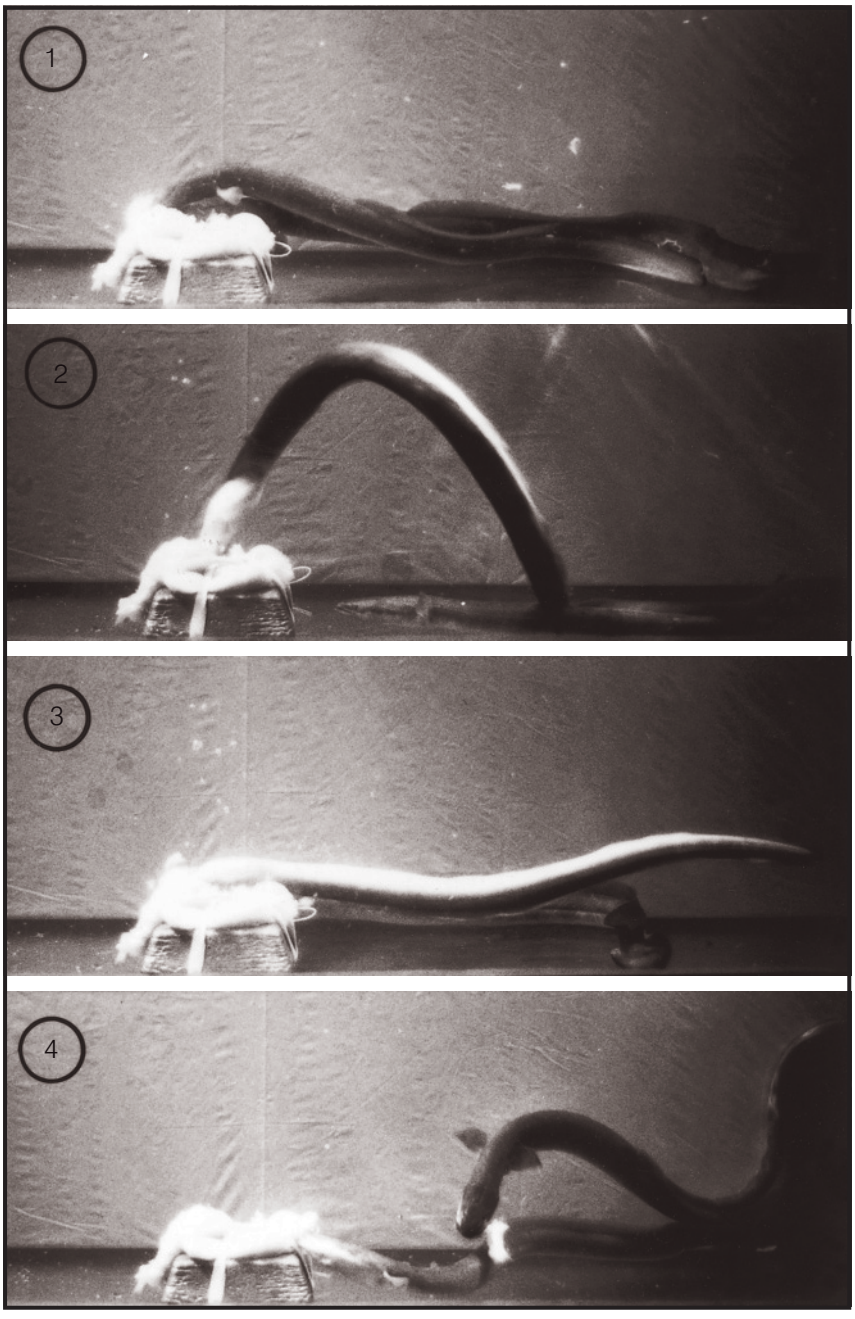


Figure 19.6

Rotational feeding in American Eels. (1) Grasp: a 50 cm eel grasps the bait (a snapper filet tied to a weight). (2) Initial torsion: the eel develops a twist in its body just prior to spinning. Note that the ventral surface of the head (light coloration) faces the camera and the ventral surface of the posterior half of the body faces upward, whereas the dorsal (dark) region between the head and midpoint of the body face the camera. (3) Spinning: after the first initial rotations, spinning continues with no apparent twisting in the body; internal forces generating the spins are not understood. (4) Withdrawal with food; the eel has removed a piece of food and is backing away from the bait. From Helfman and Clark (1986), used with permission.

to spin about their long body axis, an action not available to more conventionally shaped fishes. Without sacrificing the use of suction forces for feeding on common, small prey, rotational feeders can also overcome gape limitation and avail themselves of the occasional jackpot that a recently dead or dying fish represents (Helfman & Clark 1986; Miller 1987, 1989; Helfman 1990; Measey & Herrel 2006; De Schepper et al. 2007).

Figure 19.7
Barracuda teeth typify those of predators capable of actually dismembering prey via cutting. The teeth are pointed, flattened, and sharpened on the edges. They also fit neatly into sockets in the opposite jaw, which facilitates complete closing of the mouth during a bite, perhaps aiding the severing of prey into pieces. Photo by G. Helfman.

supplemented by mechanical grinding in the gizzards of Gizzard Shad (Clupeidae) and mullets (Mugilidae), and the gizzardlike stomach of Milkfish (Chanidae), some characoids (Prochilodontidae, Curimatidae), butterfishes (Stromateidae), and surgeonfishes (Acanthuridae). Deepsea fishes such as black swallowers (Chiasmodontidae) have highly distensible stomachs that expand to accommodate prey considerably longer than the body of the predator (see Chapter 18, The deep sea).

Scavengers, detritivores, and herbivores

Many fishes **scavenge** on dead and dying animals. A few species obtain most of their nutrition through scavenging (e.g., hagfishes) or detritivory (e.g., some minnows and suckers, curimatids, prochilodontids, mullets, some Old World cichlids), whereas others supplement predation and omnivory with scavenging (e.g., catfishes, anguillid eels). Importantly, most predators will not pass up freshly dead prey (otherwise bait would not work in hook-and-line fisheries) and most scavengers and herbivores will take advantage of easily captured live prey. In essence, although dietary specializations certainly exist, fishes are highly opportunistic and will eat available prey of the appropriate size. At Johnston Atoll in the tropical Pacific, discarded doughnuts are eaten readily at the surface by such carnivores as snake eels, butterflyfishes, and flounders, and by such herbivores as damselfishes, parrotfishes, and surgeonfishes (D. A. Mann, pers. comm).

For scavenging animals, the predation cycle is usually shortened to search, wait, manipulate, and handle, whereas for detritivores and herbivores the waiting is eliminated. The major task befalling **detritivores** is one of separating edible, fine particulate organic matter from any refractory, inedible sediments ingested. Ridges in the mouth and a maze of passageways associated with the gill rakers and epibranchial organs accomplish this in characoids. A **winnowing** process occurs in the orobranchial chambers as fishes pick up a mouthful of bottom material, sift it in the mouth, and expel inedible sediments back out the mouth or out the gill openings. Detritivores have some of the longest or most complexly folded intestines of any fishes, attesting to the resistance of detritus to enzymatic digestion (Bowen 1983).

Herbivory occurs less commonly in fishes when compared to mammals and birds. Non-teleostean fishes are exclusively carnivorous, with the possible exception of limited herbivory in the Australian Lungfish, *Neoceratodus forsteri*. In teleosts we find the evolution of **pharyngeal mills** and **gizzards** – mechanisms for rupturing cell walls and digesting plant matter. The most diverse freshwater fish taxa include substantial numbers of herbivorous species (characoids, minnows, catfishes, cichlids), and herbivores on coral reefs are among the most abundant fishes there (e.g., halfbeaks, parrotfishes, blennies, surgeonfishes, rabbitfishes). Temperate waters are relatively lacking in herbivores, although some marine families (porgies, sea chubs, Aplodactylidae, Odacidae, pricklebacks) feed heavily on plant matter (Horn 1989).

Herbivory requires accurate search and efficient handling. Herbivores, particularly those that browse on upright macroalgae and do not graze on finer algal turfs, appear to use visual cues for selecting edible versus inedible species. Herbivory is consequently a primarily daytime activity. Targeted search is necessary because plants defend themselves by being tough or by producing chemicals, often in the form of halogenated terpenoids. Herbivorous fishes show strong preferences among algal types, feeding preferentially on species that lack structural and chemical defenses, while avoiding limestone-encrusted species or algae that contain deterrent chemicals. Some of these chemicals can slow growth or cause death in fishes (Horn 1989; Hay 1991).

Specializations for handling plants relate to the difficulty with which cell walls are disrupted, cellulose is digested, or defensive structures and chemicals are overcome. Herbivorous fishes typically have long guts, high ingestion rates, and rapid gut transit times. Large quantities of plant matter are passed through the gut and relatively little nutrition is assimilated from each ingested fraction. Cell walls are broken down in pharyngeal mills or lyzed in highly acidic (pH as low as 1.5) stomachs, although con-

clusive evidence of enzymes capable of digesting cellulose (i.e., cellulase) is lacking. Unlike insects and many herbivorous vertebrates, fishes also generally lack endosymbiotic bacteria and other microbes that aid in the digestion of plant matter. The exceptions include surgeonfishes, which contain bacteria, flagellates, and peculiar protist-like organisms, and sea chubs (Kyphosidae), which possess a unique digestive tract morphology and a hindgut microflora that aids in digestive fermentation (Fishelson et al. 1985; Rimmer & Wiebe 1987). Interestingly, some sea chubs feed heavily on brown algae that are avoided by most other herbivores (Horn 1989; Kramer & Bryant 1995).

Herbivory on coral reefs is intimately linked to both shoaling and territoriality. Most herbivores either defend exclusive territories (e.g., damselfishes, adult parrotfishes, blennies, surgeonfishes) or roam about the reef in monospecific or heterospecific shoals (sea chubs, parrotfishes, surgeonfishes, rabbitfishes). Territorial defense is very successful against solitary foragers but less so against grouped foragers. Individuals in large groups sustain fewer territorial attacks and have higher feeding rates than solitary foragers or members of small groups. Hence territoriality by some fishes promotes aggregation behavior in others (Robertson et al. 1976; Foster 1985).

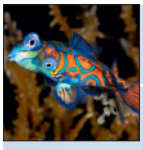
Optimally foraging fishes

Natural selection favors animals that forage efficiently, selecting foods and feeding activities that maximize the ratio of **benefits to costs** (see Hart 1993). Benefits include calories and nutrients ingested, whereas costs involve energy used up, time lost to other activities, or exposure to predators or parasites.

Fishes perform **optimally** when choosing food types, feeding locales and times, and foraging modes. As might be expected, fishes are most selective when presented with an overabundance of high-quality food and progressively less selective as food becomes less abundant or lower in quality. For Bluegill Sunfish presented water fleas (*Daphnia*) of different sizes and at differing densities, only the largest, most profitable prey are eaten when prey are abundant, but all prey are depleted equally and completely when prey are scarce. At intermediate prey densities, the largest zooplankters are consumed first, then the intermediate prey, and finally the smallest, least profitable prey (Werner & Hall 1974).

Fishes have also shown an ability to assess the relative profitability of different food patches and to switch among patches as resources are depleted. When South American cichlids, *Aequidens curviceps*, were presented with two food patches of different profitability, they aggregated in the more profitable patch in direct proportion to the difference in food availability. Fish moved between patches periodically, feeding most where food was most abundant, then switching as food was depleted. Similar results have been obtained in studies of minnows, guppies, and sticklebacks (Godin & Keenleyside 1984; Abrahams 1989).

Natural selection should also produce foragers that choose a method of food handling that gives them the **greatest relative return** for their effort. American Eels employ three modes for handling food. Small pieces of food (<85% of jaw width) can be suctioned into the mouth and swallowed. Larger pieces require dismembering. Large but soft pieces are grasped and shaken until a piece is removed, whereas large, firm foods are grasped and spun (see Fig. 19.7). In terms of net energy return and growth rate, suction is the most profitable and spinning the least profitable food type, with shaking falling somewhere between. When offered food types in a two-way choice situation, eels consistently preferred suction food over shake and spin food, and shake food over spin food, again conforming to the expectations of the cost–benefit approach (Helfman & Winkelman 1991; Helfman 1994).



Summary

SUMMARY

1. Successful predators usually search, pursue, attack, capture, and finally handle prey, using different structures and behaviors at different stages of the predation cycle.
2. Search is active or passive; detection can depend on all six senses. In active search, a fish moves through the water (zooplanktivores, tunas), whereas in passive search, a sedentary, camouflaged predator lies in wait on the bottom or in the water column (scorpionfishes versus gars). Grouped fish find food faster than solitary fish.
3. Pursuit places a predator close enough to attack prey. Chasing-type predators (carangids, billfishes) and ambushing predators (pikes, pike characins) have streamlined bodies and rely on sustained or burst speed to overtake prey. Lie-in-wait predators may use lures (anglerfishes, chacid catfishes) or may even feign death (a cichlid) to bring the prey within striking distance.

4 Attack and capture are often synonymous in fishes. Most fishes use their rapidly protrusible mouth to both overtake and suck in fleeing prey. In a few species, prey are first incapacitated prior to capture (torpedo rays, electric eels, sawfishes, thresher sharks, hammerhead sharks, billfishes). Predators on grouped prey generally try to separate an individual from the group before attacking to overcome the confusion effect.

5 Handling makes prey swallowable and digestible, such as positioning prey so it can be swallowed head-first, or through removal of spines and shells via chewing. Final digestion is mostly chemical in action, although mechanical grinding occurs in those fishes with a gizzardlike structure.

6 Many predatory fishes supplement their diets by scavenging, and some specialists rely primarily on recently dead animals or detritus for food. Handling in scavengers requires the separation of edible from inedible, either in the mouth or stomach. With few exceptions, fishes are gape-limited and cannot attack food larger than they can swallow. Large prey must be dismembered, either by chopping or crushing with the jaw and pharyngeal teeth or, in the case of many eel-like fishes, by twisting or spinning prey until swallowable pieces are broken off.

7 Herbivory is more common in tropical than temperate habitats. Herbivores must be able to identify whether plants are edible, and overcome mechanical and chemical defenses via chewing or chemical digestion; fishes generally lack endosymbiotic bacteria that break down plants. Herbivores tend to have longer guts than carnivores because of the refractory nature of plant material. Territoriality on coral reefs is common among herbivorous fishes and is often overcome by shoaling behavior in competitors.

8 Cost–benefit analyses of foraging behavior have repeatedly indicated that natural selection favors individuals that forage efficiently in terms of food types eaten, feeding locales, and methods of foraging.

Supplementary reading

SUPPLEMENTARY READING

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Chapter 20

Fishes as prey

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The critical tasks facing a prey individual are to avoid detection, evade pursuit, prevent or deflect attack and capture, discourage handling, and ultimately escape from the predator. Just as predators have evolved different adaptations at different phases in the predation cycle, so have prey developed **antipredator tactics** that correspond to cycle phases. Many of these defenses are structural, involving modified body parts or adaptive use of coloration. Other defenses are behavioral, and many defenses combine actions with structures (e.g., Godin 1997a). Defenses generally function to **break the predation cycle**, the earlier the better: an attribute such as camouflage that makes it difficult for the predator to find the prey carries less risk of injury than an attribute such as toxic skin that deters the predator during handling. As an integration of topics covered here and in the previous chapter, we end this chapter with a brief discussion of the trade-offs fishes face when their own feeding activities expose them to the threat of predation.

Avoiding detection

Camouflage

The key to lowering the probability of death during the search phase of predation is to either **avoid detection** by the predator or to **detect the predator first**. In the former case, some form of camouflage is used; in the latter case, the all-important element of surprise is eliminated. The same principles govern camouflage in both predators and prey. The task is often more difficult for prey because, unlike predators that can blend into the background and sit and wait for prey to blunder by, prey fishes must themselves search for food without being detected by predators.

It is obviously advantageous for a fish to not have to flee from a predator. The best way to accomplish this is to avoid detection by the predator in the first place. Fishes avoid detection by visually hunting predators in two chief ways, either by appearing like something **unfishlike** and therefore unrecognizable, or by **disappearing** entirely. In both categories, deception is accomplished through either reduction of **photocontrast** with the background or **disruption of the outline** of the fish. A common form of the first tactic, appearing unfishlike through photocontrast reduction, is called **protective resemblance.** Here a fish matches its background so accurately that it appears to blend in with it. Resemblance is achieved through constant or variable coloration and epidermal body growths that match surrounding objects. As most predatory animals are highly sensitive to movement, protective resemblance is usually enhanced by immobility.

Many examples among fishes of remarkable resemblances to background structures can be given. Sargassumfishes (Antennariidae) and Leafy Seadragons (Syngnathidae) hover amongst and mimic seaweed; seahorses and their relatives demonstrate some of the most spectacular examples of protective resemblance (see Fig. 15.7). Clingfishes (Gobiesocidae), shrimpfishes (Centriscidae), and cardinalfishes (Apogonidae) have long black stripes and hover among the spines of sea urchins. Yellow-spotted Gobies (Gobiidae) with greenish bodies match both the green stalks and yellow polyps of the antipatherian sea whips on which they rest. Agonid sea poachers have rugose bodies covered in brown, orange, black, white, and red that match the

sponge- and algae-covered bottom on which they are found. Green pipefishes (Syngnathidae) and wrasses (Labridae) live among green-stemmed sea grasses. Flatfishes are masters of camouflage, changing color and pattern to resemble a variety of bottom types (e.g., Fujimoto et al. 1991). Predatory fishes also employ protective resemblance and relative immobility as they lie in wait on the bottom for prey (or hide from their own predators). These predators include lizardfishes, goosefishes, stonefishes, scorpionfishes, toadfishes, flatheads, and stargazers.

Crypticity in the above examples usually involves blending into the background. An alternative tactic is to be obvious but to appear as an inedible object. This is achieved by mimicking distasteful or otherwise inedible organisms and objects. Juvenile sweetlips (Haemulidae) and batfish (Ephippidae) have the coloration and unfishlike swimming behavior of flatworms and nudibranchs, and juvenile burrfishes (Tetraodontidae) mimic opisthobranch mollusks. The invertebrates that are mimicked possess skin toxins, are brightly colored, behave conspicuously, and are avoided or rejected by most predatory fishes. Several small fishes mimic small floating sticks, blades of grass, or dead leaves, including juvenile needlefishes, halfbeaks, ephippid batfishes, lobotid tripletails, and adult nandid leaffishes (Randall & Randall 1960; Randall & Emery 1971; Moland et al. 2005; Randall 2005). That many of these instances involve juvenile fishes that "grow out" of a mimetic stage is further evidence of an antipredator function; predation pressure is often strongest on young fishes (see Chapter 24, Predation).

Some special cases involve mimicry of dangerous fishes by otherwise harmless species. The plesiopid *Calloplesiops altivelis* has a dark body with small white spots and a white-ringed ocellus or eye-spot at the posterior base of its dorsal fin (Fig. 20.1). When frightened, it swims into a crevice but leaves the posterior portion of its body in the open, expanding its dorsal, caudal, and anal fins. In this posture, it appears remarkably similar to the protruding head, eye, and mouth of the Turkey Moray eel, *Gymnothorax meleagris*

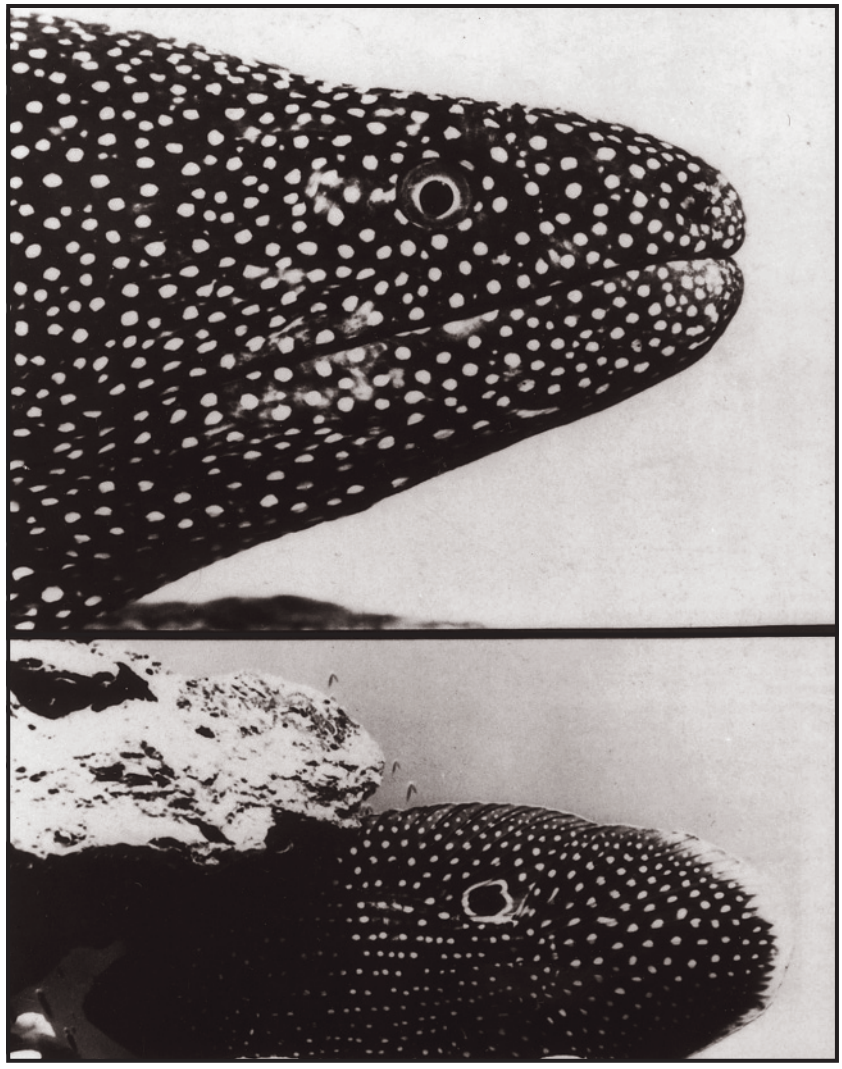


Figure 20.1
The tail region of the plesiopid reef fish *Calloplesiops* (bottom) may intimidate predators by mimicking the head of a moray eel (top), with which it occurs. From McCosker (1977), used with permission.

(Muraenidae), and may thus intimidate potential predators (McCosker 1977).

Another means of appearing unfishlike is to be **disruptively colored**. Vertebrates recognize organisms by their outlines and by the gradual shading differences that exist among regions and features within an outline. A disruptively colored fish has areas of contrasting color, usually black and white, on the body that break up the outline of the fish, making it appear unfishlike. This is one explanation for the bold coloration of some reef fishes such as humbug damselfishes, Rock Beauty Angelfish, and some croakers, as well as the vertical barring and dorsal spots of many shallow water species (sculpins, Black-banded Sunfish, darters, cichlid angelfishes, jacks, barracudas, tunas) that will be viewed by the flickering light of vegetated areas or created by wavelets passing overhead (McFarland & Loew 1983) (Fig. 20.2A). Even strikingly colored reef fishes, along with their less colorful, shallow water counterparts on reefs and in temperate lakes and kelp beds, assume a dark and light, blotchy coloration when resting at night. This disruptive pattern presumably breaks up their outlines and makes them more difficult to discern at low light levels. Disruptive coloration is also a reasonable explanation for the common occurrence of split-head coloration in many lurking predators (Fig. 20.2B) (see Chapter 19, Pursuit).

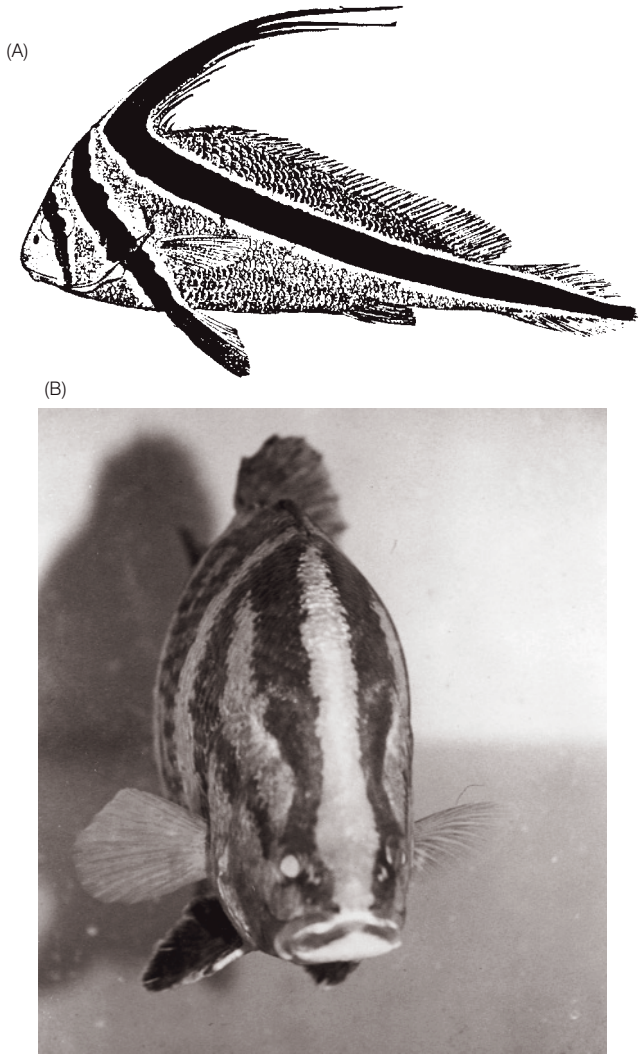
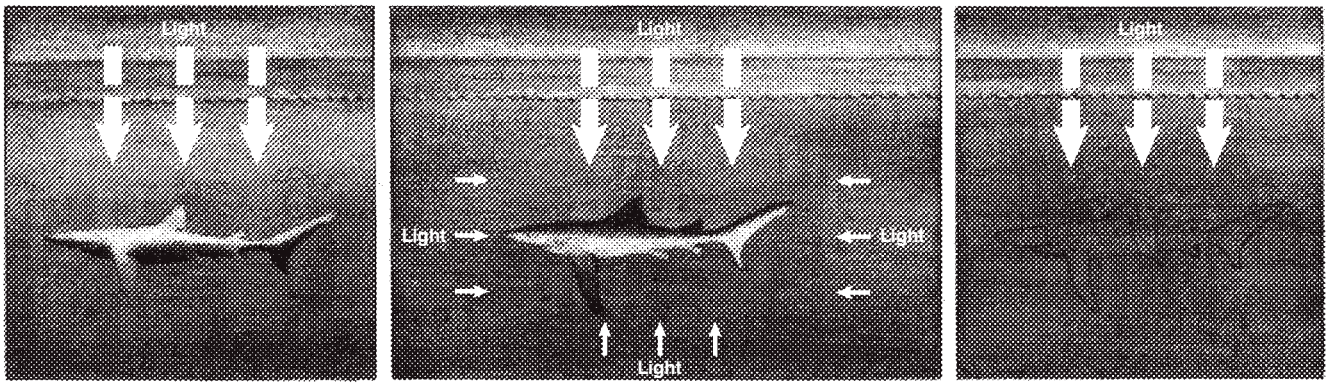


Figure 20.2
Examples and functions of disruptive coloration in fishes. (A) The Jacknife Fish, *Eques lanceolatus*, may use boldly contrasting, dark and light regions to emphasize those parts of its outline that are not fishlike in appearance, thus momentarily confusing a potential predator. (B) Many lurking predators possess a dark or light interorbital stripe that could disrupt their head outline when viewed head-on, making recognition by prey momentarily difficult. This large (*c*. 45 cm) Japanese Snook (probably *Lates japonicus*) has a distinctive, light colored interorbital stripe. (A) from Cott (1957), used with permission; (B) photo by J. DeVivo.

Invisible fishes

Protective resemblance and disruptive coloration are camouflage tactics available to all organisms, regardless of habitat (Cott 1957; Edmunds 1974; Lythgoe 1979). Coloration that makes an animal literally disappear from view, rather than blend in with its background, exploits unique features of the distribution of light underwater. *In air*, all portions of the visible spectrum, from deep blue to deep red (*c*. 400–700 nm) are well represented. Hence objects of all possible colors can be found in most habitats. In addition, brightness varies substantially and irregularly as a function of sun and viewing angle. The brightest part of the sky may be the horizon during early morning and late afternoon. The ground, vegetation, or objects below an observer or viewed laterally may be as bright or brighter than objects overhead.

In water, however, light has a much more predictable distribution, particularly in open water situations where the bottom is not visible. Sunlight is refracted at the water's surface, being bent downward even at relatively low sun angles. Hence the brightest light is consistently directly overhead or **downwelling**. Water molecules act as a powerful filter, both **absorbing** and **scattering** light; light attenuation is even stronger if dissolved or suspended particles that cause turbidity are present. Since all light underwater, with the minor exception of bioluminescence, originates as sunlight, objects viewed from above or horizontally will reflect light that has passed through the water filter. **Upwelling** light consists of light photons that have passed down and then back up again through the water column and is the weakest component; upwelling light is typically only about 1% as strong as downwelling light. Horizontal **space light** is intermediate in strength, but again consists of light that has first passed vertically down and then horizontally through the water; space light is on average about 5% as strong as downwelling light.



(A) (B) (C)

Figure 20.3

Countershaded fishes disappear in the water column because their graded coloration reflects light in a manner that makes them match natural background light. (A) A *uniformly colored* gray fish illuminated primarily from above (= *natural lighting*) would have a relatively bright dorsum and a relatively dark ventrum. (B) A *countershaded* fish viewed under unnaturally uniform illumination, as in flash photography, is not camouflaged because it contrasts with the gradient of illumination of background light. (C) In a *countershaded* fish viewed under *natural lighting* conditions, the gradual transition from dark dorsum to light ventrum, which is opposite to the actual distribution of background light, has an averaging or canceling effect. In this way the top of the fish is seen as dark against dark, the middle as intermediate brightness against intermediate, and the light belly as light against light. All color-background combinations eliminate the contrast between the fish and its background.

The attenuation of light with depth is also very **symmetrical around the vertical**, which means that a diver measuring light at 45° from the vertical will see the same quantity and quality of light whether the meter is pointed at a 45° angle north, south, or in any other direction. Similarly, light measured 90° off vertical (i.e., horizontally) will be identical ahead of and behind a viewer, etc. These two physical characteristics of light in water – **uniform reduction with depth** and **uniform attenuation around the vertical** – are primary influences on fish coloration, particularly in the context of camouflage tactics that render the fish invisible.

Invisibility can be accomplished via three mechanisms: countershading, silvery sides, and transparency. **Countershaded** fishes grade from dark on top to light on the bottom (Fig. 20.3). The actual color or shade of the fish is less important than: (i) the strength of the light that the fish reflects, which differs at different angles from the horizontal; (ii) the background light against which the fish will be compared, and (iii) the viewing angle of the observer. Countershading is easiest to understand when viewing a fish from above. A fish with a dark dorsum absorbs bright downwelling light, thus presenting a dark target against the dark background of dim upwelling light. However, most fishes are viewed by their predators or prey from the side, and here the intricacies of countershading work best. When viewed from slightly above the horizontal, the darker dorsolateral surface of the fish absorbs relatively bright downwelling light, creating a dark target that is seen against the darkened background of slightly upwelling light. Similarly, if viewed from slightly below the horizontal, a light-colored ventrolateral surface reflects weak upwelling light, creating a relatively bright target seen against the lighter background of slightly downwelling light. A countershaded fish disappears into the background because the gradation of its color is opposite to the distribution of light in water, which creates a target that is identical to the background. The fish *reflects light that is roughly equivalent to the background against which it is seen at all viewing angles*, dark against dark, light against light, intermediate against intermediate (Fig. 20.4). The same effect is reached in the mesopelagic region by fishes with dark backs and ventral bioluminescence (see Chapter 18, Energy conservation).

Light direction	Intensity of Light	Intensity of fish reflectivity	Result
Downwelling ↓	+++	−−−	0
↘	++	−−	0
Spacelight →	−	+	0
↗	−−	++	0
Upwelling ↑	−−−	+++	0
Vertical upwelling ↑	−−−−	+++	−

Figure 20.4

Presumed interaction between illumination and reflectivity in countershaded fishes. The "goal" is neutral color with respect to background (= 0 result). +, relatively bright; –, relatively dark; 0, neutral with respect to background. Neutrality is impossible to achieve when viewed from directly below because of the shadow cast by the fish's body.

Countershading makes even more sense if one considers how a uniformly colored fish, or one that has reverse countershading, might appear. A uniformly light-colored fish

would blend into the brighter background when viewed from positions below the horizontal because it would reflect available upwelling light. However, it would reflect even more downwelling light when viewed from above and hence become a bright target viewed against the dark background of weak upwelling light. Conversely, a uniformly dark fish would absorb downwelling light and appear dark against the relatively dark upwelling background, but it would also absorb weak upwelling light and appear as a dark object against a bright background when viewed from below.

Reverse countershading would make the fish conspicuous at all angles of viewing, light against dark from above, and dark against light from below. Reverse countershading occurs in fishes, but these exceptions prove the rule that countershading is camouflage. Many male fishes, such as sticklebacks, sunfishes, cichlids, and wrasses, take on bright dorsal or dark ventral colors during the breeding season, a time when conspicuousness helps them attract females and repel territorial intruders. The best proof-by-exception comes from the reversely countershaded mochokid upside-down catfishes which feed on the undersides of leaves and even swim in open water in an upside-down orientation. A predacious Lake Malawi cichlid, *Tyrannochromis macrostoma*, exhibits reverse countershading and often attacks prey while upside down (Stauffer et al. 1999). Colorful reef fishes often superimpose their bright coloration over a countershaded body and vary the dominant color pattern depending on whether they are engaged in social interactions or avoiding predators (see Box 22.1).

It is not immediately obvious that silvery sides make a fish invisible. **Mirror-sided** fishes include some of the world's most abundant and commercially important species, including herrings, anchovies, minnows, salmons, smelts, silversides, mackerels, and tunas. These and other mirror-sided fishes are predominantly open water, pelagic species that take advantage of the unique light conditions that prevail underwater. To understand how mirror sides work, one must imagine a piece of plate glass suspended in midwater (Fig. 20.5A). The glass is invisible because the background light passes right through it; an observer sees the water column background, not the glass. Because light attenuates uniformly with depth and is distributed symmetrically around the vertical, a flat mirror suspended underwater achieves the same effect as clear glass. The mirror reflects light of an intensity and color that is identical to the light that would be passing through a piece of glass suspended at the same locale, i.e., as if the mirror were not there. Light coming from a 45° angle above the horizontal and reflecting off the mirror and into the eyes of an observer located 45° below horizontal is identical to light that would pass through the mirror if it were clear glass. An observer comparing the light reflected off the fish with the background light sees no difference; the mirror, or fish, consequently disappears into the background.

Crucial to the function of mirror sides is that the fish maintains a vertical orientation at all times, since any deviation from verticality will reflect light that is either brighter or darker than the background (Johnsen & Sosik 2003). Anyone who has watched a school of bait fishes has witnessed periodic bright flashes as individuals deviate from vertical swimming. Mirror-sided fishes maximize verticality by being laterally compressed. The guanine and hypoxanthine crystals that actually reflect the light are embedded in the scales and skin and are stacked together in platelets. The reflecting crystals are separated by a space equal to about one-quarter of the wavelength of the light usually reflected, the theoretical optimum spacing for achieving reflectivity. Whereas the scales and skin conform to the curvature of the body, the **reflecting platelets** in the scales have a vertical orientation, even in regions where the body

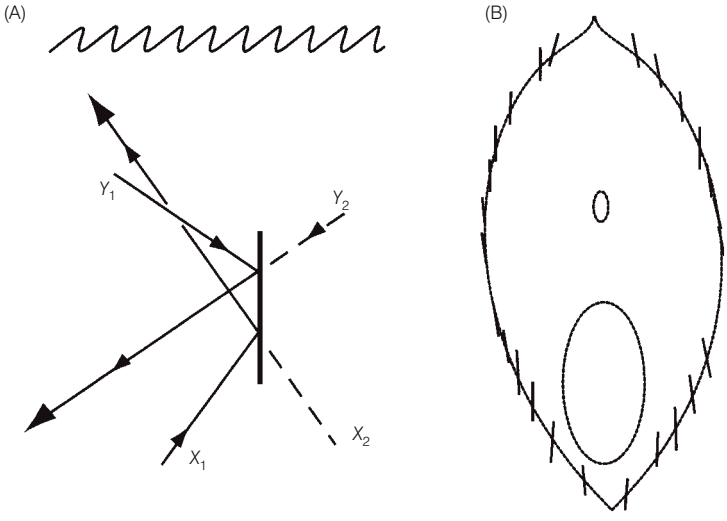


Figure 20.5

The functional morphology of mirror sides in fishes. (A) A clear plate of glass suspended in water is invisible because background light passes directly through it (extensions of dashed lines X_2 and Y_2 to the observer's eyes); an observer sees no difference between the glass plate and its background. A mirror suspended in water also disappears because light reflected off the mirror (solid lines X_1 and Y_1) is identical to the background light that would pass through the object if it were clear (dashed lines). (B) Cross-section through the body of a Bleak (*Alburnus alburnus*) to show orientation of the reflective platelets in silvery fishes. The platelets are embedded in the skin and scales and are oriented vertically, even along the curved surfaces of the fish. After Denton and Nicol (1965).

is curved (Denton & Nicol 1962, 1965; Denton & Land 1971) (Fig. 20.5B).

The third means of achieving invisibility is via relative **transparency**. This is a characteristic of fishes that live in very clear water immediately below the surface where the effects of sun angle are strongest and symmetrical distribution around the vertical is weakest. Halfbeaks and needlefishes fall into this category, along with some specialized freshwater forms such as the X-ray Tetra, *Pristella maxillaris*, and Glass Bloodtail, *Prionobrama filligera* (Characidae); African and Asian Glass Catfish (Schilbeidae, Siluridae); bagrid catfishes in the genera *Chandramara* and *Pelteobagrus*; a gymnotid knifefish, *Eigenmannia*; and the Glass Fish, *Chanda* (Ambassidae).

Larvae and young juveniles of many fishes are pelagic and transparent, their pigmentation developing along with their later habitat preferences (see Chapter 9, Larvae). The body musculature and to some extent the bones of such fishes are translucent and these fishes are consequently difficult to see. However, certain structures, most notably the eye, brain, and gonads, apparently cannot function in a transparent state; the gut also often contains prey that is opaque or quickly turns opaque when digested. These pigmented organs often have a silvery coating. The function of this silver film is poorly understood. It might reflect light as do the silver platelets in scales as described above, or the coating could shield delicate structures from harmful ultraviolet radiation that penetrates into clear, shallow water.

Early detection

Predator–prey interactions often occur over a period of tens of milliseconds. With such rapid reaction times, predators generally require an **element of surprise** to be successful. The element of surprise can be eliminated if prey detect the predator before the predator detects the prey, or at least if the predator is seen before it gets within striking distance. Early detection can be achieved through the collective vigilance of a shoal: fish in shoals detect an approaching predator more quickly than do solitary fish (Magurran et al. 1985; Milinski 1993).

Many shoals, as well as solitary fish, gain a **relative visual advantage** over approaching predators by hovering under structure such as floating logs or vegetation, undercut banks or coral ledges, or overhanging trees or artificial structures such as docks and bridges. Under appropriate conditions, a shaded fish can see an approaching fish in sunlight as much as twice as far away as the sunlit fish can see the shaded fish (Fig. 20.6). This phenomenon can be easily experienced by a diver approaching a ledge or dock; objects in the shadow of the ledge are difficult to discern until the observer swims into the shade of the object. The implications for predators lurking or prey hiding in shade are obvious; a predator approaching a shaded prey fish will lose all of the advantages of surprise because the predator will be spotted long before it can see the prey. Prey careless enough to pass near shaded structure are likely to be captured by predators lurking undetected within the darkened region.

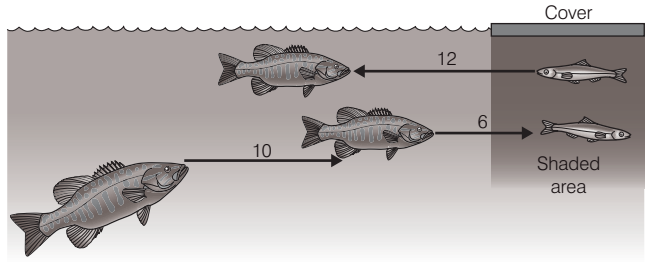


Figure 20.6

The advantage to fishes of hovering in shade. On a sunny day in a lake, a shaded observer has a relative visual advantage over sunlit observers. When horizontal visibility is 10 m, a shaded observer can detect sunlit objects 12 m away, which is approximately 1.2 times better visibility than experienced by a sunlit observer viewing a sunlit target (= a 20% advantage over ambient conditions). More significantly, the sunlit observer cannot see an object in the shade until it is 6 m away, which gives the shaded observer a 100% advantage over the sunlit observer. The relative visual advantage decreases on cloudy days, as does the attractiveness of overhead objects. After Helfman (1979b, 1981a).

The visual advantages and disadvantages around shade arise as a result of physical and physiological phenomena associated with the way in which the vertebrate eye responds to stimuli of different strengths. Vertebrate sensors *adapt rapidly to the strongest background stimulus present*. Sensitivity of the eye to light is determined by the brightest features of the environment: the eye becomes relatively incapable of seeing dimly lit objects against a bright background. An observer in a darkened room is hidden from the view of people in sunlight outside the room, but the sunlit people are easily seen by the shaded voyeur. In water, this effect is heightened by turbidity. As light enters water, it reflects off particles such as phytoplankton and silt. When looking horizontally underwater on a sunny day, particles are particularly obvious as bright blotches. Particles closest to the observer's eyes are the brightest because the light reflected off them travels the shortest distance. Turbidity therefore creates a bright region adjacent to the observer, a **veil of brightness** that intervenes between the eye and more distant targets (Lythgoe 1979). The eye quickly adapts to this bright region, and objects farther away in the darker background of space light become more difficult to detect.

The eye's adaptation to bright background plus veiling brightness combine to explain the relative visual advantage of a fish in shade. The shaded fish's eye is adapted to low illumination levels and hence can see objects in the shade as well as more brightly lit objects outside the shade. Veiling brightness is reduced because the overhead object shades out the sunlight closest to the eye, which eliminates the

strongest component of the veil. Observers in the sunlight have their view obscured by reflecting particles and must see with an eye which has been desensitized to dim light because of the surrounding bright conditions.

Hovering in shade is a tactic commonly employed by resting fishes. Many nocturnally active fishes form **daytime resting schools** in shaded regions by day, including various herrings, silversides, squirrelfishes (Holocentridae), glasseyes (Priacanthidae), snappers, and copper sweepers (Pempheridae). Diurnally active fishes also hover in shade when resting, including various suckers (Catostomidae), centrarchid sunfishes, jacks (Carangidae), and goatfishes (Mullidae). The relative advantage accrues to predators as well as prey and it is not unusual for solitary, lurking predators to hover in shaded areas and strike at prey that pass by (e.g., trout, pickerel, snook (Centropomidae), Largemouth Bass, barracuda).

Shoaling and search

The antipredation benefits of group formation apply to all phases of the predation cycle, including search. Fish in a shoal have a lower probability of being found by a predator than the same fish distributed solitarily (Brock & Riffenberg 1960). Shoals are undoubtedly more conspicuous than solitary fish, so providing no camouflage value, although an inhibitory function may exist because, at the edge of visibility, a shoal may be mistaken for a large fish and therefore be avoided by an approaching predator (Pitcher & Parrish 1993). Shoal formation is probably common in prey fishes because of the necessity to move and find food, particularly among herbivorous and planktivorous fishes. Highly evolved protective resemblance is not an option for such fishes; hence group formation is an alternative.

Upon detection of a predator, fish in shoals typically shift to **polarized, schooling tactics**. Behaviors are emphasized that preserve the integrity of the threatened group (Pitcher & Parrish 1993). Subgroups stream toward the main group (but move as coordinated units, not as individuals), interindividual distances decrease, and movements become synchronized among school members. Heterospecific shoals (those containing more than one species) sort out by species, conspecifics associating with individuals of their own species and size. If few conspecifics exist, members of the minority species may seek shelter rather than wind up as the odd members of a school (e.g., parrotfish, Scaridae; Wolf 1985).

In some situations, members of the prey group will actually move away from the shoal, approach the predator, and then return to the shoal. These **predator inspection visits** have been witnessed in Mosquitofish and Guppies (Poeciliidae), sticklebacks (Gasterosteidae), Bluegills (Centrarchidae), and gobies (Gobiidae). The behavior may: (i) allow prey fish to assess the identity, motivational state, or other traits of the predator; or (ii) inform the predator that it has lost the element of surprise and that an attack is unlikely to be successful (Magurran 1986a).

Prey can also discourage a searching predator by behaving aggressively. Several prey species actually attack potential predators and drive them from the area. This behavior, best known from bird studies and commonly called **mobbing**, has been documented for individuals or groups of squirrelfishes, snappers, grunts, goatfishes, butterflyfishes, damselfishes, wrasses, and surgeonfishes interacting with predatory moray and snake eels, lizardfish, trumpetfish, scorpionfish, stonefish, flatheads, barracuda, and flatfish, and for Bluegill and Longear sunfish and Largemouth Bass interacting with turtles and water snakes. Mobbing fish may contact the head or tail of the predator, or may display in front of the predator by swimming in place and erecting dorsal spines and rolling the body. Mobbing reduces the predation rate in an area because mobbed predators take longer to return to an area than do predators that are ignored (Motta 1983; Ishihara 1987; Hein 1996). Predators may leave an area because the physical attacks of the mobbing fish are injurious or because the actions of the mobbers notify other prey individuals to the presence of the predator, which lowers the predator's potential success in the area, analogous to the alarm calls of birds and small mammals (Helfman 1989).

Either inspection or mobbing might explain why some prey converge on or follow predators immediately after a successful attack on the group. This action has been observed in Yellow Perch attacked by Pike, in snappers attacked by jacks, in bluegill attacked by pickerel, in territorial damselfish attacked by several predators, and in planktivorous damselfish attacked by trumpetfish (Nursall 1973; Potts 1980; Dominey 1983; Ishihara 1987; G. S. Helfman, pers. obs.).

The focus of this discussion has been on avoiding detection by visual predators. However, many nocturnal predators and those that live in turbid habitats rely heavily on acoustic, bioelectrical, and chemical cues to find prey. Pacific Herring, *Clupea pallasii*, respond to sounds such as those emitted by echolocating dolphins by ceasing to feed, dropping in the water column, and schooling actively; fish already in schools drop in the water column and increase their swimming speed (Wilson & Dill 2002). Another clupeid, the American shad, *Alosa sapidissima*, first moves away from an echolocation sound and then swims erratically if the sound strengthens (Popper et al. 2004).

Little else appears to be known about mechanisms for confusing predators or avoiding detection via non-visual channels. In terrestrial environments, both predators and prey possess attributes that function to muffle sounds, such as the serrated feathers on the leading edge of owls' wings, or the pads on the feet of felids (or "quiet as a mouse"). In contrast, sound is difficult to localize underwater. Localization requires some difference in timing or amplitude upon arrival of a sound at members of a pair of receptors. Sound

travels relatively rapidly in water (4.5 times faster than in air) and hence arrives on both sides of a fish at very nearly the same time. Predators often know that prey exist in the area but cannot tell in what direction or how far away. Sharks and a few teleosts (e.g., cod, Gadidae; squirrelfishes, Holocentridae; cutlassfishes, Trichiuridae) have been shown to localize sound and this ability might encourage selection for acoustic dampening structures or behaviors in prey.

Comparatively little is known about the behavioral ecology of electrolocalization (see Chapter 22, Electrical communication), whether prey somehow insulate their electrical output or maximize their ionic similarity with their surroundings to avoid detection by passive and active electrolocators. Chemical detection of prey is well known (see Chapter 6). It has been suggested, although not demonstrated, that the mucous cocoons that many parrotfishes secrete from their gills while resting at night could seal off chemical cues used by predators such as moray eels (Winn & Bardach 1959), although tactile predators could also be deceived or deterred, especially given that parrotfish dash away when the cocoon is contacted (Videler et al. 1999; see Chapter 23, Light-induced activity patterns).

Evading pursuit

Once a predator finds and recognizes prey, pursuit is likely. Antipursuit tactics involve discouraging the predator due to real or feigned unpalatability, shelter seeking, outdistancing or outmaneuvering the predator, or disappearing into the background.

Some fishes possess stout, sharp, sometimes poison-laden spines that can be used in defense against predators. Others possess toxic chemicals in their skin and internal organs. "Noxious" prey typically advertize their unpalatability with coloration and movement that make them and their defenses quite evident. Such **aposematic** ("warning") coloration or behavior is typical of animals that are dangerous or inedible (e.g., many bees, wasps, caterpillars, butterflies, bufonid toads, porcupines, skunks). Deliberate, slow movements aid learning of the warning signal without eliciting attack from predators that are otherwise conditioned to pursue rapidly fleeing prey. By advertizing their inedibility, prey short-circuit the predation cycle at an early phase, saving the energetic costs of flight and the possible injury costs of being handled; predators in turn save time and energy and avoid potential injury or possible death.

Many fishes with obvious defenses have bold or bright coloration that could provide a warning to predators. The scalpel-like enlarged scales in the caudal peduncle of surgeonfishes (Acanthuridae) may be surrounded by a bright yellow or orange patch. Lionfish (Pteroidae) have contrasting red, black, and white fins and a stately posture that accentuates their poisonous fin spines. Weeverfishes (Trachinidae) erect their dark-colored, highly venomous dorsal fins when disturbed. Many pufferfishes (Tetraodontidae, and other tetraodontiforms), including the famous *fugu* puffers served in exclusive Japanese restaurants, contain powerful **tetradotoxins** in their skin, liver, and gonads. These fishes have contrasting rather than countershaded body markings and move about in exposed locations during the day. Some plotosid marine catfishes with exceedingly powerful spine venoms have contrasting dark and light coloration and shoal conspicuously during the day, a very uncatfishlike activity time.

Many zooplanktivores take shelter in bottom structure when pursued by predators. Hence, anthiine serranids, fusiliers (Lutjanidae), butterflyfishes (Chaetodontidae), damselfishes (Pomacentridae), wrasses (Labridae), and surgeonfishes (Acanthuridae) will dive toward the coral when disturbed. Morphology and behavior correlate strongly with vulnerability among these fishes. Small species and small members of large species feed closer to the bottom to compensate for their slower swimming speeds. Species that forage farther from the bottom tend to have more fusiform bodies and more deeply forked tails, both characteristics of faster swimming fishes (Davis & Birdsong 1973; Hobson 1991; see Chapter 8) (Fig. 20.7). Many fishes are permanently associated with holes, cracks, or tubes in the bottom to which they retreat when threatened (e.g., garden eels, Congridae; jawfishes, Opisthognathidae; tilefishes, Malacanthidae; tubeblennies, Chaenopsidae; hover gobies, Gobiidae). A few, such as the razorfishes (*Hemipteronotus*, Labridae), dive into sand with incredible speed. Fishes associated with macrophyte beds in lakes and on reefs typically use the vegetation as shelter when pursued (e.g., centrarchid sunfishes, cichlids, rabbitfishes, kelpfishes).

Evading a pursuing predator in open water requires superior speed or maneuverability. The odds here favor the predator, since predators are of necessity larger than their prey and larger fishes can usually swim faster. Some empirical studies show that prey accelerate faster than predators, perhaps because escape often involves relatively quicker C-start maneuvers whereas a predatory attack utilizes S-start activities (Dominici & Blake 1997). Also, small size enhances maneuverability and permits tactics unavailable to large predators.

To outdistance a predator, small pelagic prey can take advantage of the drag reduction that can be gained by becoming **airborne**, a tactic used most effectively by the exocoetid flyingfishes (Davenport 1994). Flyingfishes commonly double their speed after emerging into the air, accelerating from about 36 km/h in water to as much as 72 km/h while airborne. They typically take off into the wind and travel for 30 s and as far as 400 m in a series of up to 12 flights. Multiple flights are interspersed with periods of rapid taxiing when only the beating, elongate lower lobe of the tail fin contacts the water surface. Fish may reach an altitude of 8 m. Refraction at the water surface makes them undetectable by predators except when a calm sea and

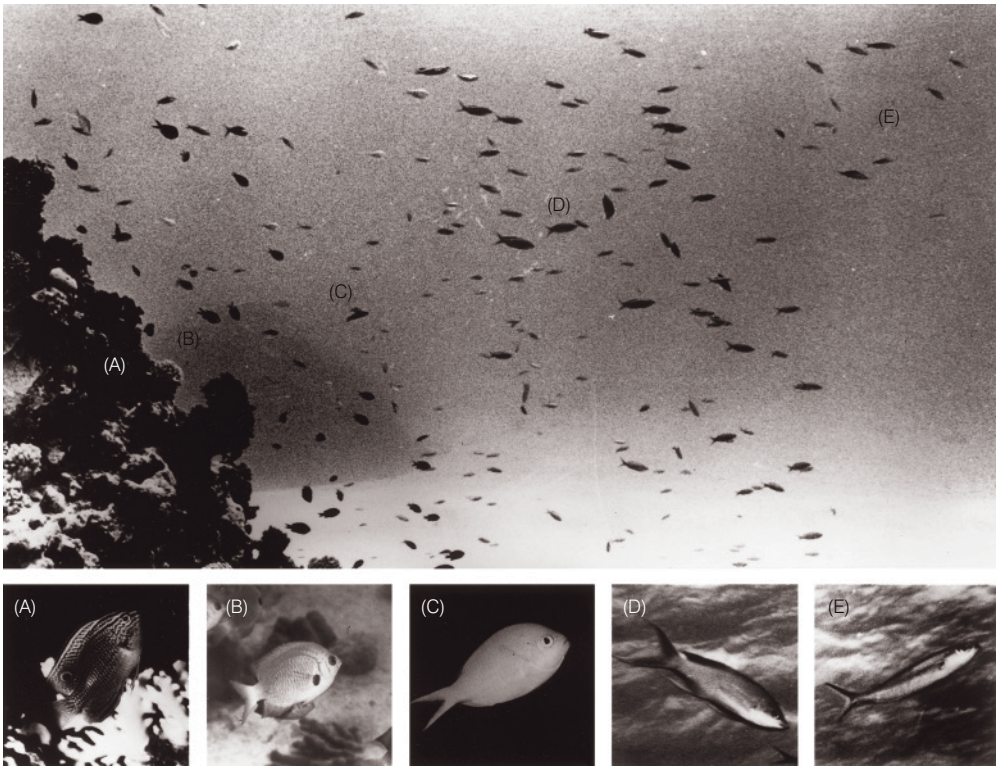


Figure 20.7
Predator avoidance has shaped body morphology in zooplanktivorous reef fishes. Fishes that feed close to protective structure tend to be more deep-bodied with square or rounded tails, those that forage higher in the water column are more streamlined with forked tails. All these fishes dive for the coral when threatened by predators. Streamlining may also facilitate holding the fish's position in the stronger currents higher above the reef. Lettering on the photograph of the reef indicates the zones where the five different fishes typically feed: (A–C) damselfishes (pomacentrids), (D) *Anthias* (a serranid), (E) *Pterocaesio* (a lutjanid). From Hobson (1991), used with permission.

bright sun create a visible shadow. Hence the flyingfish's re-entry point would be largely unpredictable, particularly if it followed a curving flight path. Flyingfishes glide rather than fly, gliding efficiency depending largely on wing surface area divided by body mass. Flyingfishes come in two-winged varieties with enlarged, cambered (curved) pectoral fins and four-winged varieties that also have enlarged pelvic fins. These fishes are of necessity small, never exceeding 50 cm in length. A 100 g flying fish has a total pectoral fin surface area of about 200 cm^2. For a 100 kg tuna to have proportionally large lifting surfaces, its pectoral fins would each have to be about 100,000 cm^2 in area.

Other "flying" fishes include the African freshwater Butterflyfish, *Pantodon* (Osteoglossidae), and the South American freshwater hatchetfishes (Gasteropelecidae), the latter species generating flying forces by vibrating its pectoral fins via pectoral muscles that may account for 25% of its body weight. The greatly enlarged pectoral fins of adult dactylopterid flying gurnards are expanded during cruising over the bottom; these fish have never been observed airborne. Many fishes leap into the air when escaping predators, including minnows (Cyprinidae), halfbeaks (Hemiramphidae), needlefishes (Belonidae), sauries (Scomberesocidae), cyprinodontids, atherinids, Bluefish (Pomatomidae), mullets (Mugillidae), and tunas and mackerels (Scombridae). And some predators (dolphinfishes, mackerels, tunas, billfishes) leap into the air in horizontal pursuit of prey, but how these leaps are timed and aimed remains unstudied. Flyingfishes do have one advantage over airborne predators: a flyingfish's cornea is flattened, which gives it the ability to focus both in water and air. Other fishes have a curved cornea, which only allows focusing in water. A remarkable convergence on the "flyingfish morphology" occurred among at least one chondrostean in the Triassic. The perleidiform, *Thoracopterus*, possessed expanded pectoral and pelvic fins, a longer lower caudal lobe, and other traits suggesting that it too glided out of the water (see Fig. 11.21).

Preventing and deflecting attacks

When actually attacked, a prey fish can make a quick evasive move, employ an active defense, rely on passive structural defenses to deflect the predator, or use a combination of actions. Rapid, **fast start** escape movements that lead to maximal acceleration away from the attacking predator are almost universal among fishes, developing early in the ontogeny of larvae and continuing to function into adulthood relatively unchanged (Webb 1986). Fast start escape movements occur in response to visual, acoustic, tactile, electrical, and water displacement stimuli. The reaction to water displacement is significant since many predators of small fishes use suction feeding, which means that a larva would experience the water around it suddenly moving toward a predator. Anatomical and behavioral features of this escape response indicate that it operates near the

physical and temporal limits of nerve conduction and muscle contraction, emphasizing the importance of predation during early life as well as later in most fishes.

Responses of aggregated prey

Shoals under attack perform a series of identifiable maneuvers, elements of which have been noted for groups of minnows and shiners (Cyprinidae), Yellow Perch (Percidae), snappers (Lutjanidae), and sand lances (Ammodytidae), among others (Pitcher & Parrish 1993). The tactic employed is dependent on the type of predator and the intensity of its attack (Fig. 20.8). Shoals generally avoid a slowly approaching predator by maintaining about a 5–15 prey body length space between the predator and the group. Often predators will swim slowly through a prey school, at which time the school separates ahead of the predator and then closes back together behind it, basically creating a prey-free vacuole around the predator. The function of the predator's slow maneuver is unclear; possibly the predator is testing for injured prey or hoping to catch an inattentive individual off guard. In more concerted attacks, prey expand rapidly out from the point of attack, scattering in different directions and fleeing the scene or seeking refuge in nearby structure.

Group membership may reduce the statistical likelihood of an individual being attacked by a predator, producing a **dilution** or **attack abatement effect**. If a predator only consumes one or a few prey once it encounters a group, then the likelihood of any one individual being eaten decreases as group size increases. An additional benefit of grouping includes the passage of information about a predator to individuals unexposed to the predator. This is termed the **Trafalgar effect**, after the Battle of Trafalgar, when Admiral Nelson sent information through his fleet using flag codes, informing ships on the far side of the fleet about the enemy's actions (Pitcher & Parrish 1993).

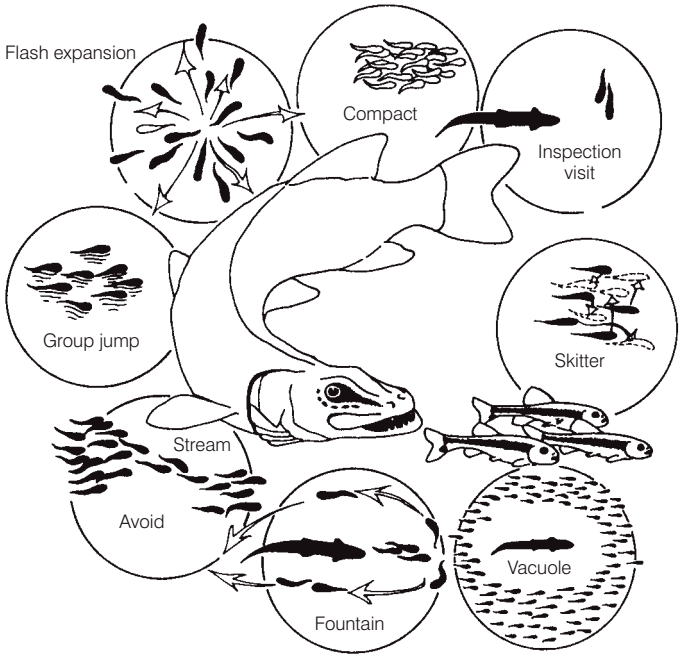


Figure 20.8
The graded responses of minnows under attack. Responses increase in intensity as the predator's actions become more threatening. The hierarchy of responses begins at the top ("compact") and proceeds clockwise to "flash expansion". From Magurran and Pitcher (1987), used with permission.

The most widely demonstrated cause of a decrease in predator success is the **confusion effect**. In studies with Largemouth Bass feeding on minnows, Pike feeding on perch, sticklebacks feeding on water fleas, and jacks feeding on anchovies (Godin 1986; Landeau & Terborgh 1986), it has been shown that predators catch fewer prey from large than from small schools. Success declines because the predator switches targets as it moves through the school, apparently confused by the number of multiple, edible objects moving across its field of vision. Specific behaviors seemingly function to increase confusion. In **skittering**, as displayed by minnows, an individual accelerates rapidly, rises in the water column, and then quickly rejoins the group. **Protean** behavior, seen in anchovies and silversides (Engraulidae, Atherinopsidae, Atherinidae), involves quick, uncoordinated up-and-down movements by several adjacent individuals just prior to resumption of polarized schooling. **Roll-and-flash**, often seen in herring (Clupeidae) schools, occurs when an individual rotates on its long body axis and reflects bright sunlight; it then returns to a normal upright position. The eye is quickly drawn to the point of the flash, but the fish seemingly disappears when upright orientation is resumed (a similar distractive function has been proposed for ink-squirting in octopods and squid under attack). The physiological basis of the confusion effect is poorly understood, although it may relate to an "information overload" problem whereby the predator's capacity for processing information is exhausted by the sheer number of objects in the visual field (Milinski 1990). Both invertebrate and vertebrate predators are subject to the confusion effect, as anyone who has ever attempted to net individual fish from a school in a large aquarium can attest. Not surprisingly, prey fish choose to join the larger of two schools when given an opportunity, and the speed at which this decision is made increases when predators are present (Hager & Helfman 1991).

Discouraging capture and handling

Capture refers to initial ingestion of the prey; in fishes this involves taking the prey into the mouth. Defenses against capture exploit the gape limitation that constrains most predators to feeding on prey small enough to be swallowed whole (see Box 19.2). Hence many anticapture adaptations

involve permanent or temporary increases in prey body size and elaboration of body armor that make it difficult to: (i) bring prey into the mouth; (ii) close the mouth once the prey are there; or (iii) swallow captured prey. Many fishes have dorsal and anal fins that appear out of proportion to their bodies, or bodies with exaggerated depth, such as citharinids, silver dollars (Characidae), veliferids, snipefishes (Macrorhamphosidae), crappies (Centrarchidae), fanfishes (Bramidae), manefish (Caristiidae), butterflyfishes (Chaetodontidae), tangs (Acanthuridae), Moorish Idols (Zanclidae), and spikefishes (Triacanthodidae). The exaggerated body humps on endemic Colorado River suckers and minnows have been interpreted as an evolved defense against gape-limited Colorado Pikeminnows (Portz & Tyus 2004; see Fig. 26.3). Greatly elongate dorsal, pelvic, and anal fins in many larval fishes (e.g., ribbonfishes, seabasses) may also function to reduce predation. Spiny pufferfishes increase their body depth and volume by inflating their stomachs with water and erecting their spines; the spines are modified scales with three-pronged, interlocking bases embedded in the puffer's skin that prevent their depression (Box 20.1).

The evolutionary development of spines that defines the Acanthopterygii accomplishes a similar defense. Predators

Box 20.1

BOX 20.1

The functional morphology of pufferfish inflation

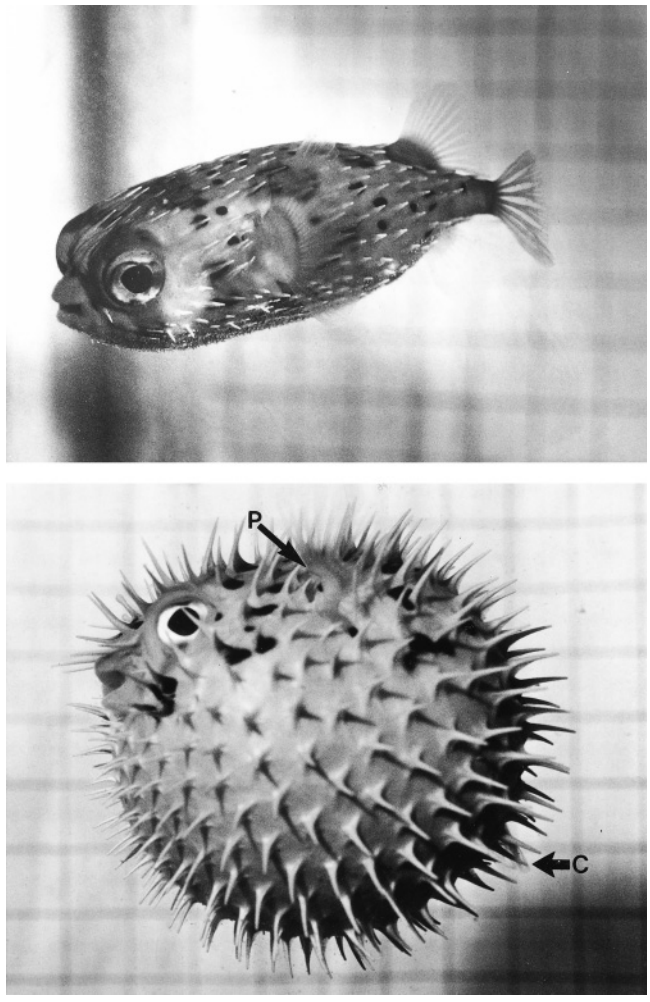
Camouflage, due to countershading, disruptive coloration, or invisibility, functions during the search and detection phases of predatory behavior. Many fishes have placed less emphasis on crypticity and instead discourage attacks using traits that make them less desirable as prey. The scales and spines of squirrelfishes, lionfishes, rabbitfishes, and surgeonfishes, among many others, provide such mechanical defenses. Antihandling adaptations reach an extreme of specialization in the porcupinefishes, balloonfishes, and spiny pufferfishes (Diodontidae), where jaw musculature and bones, skin, stomach, scales, body musculature, and peritoneal cavity have all been modified to contribute to a coordinated defensive tactic in which a threatened fish turns itself into an inedible, spiny sphere (Brainerd 1992; Wainwright et al. 1995).

Balloonfish, in response to attacks by fishes or birds, increase their volume three-fold by pumping water or air into their stomach (Fig. 20.9). The pumping mechanism involves rhythmic mouth cavity expansions and compressions that are driven by specialized muscles and unique couplings of the mouth floor, branchiostegals, and pectoral girdle. Pumping is rapid, taking about 15 s and 40 separate puffs to complete. Stomach pressure and the force exerted by each puff increase as the stomach fills, analogous to a human inflating a balloon. The stomach, which has lost its digestive function, rests in a folded state and then expands 50–100-fold when filled with water. When a balloonfish is fully inflated, the unique peritoneal cavity, now filled by the expanded stomach, extends anteriorly to the tip of the dentary, dorsally around the body musculature, and posteriorly around the dorsal and anal fins. In related tetraodontiforms that do not puff up, such as triggerfishes, the peritoneal cavity is limited to the anterior ventral quarter of the body.

The skin of the balloonfish plays an integral role during inflation. Both the dermis and epidermis contain numerous internal microfolds that make a puffer's skin highly stretchable. The skin can stretch about eight times more than other types of fish skin. When the skin is finally stretched to the point of stiffening, this rigidity aids in the erection and anchoring of the spines. The spines themselves are modified scales, and are among the longest and most elaborate of all teleost scales. Collagen fibers in the skin attach to a forward pointing process at the base of each spine. As the skin is stretched, a posterior pulling force is applied to the forward pointing process, levering the spine into an erect position. In most fishes, the skin is tightly bound to the body musculature by a cross-helix of collagen fibers and may serve as an external tendon that contributes to locomotion (see Chapter 8, Locomotion: movement and shape). In conjunction with high stretchability, the skin of the balloonfish lacks such tight attachment to the underlying musculature, and the special orientation of the collagen fibers in the dermis prevents the transmission of force from muscles to skin. Locomotory capability has been traded off in favor of inflation; puffers consequently swim via a unique combination of pectoral and median fin undulations referred to as "diodontiform" swimming, which is a modified form of tetraodontiform swimming (see Table 8.1). In an inflated balloonfish, which is more spherical than any other vertebrate, a "stiff skin surrounding a ball of incompressible water provides a rigid framework for the support of the spines", creating an object too large and too difficult for most predators to swallow (Brainerd 1992, p. 17a).

Figure 20.9

Balloonfish inflate themselves with water in response to being handled by potential predators. They undergo a three-fold increase in volume, which turns them into a sphere with projecting spines. Extremities that might offer a predator a grasping point, such as the caudal (C), pectoral (P), and other fins, sit largely within the protective framework of the spines when the fish is inflated. Inflation occurs as water is pumped into the stomach, which expands up to 100-fold to fill an unusually large peritoneal space. The spines are embedded in a highly derived, stretchable skin. From Brainerd (1992), used with permission.



focus their attacks on the center of mass of the body, which is often where the prey's body is deepest; this depth is increased by erectable spines. A temporary increase in depth can be achieved by erecting the dorsal, pelvic, and anal fins with their stiff armament. A Bluegill Sunfish increases its body depth by about 40% by erecting its fins, making it a larger and hence less desirable food item for most predators. Erecting fins as a predator approaches may be a way of discouraging the predator before it attacks.

The effectiveness of erected spines in preventing passage of prey towards the predator's throat can be enhanced by additional structures. Sticklebacks lodge themselves in the mouths of predators such as pike by locking their dorsal and pelvic spines, forcing the predator to break the spines before swallowing can occur. In leiognathid ponyfishes, the dorsal and anal fin spines, positioned opposite one another where the body depth is greatest, have a locking mechanism (Nelson 2006). Triggerfishes link the first two dorsal spines to prevent depression of the dorsal fin. Triggerfishes can wedge themselves into a crevice or a predator's mouth and lock the spines; the second spine (the "trigger") has to be pushed posteriorly to depress the dorsal fin (see Chapter 15, Order Tetraodontiformes; Fig. 15.27). Indo-Pacific rabbitfishes (Siganidae) possess several unusual spine adaptations. The first dorsal spine points forward ("retrorse") instead of up, which could inhibit head-first swallowing by predators, and each pelvic fin has hard spines at the leading and trailing edge of the fin. These are difficult fish to handle without getting punctured and the spines are covered with a toxic slime that causes painful wounds, at least in humans.

Most defensive morphological traits appear to be evolved responses to the threat of predation, such as

pelvic spine length and degree of armor plating of sticklebacks in populations that vary in predation pressure (e.g., Vamosi 2005). However, other adaptations involve more immediate phenotypic changes induced in individuals by predators. Crucian Carp (*Carassius carassius*), Eurasian Perch (*Perca fluviatilis*), and Roach (*Rutilus rutilus*) have been shown experimentally to react to the presence of predators by changing body proportions or fin placement and shape. Carp and perch increase body depth during growth, whereas roach move the dorsal fin posteriorly and the pelvic fins anteriorly and widen the anal fin. Although these responses are complicated by intervening variables of food availability and population density, the evidence indicates that the changes are induced by chemicals released by predators. Increased body depth would make prey harder to swallow, and the fin changes in roach are thought to improve swimming ability during escape (Holopainen et al. 1997; Eklöv & Jonsson 2007).

Dermal and epidermal defenses also play an important role in resisting capture and in complicating handling. Many fishes exude mucus upon capture. This slime may make the fish slippery and harder to hold (hagfishes, anguillid eels), but in many the slime or other skin secretions contain distasteful substances that cause rejection by the predator (some moray eels, Muraenidae; marine catfishes, Ariidae; toadfishes, Batrachoididae; clingfishes, Gobiesocidae; soapfishes, Serranidae; gobies, Gobiidae; trunkfishes, Ostraciidae) (Hori et al. 1979; Smith 1992; Shephard 1994). Coral reef gobies in the genus *Gobiodon* secrete skin toxins that cause loss of equilibrium and even death in predators (Schubert et al. 2003). The toxins are water soluble, thus maximizing their detectability to nearby potential enemies. Toxicity varies across species, the most toxic gobies being the most active and brightest colored, again corresponding with predation risk. Goby skin toxins may also affect the attachment behavior of external parasites (Munday et al. 2003). In certain soleid flatfishes, toxic steroid aminoglycosides secreted from glands at the base of the dorsal and anal fins have a repellent effect on predators such as sharks (Primor et al. 1978; Tachibana et al. 1984).

External defenses in some species include a thickened or hardened dermis (e.g., the ganoid scales of lepisosteid gars and polypterid bichirs, the carapace made up of scale plates in ostraciid boxfishes, and the toughened skin of balistid leatherjackets). Populations of Three-spine Sticklebacks, *Gasterosteus aculeatus* (Gasterosteidae), that co-occur with predators have more lateral bony scutes and longer dorsal spines than do comparatively predator-free populations (Reimchen 1983; FitzGerald & Wootton 1993). Many shoaling species have easily dislodged, deciduous scales which may allow them to slip away from predators, analogous to the easily shed wing scales of moths and butterflies.

A special case of a handling-induced antipredator response in shoaling fishes and a few other species is the production of and reaction to alarm chemicals. **Alarm reactions** are best known in ostariophysans, where they were first discovered (see Chapter 14, Subdivision Otocephala, Superorder Ostariophysi). Substances and reactions also occur in some salmonids, livebearers, sculpins, darters, Yellow Perch, cichlids, and gobies, and are suspected in galaxiids, killifishes, and silversides (Smith 1986, 1992; Chivers & Smith 1998; Brown 2003). The **alarm substance** is released when the skin of a fish is broken, such as during a predatory attack.

Reactions depend on the species and the situation. Shoaling fishes often react by schooling tightly and moving away from the area where the alarm substance is released. Some solitary cyprinids sink to the bottom, whereas benthic species (gudgeon, Cyprinidae; loach, Cobitidae; suckers, Catostomidae) freeze in place, utilizing their cryptic coloration to avoid detection. When alarm substances are in the water, overhead predators cause shiners (Cyprinidae) to hide in vegetation, whereas fish predators elicit a strong schooling response. The alarm reaction spreads as additional individuals detect the alarm substance or as they react visually to schoolmates. Many fishes show an alarm reaction to water in which predators have been kept, indicating again the probable importance of chemical interactions among fishes (see Chapter 22, Chemical communication); some minnows even show alarm reactions when exposed to the feces of a predator that has fed on conspecifics (Brown et al. 1995). Juvenile convict cichlids, *Archocentrus nigrofasciatus*, show increasing levels of alarm reaction to increased concentrations of alarm substance (Brown et al. 2006).

Some fishes use nonchemical channels to transmit alarm signals. Visual signals induced by predators include increased fin flicking rates in schooling characins and in parental cichlids guarding young, head bobbing by gobies, and inspection visits and mobbing as discussed above. Many fishes emit **distress sounds** when held, prodded, or speared (e.g., catfishes, grunts, drums, triggerfishes). At least three families of fishes (cods, squirrelfishes, groupers) produce distinctive sounds when confronted with predators. Squirrelfishes produce a staccato sound that causes conspecifics to take refuge or inspect the predator (Myrberg 1981; Smith 1992).

The adaptive significance of responding to an alarm signal is obvious: it is advantageous to know that a predator is active in an area and to take appropriate action. Coordinated flight behavior within a school lessens a predator's chance of additional success. Further exploration of prey responses have shown additional benefits, including facilitated learning and recognition of predators and dangerous habitats, induced morphological changes in prey, and adap-

tive shifts in life history characteristics (e.g., Chivers & Smith 1998).

The evolution of an ability to generate an alarm substance or signal is more problematic. Unless there is a high probability that schoolmates are close genetic relatives (e.g., **kin selection**), little benefit accrues to an altruistic, injured individual that produces an alarm substance and is consequently deserted by its schoolmates. One possible advantage to producing a rapidly diffusing alarm chemical is that it might attract other predators, including predators larger than the one that caused the initial injury. Such larger predators could frighten the initial attacker into leaving the area, thus allowing the injured prey to escape (Mathis et al. 1995, Chivers et al. 1996; see Chapter 22, Acoustic communication).

Balancing foraging against predatory threat

It is important to realize that most predators are also prey and that foraging decisions often must be made in the context of danger to the feeder. These conflicting demands create a **foraging–predation risk trade-off**. What evidence exists to suggest that foraging fishes take into account risk to their own survival when choosing among food types, locales, and methods? Sticklebacks feed more slowly and gobies eat less in the presence of predators, even when the predators are behind a transparent partition (Magnhagen 1988; Milinski 1993). Juvenile Coho Salmon are less willing to travel long distances to intercept floating prey when presented with photographs of large predatory trout (Dill & Fraser 1984). Juvenile Black Surfperch (Embiotocidae) shift from feeding in low-growing, exposed algae when predatory kelp bass (Serranidae) are absent to feeding in tall, bushy algae when predators are present (Holbrook & Schmitt 1988a). Herbivorous minnows and loricariid catfishes abandon shallow areas of high algal productivity for deeper, less productive areas to avoid both predatory birds and fishes (Power 1987). Juvenile Bluegill grow fastest when feeding in open water on zooplankton. When Largemouth Bass are released in the open water areas, smaller, more vulnerable Bluegill move into vegetated areas where they have lower mortality rates from predation but also grow more slowly because of lower food intake. Bluegill too large to be swallowed by the bass remain in the open water areas (Werner et al. 1983). Similar trade-offs and attendant costs have been shown in such fishes as Ocean Pout and Guppies (e.g., Botham et al. 2006; Killen & Brown 2006).

The balance between foraging and predation risk is shown by studies that vary the degree of threat and the strength of the reward. Minnows and surfperch will risk feeding in patches where predators are present if food densities are high; otherwise they avoid patches with predators (Gilliam & Fraser 1987; Holbrook & Schmitt 1988b). Additional factors can affect the decision process. Hunger or parasite loads cause sticklebacks to resume feeding sooner after exposure to predators and also cause fishes to feed closer to potential predators (Godin & Sproul 1988; Milinski 1993). When offered food in the presence of a cichlid predator, female Guppies will accept more risk for more reward whereas male Guppies avoid the predator regardless of food availability, implying that reproductive output is more dependent on food intake in females than in males (Abrahams & Dill 1989; see also Chapters 21, 22).

Finally, prey fish do not feed or avoid predators in an all-or-nothing fashion. They appear to weigh the potential threat from a predator and to take action appropriate to the degree of threat. This **threat sensitivity** is evident in individuals and groups. Territorial damselfishes respond more strongly to larger than to smaller predators and to predators in a strike pose than to searching predators. The strength of the flight behavior elicited also increases as the predator draws closer (Helfman 1989). Minnows in shoals also employ a graded series of escape responses that increase in strength and effectiveness as a pike escalates its attack (see Fig. 20.8), and sticklebacks spend progressively less time foraging as predatory trout increase in number (Fraser & Huntingford 1986; Magurran & Pitcher 1987). Threat sensitivity – to chemical and visual cues and sometimes involving learning by observing avoidance behavior in conspecifics – has also been shown in rainbowfish, sticklebacks, sculpins, and cichlids (Bishop 1992; Brown & Warburton 1997; Chivers et al. 2001; Brown et al. 2006). Threat sensitivity makes good Darwinian sense. A prey individual that is capable of assessing just how threatening a predator is and that is able to devote an appropriate amount of time and energy avoiding the predator will have more time for other fitness-influencing activities (feeding, breeding, defending a territory or young) than will an individual that flees or hides any time a predator arrives in the area.

Summary

SUMMARY

1. To escape predators, prey must avoid detection, evade pursuit, prevent or deflect attack and capture, and discourage handling. Different behaviors and structures achieve these different functions. Detection is avoided by various types of camouflage that make a prey appear unfishlike or inedible, blend into its background, or just disappear. Tactics employed include protective resemblance, mimicry, disruptive coloration, countershading, mirror sides, and transparency. Shoaling may increase the ability of prey to detect and assess approaching predators, as does hovering under shade-producing objects.
2. To discourage pursuit, a prey fish can demonstrate or feign unpalatability, outdistance or outmaneuver the predator, or seek shelter in the bottom, in vegetation, or in the water column. Some fishes with toxic skin or spines advertise these structures via color or behavior (surgeonfishes, lionfishes, weeverfishes, pufferfishes). Many fishes dive into holes in coral or rocks or into the sand when pursued. Open water species must outdistance a predator; flyingfishes leap from the water and glide at twice their swimming speed.
3. An attack can be prevented by quick evasive action, or by active or passive defense. Rapid, fast start moves are almost universal among fishes from early ontogeny on. Schooling fishes undergo a series of maneuvers when attacked; aggregating functions particularly well during attack because multiple targets presented by the prey confuse the predator.
4. Capture is commonly discouraged by exploiting the gape limitation of most predators. Prey fishes increase their body size by erecting their spines. Balloonfishes combine an inflatable stomach, stretchable skin, and scales modified into long, stout spines to create an inedible object. Easily displaced scales may allow prey to slip out of the mouth of a predator. Slime and toxic or distasteful skin secretions also discourage capture (moray eels, toadfishes, soapfishes, soleid soles, trunkfishes). Specialized skin cells in ostariophysan and a few other fishes secrete an alarm substance that warns schoolmates of an attack. Alarm substances and alarm calls may also attract secondary predators, which could frighten the first predator into releasing a victim.
5. Foraging places fishes at risk of becoming prey themselves. Thus many fishes must trade-off their own foraging against the risk of predation. Experimental studies have shown that fishes often give up foraging opportunities when threatened by predators, but will risk greater threats when exceptionally hungry or when the rewards are high enough. Prey are sensitive to the degree of threat presented by a predator and are able to take evasive action proportional to the degree of threat.

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Chapter 21

Fishes as social animals: reproduction

Chapter contents

CHAPTER CONTENTS

Evolutionary success is determined by an individual's ability to place genes in future generations, relative to the success of conspecifics. To transmit genes, individuals must mate with conspecifics. However, many fish species are relatively solitary as adults. During breeding seasons, fish must overcome individualistic habits and seek out potential mating partners. Suitable spawning habitats and substrates must be found or even modified into nests, activities of males and females must be synchronized, and tactics for avoiding hybridization (**species isolating mechanisms**) should be employed. Aggregations of reproductively active individuals create potential competition for spawning sites and partners, eliciting territorial and mate choice behavior. Courting and spawning may distract the attention of participants and thus make them more vulnerable to predators. After spawning, many species engage in varying degrees of parental care. All these activities and characteristics constitute the diverse mating systems of fishes. Our emphasis here will be on the diversity of mating systems, with focus on patterns and adaptations where they can be identified.

Reproductive patterns among fishes

Important components of a **breeding system** include frequency of mating, number of partners, and gender role of average individuals (Table 21.1). Fishes show greater diversity in these traits than do other vertebrates. Most fishes follow the mammalian and avian norm of remaining one gender throughout adult life, but many fish species change sex and some are parthenogenetic, producing young from unfertilized eggs (see Chapter 10, Determination, differentiation, and maturation; Chapter 24, Life histories and reproductive ecology). Some fishes retain a single mate, perhaps for life, others mate promiscuously, and a few are haremic. And in some fishes, a single breeding system may not characterize the entire species.

Lifetime reproductive opportunities

Most fishes are **iteroparous**, spawning more than once during their lives (e.g., sharks, lungfishes, sturgeons, gars, tarpons, minnows, trouts, codfishes, seabasses). However, some well-known species are **semelparous**, spawning one time and dying. Semelparity characterizes most salmon of the genus *Oncorhynchus* (e.g., Pink, Chum, Chinook, Coho, and Sockeye salmon). These fishes hatch in fresh water, migrate to the sea for a period of 1–4 years, and then return to their **natal** (birth) stream where they spawn and die. Although the life cycle of females appears to be relatively fixed across a species, intrapopulational

Table 21.1

A summary of components of breeding systems in fishes, with representative taxa. Accurate categorization is often hampered by the difficulty of following individual fish over extended periods in the wild. Although families are listed for some components, exceptions are common within a family. Modified from Wootton (1990), used with permission.

I. *Number of breeding opportunities*
- A. Semelparous (spawn once and die): lampreys, river eels, some South American knifefishes, Pacific salmons, Capelin
- B. Iteroparous (multiple spawnings):
  1. A single, extended spawning season: most annuals (rivulines)
  2. Multiple spawning seasons: most species (elasmobranchs, lungfishes, perciforms)

II. *Mating system*
- A. Promiscuous (both sexes with multiple partners during breeding season): herrings, livebearers, sticklebacks, greenlings, epinepheline seabasses, damselfishes, wrasses, surgeonfishes
- B. Polygamous:
  1. Polygyny (male has multiple partners each breeding season): sculpins, sunfishes, darters, most cichlids; or polygyny (haremic): serranine seabasses, angelfishes, hawkfishes, humbug damselfishes, wrasses, parrotfishes, surgeonfishes, trunkfishes, triggerfishes
  2. Polyandry (female has multiple partners each breeding season): anemonefishes (in some circumstances)
- C. Monogamous (mating partners remain together for extended period or the same pair reforms to spawn repeatedly): bullheads, some pipefishes and seahorses, *Serranus*, hamlets, jawfishes, damselfishes, tilefishes, butterflyfishes, hawkfishes, cichlids, blennies

III. *Gender system*
- A. Gonochoristic (sex fixed at maturation): most species (e.g., elasmobranchs, lungfishes, sturgeons, bichirs, bonytongues, clupeiforms, cypriniforms, salmoniforms, beryciforms, scombroids)
- B. Hermaphroditic (sex may change after maturation):
  1. Simultaneous (both sexes in one individual): *Kryptolebias*, hamlets, *Serranus*
  2. Sequential (individual is first one sex and then changes to the other):
     - a. Protandrous (male first, change to female): anemonefishes, some moray eels, *Lates calcarifer* (Centropomidae)
     - b. Protogynous (female first, change to male): *Anthias*, humbug damselfishes, angelfishes, wrasses, parrotfishes, gobies
- C. Parthenogenetic (egg development occurs without fertilization):
  1. Gynogenetic: *Poeciliopsis*, *Poecilia formosa* (no male contribution, only egg activation)
  2. Hybridogenetic: *Poeciliopsis* (male contribution discarded each generation)

IV. *Secondary sexual characteristics* (traits not associated with fertilization or parental care)
- A. Monomorphic (no distinguishable external difference between sexes): most species (clupeiforms, carp, most catfishes, frogfishes, mullets, snappers, butterflyfishes)
- B. Sexually dimorphic:
  1. Permanently dimorphic (sexes usually distinguishable in mature individuals): *Poecilia*, anthiine seabasses, dolphinfishes, *Cichlasoma*, some angelfishes, wrasses, parrotfishes, chaenopsid blennies, dragonets, Siamese Fighting Fishes
  2. Seasonally dimorphic (including color change only during spawning act): many cypriniforms, Pacific salmons, sticklebacks, lionfishes, epinepheline seabasses, some cardinalfishes (female), darters, some angelfishes, damselfishes, wrasses, blennies, surgeonfishes, porcupinefishes (female)
  3. Polymorphic (either sex has more than one form): precocial and adult male salmon; primary and secondary males in wrasses and parrotfishes

V. *Spawning site preparation* (see Table 21.2)
- A. No preparation: most species of broadcast spawners (e.g., herring)
- B. Site prepared and defended: sticklebacks, damselfishes, sunfishes, cichlids, blennies, gobies

VI. *Place of fertilization*
- A. External: most species (lampreys, lungfishes, Bowfin, tarpons, eels, herrings, minnows, characins, salmons, pickerels, codfishes, anglerfishes, sunfishes, marlins, flatfishes, pufferfishes, porcupinefishes)
- B. Internal: elasmobranchs, coelacanths, livebearers, freshwater halfbeaks, scorpionfishes, surfperches, eel-pouts, clinids
- C. Buccal (in the mouth): some cichlids

VII. *Parental care* (see Table 21.2)
- A. No parental care: most species
- B. Male parental care: sea catfishes, sticklebacks, pipefishes, greenlings
- C. Female parental care:
  1. Oviparity with post-spawning care: *Oreochromis*
  2. Ovoviviparity without post-spawning care: rockfishes (*Sebastes*)
  3. Viviparity without post-spawning care: elasmobranchs, *Poecilia*, surfperches
- D. Biparental care: bullheads, discus, *Cichlasoma*, anemonefishes
- E. Juvenile helpers: some African cichlids (*Lamprologus*, *Neolamprologus*, *Julidochromis*)

differences in male cycles are common (see below, Alternative mating systems and tactics).

Other semelparous fishes include lampreys, anguillid (freshwater) eels, and the osmeriform southern smelts (Retropinnidae) and galaxiids of Australia and New Zealand (McDowall 1987). American Shad (*Alosa sapidissima*) are semelparous in southern locations (30–33°N), largely iteroparous at northern latitudes (41–47°N), and variably iteroparous at intermediate latitudes (Leggett & Carscadden 1978). With the exception of such annual fishes as aplocheiloid rivulines, semelparous fishes are diadromous or include at least one major migratory phase in their life cycle. Anguillid eels show sex-based differences in tactics within an overall semelparous strategy. Males often mature rapidly (*c*. 3–6 years) and at a uniformly small size (30–45 cm) regardless of locale, whereas females are consistently longer (35–100 cm) and may mature quickly (4–13 years) at low latitudes or slowly (6–43 years) at high latitudes. Slow maturing females grow larger and produce more eggs than smaller, faster maturing females. In American eels, males have a relatively restricted geographic distribution, occurring primarily in estuaries of the southeastern United States, whereas females are found throughout the North American range of the species and in all habitats. As far as is known, all members of an anguillid species migrate to the same oceanic region to spawn and die (Sargasso Sea in the western Atlantic for American and European eels, the Philippine Sea for Japanese eels) (Helfman et al. 1987; Jessop 1987; see Chapter 23, Representative life histories of migratory fishes).

Mating systems

Mating systems are defined by the number of mating partners an individual has during a breeding season (Table 21.1). The three most common categories are promiscuous, polygamous, and monogamous. **Promiscuous** breeders are those in which little or no obvious mate choice occurs, where both males and females spawn with multiple partners, either at one time or over a short period. Such spawning has been documented for the Baltic Herring (Clupeidae), Guppies (Poeciliidae), Nassau Groupers (Serranidae), humbug damselfish colonies (Pomacentridae), cichlids, and the Creole Wrasse (Labridae) (Thresher 1984; Barlow 1991; Turner 1993).

Polygamy, where only one sex has multiple partners, takes multiple forms. **Polyandry**, where one female mates with several males (and presumably not vice versa), is relatively uncommon, so far documented only in an anemonefish (Pomacentridae) (Moyer & Sawyers 1973). Polyandry might also be descriptive of female ceratioid anglerfishes which have more than one male attached (see Chapter 18, The deep sea). **Polygyny** is the most common form, involving males as the polygamous sex. Territorial males that care for eggs and young are frequently visited by several females, as in sculpins, sunfishes, darters, damselfishes, and cichlids. Polygyny can also develop into **harem formation**, where a male has exclusive breeding rights to a number of females that he may guard. Harems have been observed in numerous cichlids and in several coral reef families (e.g., tilefishes, anthiine serranids, damselfishes, wrasses, parrotfishes, surgeonfishes, triggerfishes).

Many polygynous animals form **leks**, which are traditional areas where several males congregate for the sole purpose of displaying to females (Emlen & Oring 1977). Females are often attracted to a male in response to his central position within the lekking ground, or to the vigor of his display and bright plumage. Lekking is common in birds and mammals, in which only the female provides parental care. Some African cichlids come closest to forming true leks. Large numbers (*c*. 50,000) of male *Cyrtocara eucinostomus* congregate along a shallow 4 km long shelf in Lake Malawi and build sand nests and display to passing females each morning. Females spawn and then mouthbrood eggs elsewhere. The male aggregations break up each afternoon, when fish feed (McKaye 1983, 1991). Some fishes form "leklike" aggregations of males (e.g., Arctic Char, Atlantic Cod, damselfishes, wrasses, parrotfishes, surgeonfishes), but the display ground is also an appropriate place for launching or caring for eggs, which stretches the definition of lekking (Loiselle & Barlow 1978; Moyer & Yogo 1982; Figenschou et al. 2004; Windle & Rose 2007). In a unique variation on leklike behavior, female triggerfish (*Odonus niger*, Balistidae) form a communal display ground for 1 day before spawning, after which they all mate with a single, nearby male (Fricke 1980).

In **monogamous** systems, fish live in pairs that stay together and mate, or mate with the same individual repeatedly and exclusively, regardless of pairing at nonmating times. Strongly pairing species include North American freshwater catfishes, many butterflyfishes and angelfishes, most substrate guarding and some mouthbrooding cichlids, and anemonefishes; in the butterflyfishes, pairs may remain together for several years and probably mate for life (Reese 1975). Monogamous coral reef fishes commonly spawn with the same partner on a daily basis over an extended period without ensuing care of young, whereas freshwater species such as cichlids spawn over a limited time and then both parents typically care for the young. Monogamy has evolved independently in many groups, often in conjunction with territoriality and paternal care (Whiteman & Côté 2004). Monogamy is also known in freshwater bonytongues, bagrid and airsac catfishes, and snakeheads, and among at least 18 marine families, including pipefishes and seahorses, hermaphroditic hamlets, jawfishes, cardinalfishes, tilefishes, hawkfishes, damselfishes, wrasses, blennies, gobies, wormfishes, surgeonfishes, triggerfishes, filefishes, and pufferfishes (Barlow 1984, 1986; Thresher 1984; Turner 1993, Whiteman & Côté 2004).

Gender roles in fishes

Although the vast majority of fishes are **gonochoristic**, with sex determined at an early age and remaining fixed as male or female, a significant number of fishes can function as males or females simultaneously or sequentially (see also Chapter 10, Determination, differentiation, and maturation). The environmental correlates and evolutionary causes of sex change in fishes have been the subject of considerable study and speculation (Box 21.1).

Sex reversal has evolved, apparently independently, in perhaps 34 families belonging to 10 orders, including moray eels (Anguilliformes), loaches (Cypriniformes), lightfishes (Stomiiformes), killifishes (Atheriniformes), swamp eels (Synbranchiformes), flatheads (Scorpaeniformes), boxfishes (Tetraodontiformes), and at least 24 perciform families (including snooks, seabasses, tilefishes, emperors, rovers, porgies, threadfins, angelfishes, bandfishes, damselfishes, wrasses, parrotfishes, and gobies) (Devlin & Nagahama 2002; DeMartini & Sikkel 2006). Sex changers can be either: (i) **simultaneous hermaphrodites**, capable of releasing viable eggs or sperm during the same spawning; or (ii) **sequential hermaphrodites**, functioning as males during one life phase, and as females during another. Among sequential hermaphrodites, **protandrous** fishes develop first as males and then later change to females, whereas **protogynous** fishes mature first as females and then later become males. Variations on these patterns exist, such as protogynous populations with some males that develop directly from juveniles, or simultaneous hermaphrodites that lose the ability to function as one sex (Smith 1975; Warner 1978; Sadovy & Shapiro 1987; Lutnesky 1994).

Protogyny is by far the most common form of hermaphroditism, exhibited in at least 17 tropical marine families, which is about one-fifth of reef families (DeMartini & Sikkel 2006). In a classic study, Robertson (1972) found that the Indo-Pacific Cleaner Wrasse, *Labroides dimidiatus*, formed harems of one large male and up to 10 females. Breeding access to the male was determined by a behavioral dominance hierarchy or peck order, the largest female dominating the next smallest and so on. If the top (alpha) female was removed, the next largest female assumed her role and everyone else moved up a step. If the male was removed, the alpha female began courting females within an hour and developed functional testes within 2 weeks (see also Kuwamura 1984).

Protogyny in wrasses can take other forms. In the Caribbean Bluehead Wrasse, *Thalassoma bifasciatum*, fish usually begin life as predominantly yellow females or similarly colored males ("**initial phase**" coloration). Any of the initial phase fish can change into larger, "**terminal phase**" males, which also develop a blue head, a black-and-white midbody saddle, and a green posterior region. Large males set up territories over coral heads that females prefer as spawning sites. Some females are intercepted by and spawn with groups of up to 15 smaller males, but the largest, pair-spawning males have the highest spawning success. A territory-holding male may receive 40–100 spawnings per day, whereas a nearby group-spawning male may receive only one to two matings, and his sperm will often be diluted by the gamete output of other males in the group (Warner et al. 1975; Warner 1991). Other well-studied protogynous species include the anthiine serranid, *Anthias squamipinnis*, a pair-spawning species that forms large aggregations in which females may outnumber males by 36 : 1. The precision of **social control of sex change** in this species is remarkable: if nine males are removed from a large group, nine females change sex to replace them. Sex change to male in *Anthias* also occurs if the female : male ratio exceeds a threshold value (Shapiro 1979, 1987). The commonness of protogyny probably reflects the fact that most teleosts, including gonochoristic species, differentiate first as nonfunctional females.

Protandry has been reported in moray eels, loaches, lightfishes, platycephalids, snooks, porgies, threadfins, damselfishes, and crediid sandburrowers. The popular clown or anemonefishes (*Amphiprion* spp., Pomacentridae) live in groups of two large and several small individuals in an anemone. Only the two largest fish in an anemone are sexually mature, the largest individual being female and the next largest being male. Although smaller fish may be as old as the spawning individuals, the behavioral dominance of the mature pair keeps these smaller males from maturing and growing, and a dominance hierarchy exists among the smaller males. In essence, "low ranking males are psychophysiologically castrated" (Fricke & Fricke 1977, p. 830). If the female dies, the male changes sex to female and the next largest fish in the group takes over his former role and grows rapidly (Allen 1975; Moyer & Nakazano 1978). This inconvenient truth was judiciously sidestepped in the otherwise biologically accurate movie, *Finding Nemo*. In fact, Nemo's dad, Marlin, should have become Nemo's mother.

Simultaneous hermaphroditism (= cosexuality, synchronous hermaphroditism) is least common, known from only four shallow water families (muraenids, rivulids, serranids, gobies) and most of the 16 families in the deepsea order Aulopiformes (lizardfishes, Synodontidae, are the best-known exception) (Smith 1975; Warner 1978; St. Mary 2000; Devlin & Nagahama 2002). Three species of New World cyprinodontiform rivulids are capable of self-fertilization (*Kryptolebias* spp. of South America and the mangrove rivuline, *Kryptolebias marmoratus*, of North and Central America). Self-fertilization in *Kryptolebias* is internal, producing clonal populations of homozygous, genetically identical hermaphroditic fish. Functional males can be produced depending on temperature and day length (Harrington 1971, 1975; Taylor 1992). Cyprinodontiform fishes are often colonists of small streams on islands and other seasonally adverse habitats (see Chapter 18). Self-fertilization may be one means of assuring mates in low-

Box 21.1

BOX 21.1

"When the going gets tough, the tough change sex"[a]: the evolution of sex change in fishes

The topic of sex or gender change and its relationship to hermaphroditism has sparked a great deal of debate among biologists. Two questions dominate the discussion of sex-changing fishes (and of sex allocation in organisms in general). The questions are "why change sex?" and "when to change?" Answers lie primarily in the ecologies of individual species, greatly influenced by the relative reproductive success of males versus females at different sizes.

Animals change gender when, at a given size, the reproductive success of one gender becomes higher than if the individual remained the other gender (Ghiselin 1969; Warner 1975). The value of changing gender is reduced by the costs of changing, such as lost reproductive opportunities while undergoing the change and metabolic costs of altering gonads. This **size advantage model** assumes indeterminate growth and increased fecundity with increasing size; both are the norm among fishes. Reproductive success in females is generally limited by gamete production, whereas males are limited by the number of mates that they can acquire (Bateman's Principle). Males, including small males, generally produce a surplus of sperm, most of which never encounter an egg. In contrast, egg production increases with growth in females and each egg is likely to be fertilized. These circumstances would dictate that sex changers be protandrous: small females produce very few eggs but small males can fertilize many eggs. Such conditions would select for fish that began life as small but functional males and changed to female when they were large enough to produce more eggs than a small male could fertilize. For example, in pair-spawning, monogamous anemonefish, lifetime egg production of the pair is maximized by having the larger fish a female.

However, male fish often compete for females (see below), and the outcome of such competition is frequently determined by body size, with larger males winning. Hence one large, behaviorally dominant male can monopolize many females and fertilize their eggs, as in the Bluehead Wrasse and *Anthias* examples mentioned earlier. Under these circumstances, the greatest advantage accrues to the largest males and the tactic to follow is to be a female first (since small males have such limited competitive and therefore reproductive success) and then change to male because of the advantage conferred upon large males. The age or size at which an individual should change sex is probably determined by an interaction between body size and social structure (numbers of males and females, dominance hierarchies) of the population (Shapiro 1987). The size advantage hypothesis is (of course) complicated by exceptional situations, such as Bucktooth Parrotfish, *Sparisoma radians*, populations that contain large females and smaller, sex-changed males (see Munoz & Warner 2004). Sex change is an obviously rich subject for both observation and speculation.

Left unanswered is why more species of fishes and other vertebrates do not change sex. Ideas on this subject focus on the relative costs of changing sex in different taxa, the existence of dimorphic sex chromosomes (which are generally lacking in fishes), and differences in sex determination mechanisms (Warner 1978; Devlin & Nagahama 2002). Add to these the realization that evolution is a predominantly conservative process. Biological systems are complex, which is certainly a description of the reproductive systems of fishes, given the behavioral, ecological, physiological, and anatomical components involved. Alterations to complex systems are likely to destroy the homeostasis that has evolved among the components. Hence the advantages of sex change would have to be very large to overcome fitness losses due to disruption of the coevolved gene complexes that code for the systems. Sex change then becomes an alternative to gonochorism, but one that does not offer a sufficiently large advantage to overcome the costs of refitting the reproductive systems of most fishes. Gonochorism obviously works well for most species; since it isn't broken, there is little selective advantage in fixing it.

[a] From Warner (1982, p. 43).

density populations that frequently become isolated, a scenario that could also be applied to the deepsea aulopiforms.

The other species of simultaneous hermaphrodites occur among the small hamlets (*Hypoplectrus*, *Serranus*). Each individual is physiologically capable of producing sperm and eggs at the same time, but behaviorally these fishes function as only one sex at a time during a spawning bout. In Caribbean hamlets (*Hypoplectrus*), spawning bouts can last for several hours, during which time members of a pair

alternate sex roles, one fish first behaving as the "female" and releasing eggs and then behaving as the "male" and releasing sperm (Pressley 1981; Fischer & Petersen 1987). The eastern Pacific *Serranus fasciatus* is a haremic, sex-changing, simultaneous hermaphrodite: one male guards and spawns with several hermaphrodites that act as females. If the male is removed, the largest hermaphrodite changes into a male (Fischer & Petersen 1987). Serranines have separate external openings for the release of eggs and sperm (in addition to an anus), which may prevent internal or accidental self-fertilization. Self-fertilization may occur in some serranines, but only in aquaria (Thresher 1984).

One additional group of fishes departs from normal gonochoristic gender roles. Livebearers in Mexico and Texas include **parthenogenetic** "species" that are all-female but require the sperm from males of other species to activate cell division in their eggs. Parthenogenesis in livebearers takes two forms: gynogenesis and hybridogenesis (Fig. 21.1). **Gynogenetic** females are usually triploid and produce eggs that are also 3N. These eggs are activated by sperm from other species, but no sperm material is incorporated; hence daughters are genetically identical to their mothers. **Hybridogenetic** females, in contrast, are diploid and produce haploid eggs that, during the reduction division of meiosis, keep the maternal genes and discard the paternal genes. Upon mating, these eggs unite with sperm from males of another species, forming a new, diploid hybrid daughter (no sons are produced). When the daughter mates, she again produces eggs that are haploid and "female". Hence the maternal lineage is conserved and the male's genetic contribution is lost after one generation. These parthenogenetic "species" are thought to have arisen originally as hybrids between *Poeciliopsis monacha* females and males of four congeners, *P. lucida*, *P. occidentalis*, *P. latidens*, and *P. viriosa*. The males of the four species are the usual sperm donors during mating. An additional species, the Amazon Molly, *Poecilia formosa*, is diploid and gynogenetic. Sperm from two other species (*P. mexicana* and *P. latipinna*) activate the eggs, but contribute no genetic material (Schultz 1971, 1977; Vrijenhoek 1984). Natural gynogenesis has also been reported for the cyprinid *Cyprinus auratus gibelio* (Price 1984).

An immediate question that arises is how natural selection maintains males that waste gametes so wantonly. Apparently, dominance hierarchies among "donor male" populations of live-bearers exclude many males from mating with conspecific females. These are often the males that participate in the parasitized, heterospecific spawnings. **Satellite** or **peripheral males** that have very low reproductive output are characteristic of many vertebrate species (these are often the sneakers and streakers discussed below), providing an abundance of otherwise unused sperm (Moore 1984). Additionally, laboratory tests of mate preferences in sexual females show that sexual females are more attracted to males that the females observed courting gynogenetic females. Apparently a male can increase his chances of mating with a sexual female if he spends time courting asexual females because sexual females copy the choices made by female gynogens. It is not known whether sexual females prefer males that mate with sexual females over those that mate with gynogenetic females (Schlupp et al. 1994).

Certain generalities arise from surveys of sex change in shallow water fishes, as do exceptions. Sex change is largely a tropical and subtropical, marine phenomenon (Policansky 1982c; Warner 1982). Cool temperate marine and freshwater sex changers are known (e.g., loaches, bristlemouths, swamp eels, wrasses, gobies) but are relatively uncommon compared with tropical marine hermaphrodites. Patterns often follow familial lines, all members of a family being either protandrous or protogynous (although there are both protogynous and protandrous species among moray eels, seabasses, porgies, damselfishes, and gobies, and some serranids are clearly simultaneously hermaphroditic).

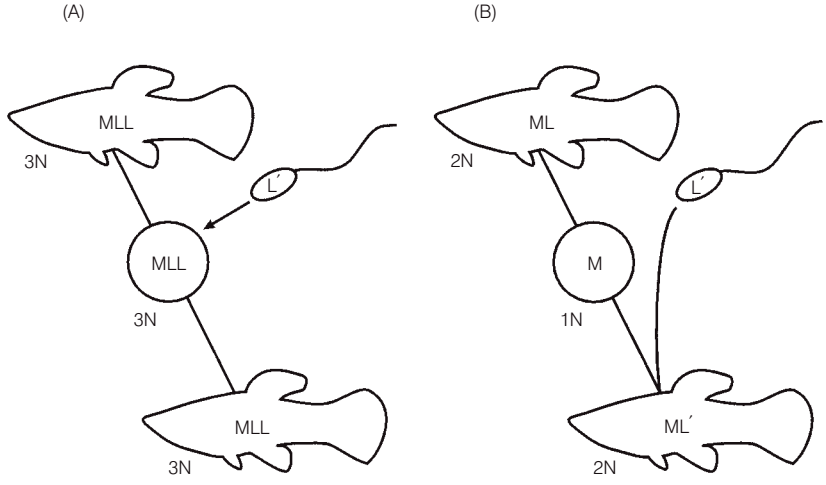


Figure 21.1

Parthenogenesis in Mexican livebearers. (A) In gynogenesis, a triploid female (designated MLL, shorthand for *Poeciliopsis monacha-lucida-lucida*) produces 3N eggs that are activated but not fertilized by sperm from a male *P. lucida* (L´). A daughter identical to the mother is produced. (B) In hybridogenesis, a diploid mother (ML, for *P. monacha-lucida*) produces haploid eggs (M) that contain only the maternal genome. Sperm from *P. lucida* (L´) combine to form a diploid daughter (ML´), but this male component will be discarded again during gamete production and all future eggs will continue to have solely *monacha* genes. After Vrijenhoek (1984) and Allendorf and Ferguson (1990).

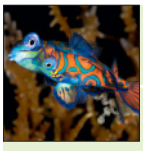
However, population differences are becoming increasingly well known in sex-changing fishes. The Cleaner Wrasse, *Labroides dimidiatus*, is haremic under some conditions but forms pairs under others. Bluehead Wrasse, *Thalassoma bifasciatum*, are dominated by territorial-spawning males on small reefs with small populations, but by group-spawning males on large reefs with dense populations. Resource limitation, either food availability or reef size, and population size are frequent determinants of variation in mating systems. Clearly, sex change and mating systems respond to environmental variability (see Thresher 1984; Shapiro 1991; Warner 1991; Devlin & Nagahama 2002; Oldfield 2005).

Courtship and spawning

Sexual selection, dimorphism, and mate choice

Some traits of an animal function primarily to attract mates or to aid in battles between members of one sex for access to the other sex. Such **sexually selected** traits confer a mating advantage on an individual; they are a subset of natural selection, which usually involves traits that confer a survival advantage. Sexually selected traits may serve no other purpose than mating and may even handicap the possessor with respect to other, fitness-influencing activities. However, sexually selected traits can also confer a positive survival advantage, such as large size in males, which provides a physical defense from predators and is also favored by females during mating (see Box 21.2). Sexually selected traits are often referred to as **secondary** sexual characteristics. **Primary** characteristics include ovipositors, genitalia, and other copulatory structures such as claspers in elasmobranchs, gonopodia or priapia in livebearers and phallostethids, or brood patches or pouches and other structures used in parental care. In some instances, a character may be both secondary and primary, serving both in mate attraction and in copulation or parental care. In sticklebacks, male sticklebacks are attracted to females with swollen bellies, but the swelling results from the female's ripe ovaries (Wootton 1976).

Secondary sexual characteristics have four general attributes: they are restricted to or are expressed differentially in one sex (usually the male), they do not appear until maturation, they often develop during a breeding season and then regress, and they generally do not enhance survival. Secondary characteristics take the form of **sexual dimorphisms** (differences in body parts between sexes), such as differences in body size, head shape, fin shape, dentition, and body ornamentation, or as **dichromatisms** (differences in coloration). We know comparatively little about electrical, chemical, and acoustic differences between the sexes, although differences in anatomy and physiology associated with these sensory modes are common (e.g., elephantfishes, salmons, minnows, gymnotid knifefishes, toadfishes, croakers, damselfishes, gobies). For example, males of the Plainfin Midshipman, *Porichthys notatus* (Batrachoididae), attract females by "humming", a sound produced by contracting large muscles attached to the gas bladder walls. The sound-producing ability and its importance in courtship are reflected in numerous differences between the sexes. Males differ from females in having larger body size, different color, larger sonic muscles, and differing neural circuitry – involving larger cell bodies, dendrites, and axons in the brain – than are found in the females (Bass 1996).



Box 21.2

BOX 21.2

Sexual selection in fishes

The major feature of **sexually selected traits** is that one sex bases its mating preferences on a character or set of characters in the other sex. The basis of mate choice is complex, involving a combination of factors related to male–male competition and female attraction, but sexually dimorphic traits serve as immediate (proximate) cues to a potential mate's ultimate reproductive quality. In nest guarding or otherwise territorial species, males typically compete for spawning sites and then females choose males based on male size and coloration, territory size and location, and quality of the oviposition substrate.

Whether male attributes versus the qualities of the site he possesses are more important is often difficult to determine (Kodric-Brown 1990). Relevant male attributes include size, which is directly correlated with intrasexual dominance in many families (e.g., minnows, salmons, sticklebacks, sculpins, sunfishes, darters, wrasses, blennies, gobies). Females actively choose larger males in many nesting

species in which males guard eggs and fry. Such a size-based preference is an adaptive choice by females: larger males are generally more effective nest guarders and hence choosing a larger male is a means of insuring better protection from egg predators (Downhower et al. 1983; Fitzgerald & Wootton 1993). Bright coloration can serve both as a dominance signal and a mate attractant (minnows, livebearers, killifishes, sticklebacks, greenlings, darters); larger males are also often the most colorful. Female choice based in part on territory or spawning site characteristics has been demonstrated in damselfishes, wrasses, triplefins, blennies, and gobies. Given the positive correlations among the many traits that may indicate male quality (e.g., size, color, health, courtship intensity, dominance, territory size, quality of paternal care), it is not surprising that females often rely on a variety of characteristics rather than a single male trait in making their choices (Kodric-Brown 1990).

It is widely held that the sex that expends the greatest energy in gamete production will be in relatively limited supply, that the other sex will compete for the limiting sex, and that the limiting sex will protect its large investment by being choosiest about mating partners. Dimorphic males and female choice are generally the rule in fishes, reflecting the greater cost of producing eggs than sperm. Evidence of the generalization can also be found in "**role reversed**" species where males become "pregnant" and carry eggs internally, such as the pipefishes and seahorses. In pipefishes, females are often the more colorful sex and males select mates based on female size and the intensity of courtship displays (Berglund et al. 1986a, 1986b, 2005). The female is also the dimorphic sex in a limited number of species, notably in some cardinalfishes, damselfishes, and porcupinefishes on coral reefs. In the first two families, males mouth brood or defend the eggs. The social conditions under which role reversal has evolved are a matter of much discussion (e.g., Vincent et al. 1992; Berglund & Rosenqvist 2003; Barlow 2005).

Several well-studied instances of sexual dimorphism and sexual selection have given us insight into how such traits evolve and function. Male swordtails (*Xiphophorus* spp., Poeciliidae) develop a colorful, elongate, lower caudal fin extension, the sword, when they mature. The sword continues to grow as the fish ages and may exceed the length of the rest of the body in older individuals. The sword serves no role in male–male interactions and may be a liability in predator avoidance. The only known function of this "elaborate, highly conspicuous ornament" is during courtship, when the male displays the sword to females (Basolo 1990a, p. 333). Females prefer to mate with males with longer swords; when given a choice between two males with different length swords, the longer sword is preferred and the strength of the preference increases as the difference between sword length increases. Hence female choice for long swords has selected for increased sword length in males. Interestingly, swordlessness is the probable ancestral condition in the genus. Platyfish are primitive congeners of swordtails, but platyfish do not develop swords. When plastic swords are surgically attached to the tails of male platyfish, female platyfish prefer males with the artificial swords over normal, swordless males. Swords in male swordtails apparently evolved in response to a **preexisting preference** in the female's information-processing system, which, when combined with natural variation in tail length, selected for males with progressively longer swords (Basolo 1990b).

As is often the case, strong selection for sexually dimorphic traits is achieved at a cost. The trade-off operating here is sexual selection "versus" conspicuousness to predators. For example, male Guppies attract females via a series of displays that are enhanced by brightly colored spots on the male's side. The largest, brightest, and most diverse spots are most attractive to females and predators alike. In Trinidad, predators are more common and diverse in lowland areas than in upland areas, and males in these predator-dense streams tend to have fewer, less intense, smaller, and less colorful spots. Hence a compromise is struck between attracting mates and attracting predators (Endler 1991). It makes little evolutionary sense that females in predator-dense areas would prefer to mate with males that were also very attractive to predators, if for no other reason than the female's sons would be relatively vulnerable. Not surprisingly, females from predator-dense areas generally do not show a preference for more colorful males (Houde & Endler 1990; J. Endler, pers. comm.). Male Guppies with larger tails also exhibited poorer swimming performance than males with shorter tails (Karino et al. 2006). Related poeciliids show similar cost–benefit phenomena. Female *Gambusia* prefer males with larger gonopodia, but a larger gonopodium is grown at a cost in fast start swimming performance needed to escape predators. Male *Gambusia* in predator-free environments tend to have larger gonopodia than males from locales with predators (Langerhans et al. 2005). Male swordtails, *Xiphophorus*, incur greater energy costs while swimming as a result of having an elongate caudal fin that females find attractive (Basolo & Alcaraz 2003).

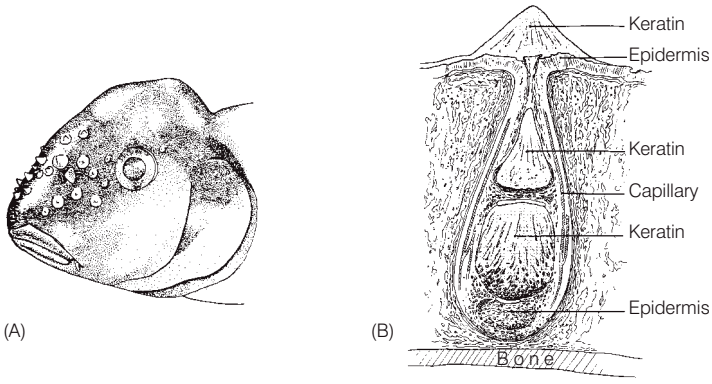


Figure 21.2

Breeding tubercles in fishes. Males of at least 25 different families develop keratinized bumps on their fins and body during the breeding season that may help maintain contact between spawning fish and stimulate females to spawn. (A) Tubercles on the head of an *c*. 15 cm long male River Chub, *Nocomis micropogon*. The swollen region on the top of the head is also characteristic of male River Chubs during the breeding season. (B) Internal structure of a tubercle from the snout of a gyrinocheilid algae eater. The tubercle consists of an outer cap of epidermal keratin, with concentrations of replacement keratin lying in a pit at the base of the tubercle that will replace the tubercle in the event of its loss. (A) from Jenkins and Burkhead (1993), used with permission; (B) from Wiley and Collette (1970), used with permission.

Whereas the vast majority of fish species show no obvious sexual dimorphisms, many species are distinctly dimorphic. Males are often the larger sex in salmon, sauries, wrasses, and clingfishes, whereas females are larger in Mackerel and Whale sharks, sturgeon, true eels, ceratioid anglers, sticklebacks, halfbeaks, silversides, livebearers, blennies, and billfishes. Male Dolphinfish (*Coryphaena hippurus*, Coryphaenidae) are larger and have a distinctly blunter head than females. During spawning migrations, male anguillid eels develop larger eyes than females, and male salmon develop distinctly concave upper and lower jaws, called **kype**, that preclude feeding. Males may have trailing filaments at the ends of their dorsal, anal, or caudal fins (characins, African rivulines, rainbowfishes, anthiine seabasses, cichlids, wrasses); enlarged median or paired fins (lampreys, bichirs, freshwater flyingfishes, minnows, characins, killifishes, livebearers, dragonets, gobies, climbing gouramis); elongate tail fins (livebearers); or have elongate, lobule-tipped gill covers or pelvic fins that are displayed in front of females during courtship (*Corynopoma*, Characidae; *Ophthalmochromis*, Cichlidae). In elasmobranchs, males may have longer or sharper teeth than females, which serve to grasp the female during courtship and copulation; females in turn may have thicker skin than males.

Differences in body ornamentation include small bumps on the body, scales, and fins of mostly male fishes in 25 different families of primarily soft-rayed teleosts. These bumps are called **nuptial** or **breeding tubercles** when of epidermal origin, or **contact organs** when of dermal origin (Collette 1977) (Figs 21.2, 21.3). Scale differences also include scale type: male cyprinodontids have ctenoid scales, whereas females have cycloid scales (Berra 2001). Other dimorphic ornaments include small hooks on the anal fins and even tail of some male characins (a kind of contact organ), and rostral papillae in male blind cavefishes, photophore patterns in lanternfishes, and pigmented egg dummies on the anal fins of cichlids. Some male minnows, cichlids, wrasses, and parrotfishes develop bony or fatty humps on the front (nuchal region) of their head.

Figure 21.3

Extreme sexual dimorphism in a male Bluehead Chub, *Nocomis leptocephalus*. This *c*. 20 cm minnow builds pebble nests on stream bottoms and attracts females with its swollen head and distinct breeding tubercles. Photo by P. Vecsei, used with permission.

Coloration differences are widespread and are usually expressed as more brightly colored males, either permanently (Bowfin, livebearers, killifishes, rainbowfishes, cichlids, wrasses, anabantids) or seasonally (minnows, sticklebacks, darters, sunfishes, cichlids). Male color change often involves development of bright or dark patches where they are most conspicuous because they break the rules of crypticity. Hence dark and light patches exist adjacent to one another, color transitions become sudden rather than gradual, or reverse countershading develops (e.g., sticklebacks, sunfishes, temperate wrasses). Conspicuousness in the breeding season reinforces the premise that animals are willing to risk an increased predatory threat for a chance to reproduce (Breder & Rosen 1966; Fryer & Iles 1972; Meisner 2005).

The importance of sexually selected, dimorphic traits as species-isolating mechanisms has become increasingly obvious in recent years as human-caused alterations of the landscape interfere with mating patterns. In Lake Victoria, where "probably more vertebrate species are at imminent risk of extinction . . . than anywhere else in the world" (Ribbink 1987, p. 22), cichlids are separated taxonomically and apparently behaviorally by color variation in males. Females discriminate among closely related male suitors at least in part on color differences. Increased algal growth, resulting from heavy runoff of nutrients from the surrounding deforested hillsides (see Chapter 26, Introduced predators), has increased turbidity and severely limited light transmission, especially at the long (red) and short (blue) ends of the visible light spectrum (Seehausen et al. 1997a) (Fig. 21.4A). Mate selection is apparently impaired by this absorption of long and short wavelengths because distinct red and blue colors in males are no longer obvious, leading to altered perception of mating colors and increased hybridization (Fig. 21.4B). "Where eutrophication turns the lights off, ecological and species diversity erode rapidly" (Seehausen et al. 1997a, p. 1810).

Other researchers have linked alterations and reductions in spawning behavior to increased turbidity. Sexual selection was relaxed under conditions of experimentally induced turbidity in the Sand Goby, *Pomatoschistus minutus*. In clear water, females showed a strong preference for larger males, but this preference weakened as water clarity was reduced (Jarvenpaa & Lindstrom 2004). Hence, increased turbidity can alter mating systems by altering the intensity of sexual selection. Other, related findings include a reduction in the intensity of red coloration in male three-spined sticklebacks in the Baltic Sea, linked to eutrophication-caused algal growth and reduced visibility (Candolin et al. 2007). Decreased spawning frequency, disrupted timing of spawning, and a 93% reduction in number of viable eggs produced by the Tricolor Shiner, *Cyprinella trichroistia*, were interpreted as a result of disrupted visual cues associated with increased turbidity and resulting changes in light transmission (Burkhead & Jelks 2001).

Visual communication is not the only mode affected by anthropogenic impacts. Species recognition in the swordtail, *Xiphophorus birchmanni*, is chemically mediated, with females preferring conspecific males based on chemical cues. Fish tested in clean water maintain that species preference. Females tested in water subjected to sewage effluent and agricultural runoff did not discriminate between conspecific males and males of *X. malinche*, with which they can hybridize. The chemical most likely to interfere with communication was identified as humic acid, "a ubiquitous, natural product elevated to high levels by anthropogenic processes" (Fisher et al. 2006, p. 1187). It seems reasonable to assume that other sensory modalities involved in courtship and species recognition, such as acoustic and electrical

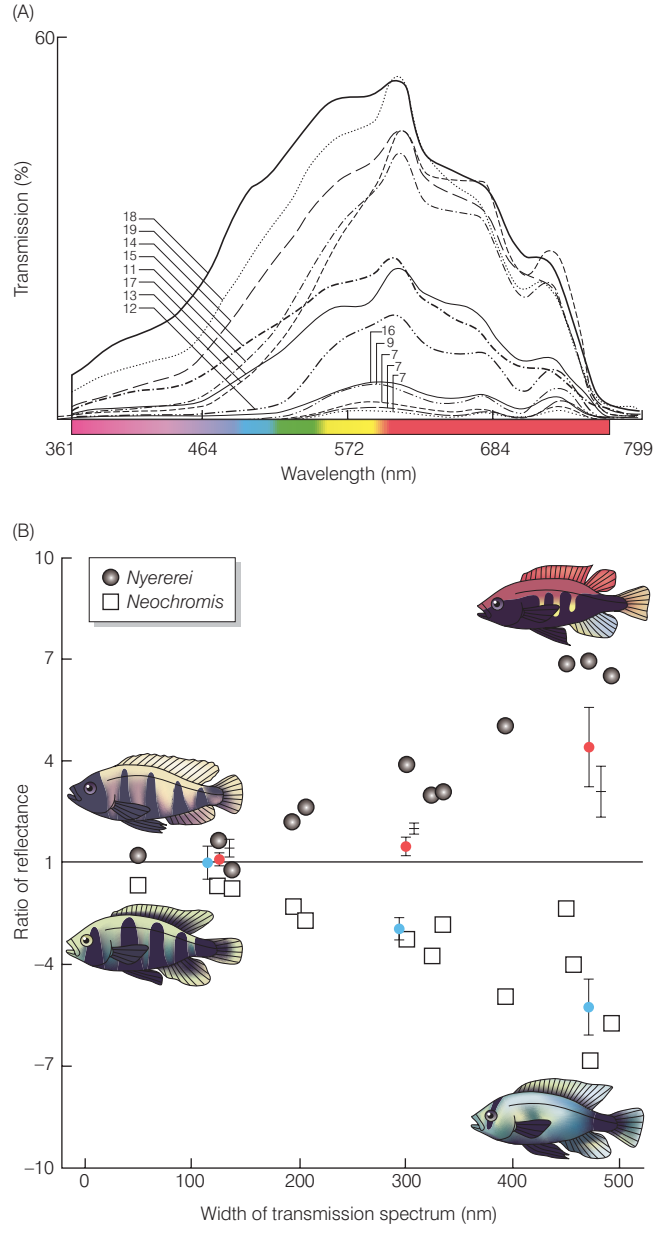


Figure 21.4

Turbidity-influenced light transmission is causing hybridization and loss of species in Lake Victoria. (A) Species richness and spectral properties at 13 sampling stations in Lake Victoria, showing that where water clarity is greater (upper curves), greater transmission of light at the short and long regions of the spectrum occurs. Where turbidity is high (lower curves), few photons at short and long wavelengths are transmitted. The number of haplochromine cichlids are shown next to the curve for each station. (B) A detectable difference in red and blue colors ("ratio of reflectance") decreases as the width of the transmission spectrum narrows. Red (*Nyererei*) and blue (*Neochromis*) males appear very similar where the spectrum is narrow (left side of graph) but the colors are easier to discriminate where the spectrum is wider (right side). After Seehausen et al. (1997a).

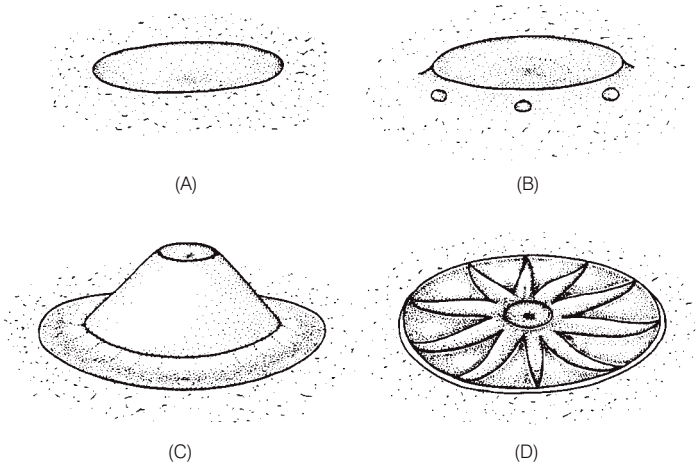


Figure 21.5

Spawning nests or bowers of African cichlids. Male cichlids construct sand structures that vary from simple pits to complex structures, where females deposit eggs just prior to picking them up in their mouths for brooding: (A) *Tilapia* (*Oreochromis*?) *andersonii* and *T. nilotica*; (B) *T. variabilis*; (C) *T.* cf. *macrochir* from Lake Bangweulu; (D) *T.* cf. *macrochir* from Lake Mweru. In the latter, radiating spokes are created by the male plowing through sand with his open mouth from the focal point to the edge. Structures vary from 15 to 150 cm across. From Fryer and Iles (1972), used with permission.

communication, could also be impaired by anthropogenic activities (e.g., Rabin & Greene 2002).

Spawning site selection and preparation

Many fishes spawn in nests. Nests may be no more elaborate than a simple depression that either or both sexes excavate in the bottom by fanning vigorously with the fins or by swimming rapidly in place (e.g., lampreys, Bowfin, trahiras, sunfishes). In lampreys and salmon, the eggs are covered with additional sand or gravel and then abandoned, whereas in other species the male remains to guard the exposed eggs. Many species spawn in a rock crevice or space on or under a shell or rock or in a hollowed log that has been excavated or picked clear of growth and debris (e.g., ictalurid catfishes, sculpins, poachers, darters, cichlids, damselfishes, clingfishes, sleepers, gobies). Some damselfishes "sandblast" a surface clean by spitting sand against it and then fanning it with their fins. The European Wrasse, *Crenilabrus melops*, lines a rock crevice with different types of algae. Softer algae at the back of the crevice serve as a substrate for spawning, whereas tougher, stickier coralline algae are packed into the outer portion of the crevice to protect the eggs.

Burrows are excavated and later guarded by lepidosirenid lungfishes, ictalurid catfishes, jawfishes, tilefishes, and gobies. Males of some stream minnows construct nest mounds by piling as many as 14,500 small stones, 6–12 mm in diameter, that are carried in the mouth to the nest site from as far as 4 m away (e.g., *Nocomis*, *Semotilus*, *Exoglossum*). Eggs deposited by the female fall into the interstices between the stones and are covered by additional stones; the nest is guarded and kept free of silt by the male (Breder & Rosen 1966; Keenleyside 1979; Potts 1984; Thresher 1984; Wallin 1989, 1992; Johnston 1994). In African cichlids, males build nests in sand, some of elaborate design (Fig. 21.5). These structures have been likened to the bowers of bowerbirds because they are primarily display, courtship, and spawning stations from which the female picks the eggs up in her mouth almost as quickly as they are laid (Fryer & Iles 1972; McKaye 1991).

Nests can also be constructed of intrinsically produced materials, sometimes combined with extrinsically gathered objects. Gouramis and Siamese Fighting Fishes (Anabantoidei) and Pike Characins produce bubble or froth nests, consisting of mucus-covered bubbles that stick together in a mass. Some anabantoids add plant fragments, detritus, sand, and even fecal particles to the bubble mass. Male sticklebacks pass a mucoidal, threadlike substance manufactured in the kidneys out through the cloaca, using it to bind together pieces of leaves, grasses, and algal filaments that create a cup or tunnel nest in which a female deposits eggs. All of these structures are tended by the male following spawning (Wootton 1976; Keenleyside 1979).

Courtship patterns

Courtship is the series of behavioral actions performed by one or both members of a mating pair just prior to spawning. Courtship has several functions that maximize efficiency of the spawning act. Courtship aids in species recognition (a pre-mating species-isolating mechanism), pair bonding, orientation to the spawning site, and synchronization of gamete release. Courtship is often necessary to overcome territorial aggression by the male, who might otherwise drive the female away from the site (in many species, males already have eggs in their territories and must guard against predation by conspecifics of both sexes). Courtship may be relatively simple (as in herring), or may involve a large number or a complex progression of displays and signals by one or both members (e.g., *Corynopoma*, Characidae; Guppies; sticklebacks).

During courtship, individuals frequently change color from their normal, countershaded patterns to bolder, contrasting color patterns. In many species (e.g., minnows, silversides, cichlids) existing body coloration intensifies or the head becomes dark relative to the remainder of the body. Sound production during courtship, usually by the male, occurs in many fish families (sturgeons, minnows, characids, codfishes, toadfishes, sunfishes, grunts, sciaenids, darters, damselfishes, cichlids, blennies, gobies), often in accompaniment with visual displays involving exaggerated or rapid swimming patterns, erection of fins, and jumping out of the water (Fine et al. 1977; Myrberg 1981, 2002; Lugli et al. 1997; Johnston & Johnson 2000; Lobel 2001; Johnston & Phillips 2003). Chemical stimulants are also involved. Male Goldfish, Zebra Danios (Cyprinidae), and gobies begin courtship activities when exposed to water that held a gravid female, and gravid female gobies are attracted to male-produced androgynous substances (Hara 1982; Stacey & Sorensen 1991). Species and sex recognition during courtship in cichlids occurs more quickly when individuals receive both visual and chemical cues from potential mates (Barlow 1992).

Some appreciation of the evolutionary premium placed on successful courtship can be gained by realizing that the gas bladder muscles that produce the boatwhistle mating call of the male Oyster Toadfish, *Opsanus tau* (Batrachoididae), contract at a rate of 200 Hz. This makes them the fastest contracting vertebrate muscles known, the next closest being the shaker muscles at the base of the tail of rattlesnakes, which contract at only half that rate (Rome et al. 1996).

The spawning act

The final act of spawning may take place in the water column, above the bottom, in contact with plants and rocks, and in some special cases, out of water. In external fertilizers, behaviors associated with spawning often involve rapid swimming, quivering, vibrating, fin spreading, and enfolding of the female with the male's fins or body. The breeding tubercles and contact organs common in many fishes (see above) may help maintain contact between members of a pair and may also stimulate the female. Internally fertilizing species also engage in elaborate courtship sequences. Male Guppies perform a variety of actions involving following, luring, biting, and sigmoid swimming that display their fins and body coloration until a female allows them to approach and copulate. The sequence and types of displays by the male serve as a species-isolating mechanism in that females reject males of the wrong species after viewing their courtship displays (Keenleyside 1979).

Species-specific sounds may also be produced during the spawning act itself. For example, in the simultaneously hermaphroditic hamlets, the "male" emits a courtship call and the "female" a spawning call. As individuals switch roles during a prolonged spawning bout, they also switch the sounds they produce (Lobel 1992).

Although the great majority of fishes spawn as part of large groups, **pairing** of individual males and females within these groups is common. Short-term pair formation probably assures efficient gamete release and fertilization; haphazard release of gametes could result in a large proportion of eggs going unfertilized because sperm become inviable and are rapidly diluted in open water, and eggs become unfertilizable within minutes after release (Hubbs 1967; Petersen et al. 1992). Codfishes spawn in large aggregations, but males establish small territories, actively court individual females using visual, tactile, and acoustic signals, and the pair moves synchronously to the surface where gametes are released while the genital openings of both fish are in close contact (Brawn 1961). Aggressive defense of females and pair spawning also occurs in schooling tunas (Magnuson & Prescott 1966). Pair spawning characterizes most epinepheline seabasses, which also form large breeding aggregations.

Group spawning, involving more than two fish, usually involves one female accompanied by several males (Fig. 21.6). This is the pattern in group-spawning minnows, suckers, salmon, smelt, wrasses, and surgeonfishes. In groups of Bluehead Wrasse, males release sperm in direct proportion to the number of eggs released by the female and the number of competing males in the group (Shapiro et al. 1994). In fishes with alternative mating systems, such as wrasses and parrotfishes on coral reefs, some individuals spawn as pairs whereas others spawn in multiple male groups (see above). Truly random spawning associations, as described for promiscuous species, occur most frequently in water column spawners or in such benthic spawners as herring (Keenleyside 1979).

Water column spawners on coral reefs often rush rapidly upward and release their gametes at the top of the rush, sometimes near the surface. Speeds approach 40 km/h in the Striped Parrotfish, *Scarus croicensis* (Colin 1978). This pattern has been observed in more than 50 species in over 18 families. Its function(s) are debated. Movement up in the water column places the eggs out of reach of many benthic or near-benthic invertebrate and vertebrate zooplanktivores and into currents that promote dispersal. However, by moving away from the reef, spawning adults face the conflicting threat of piscivores (e.g., Sancho et al. 2000a, 2000b). Not surprisingly, well-defended spawners (e.g., larger seabasses, trunkfishes, porcupinefishes) move higher in the water or spawn more slowly than smaller, more vulnerable species (Thresher 1984). For many species, the spawning rush may serve as a final synchronizing event in the courtship sequence and may also help evade the sneakers and streakers that abound close to the reef (e.g., Sancho 1998). Left unanswered is the question of why surface rushes are uncommon in other habitat types.

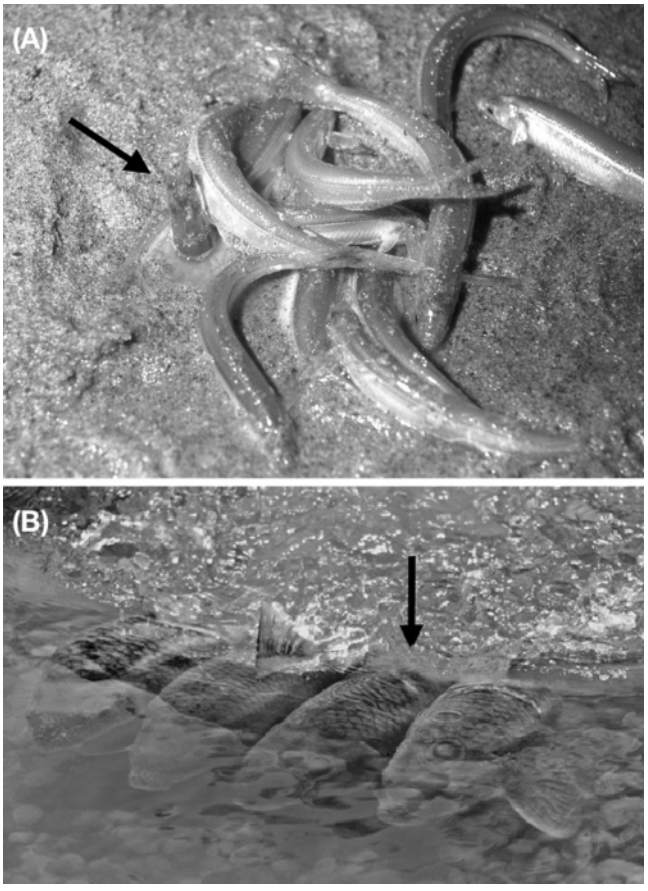


Figure 21.6
Spawning frequently involves multiple males and a single female. (A) California grunion (Atherinopsidae) spawn on beaches at the top of the tide zone, a single female (arrowed) assuming a head-up position in the sand while males encircle her and release milt. (B) Robust Redhorse Suckers (*Moxostoma robustum*, Catostomidae) typically spawn over gravel and cobbles in groups of three, a single female (arrowed) flanked on either side by a male. In this group, the female has one male on her left and two on her right. (A) photo courtesy of M. Horn; (B) photo courtesy of B. Freeman.

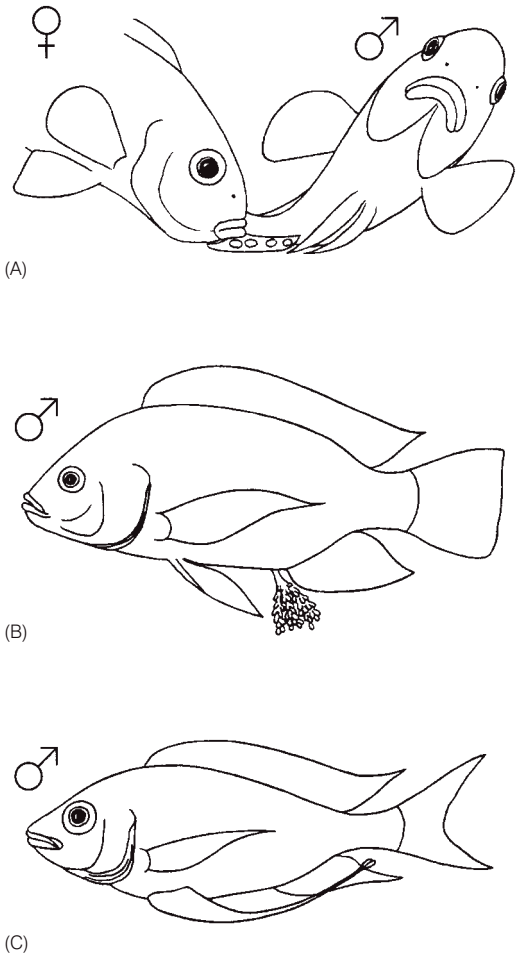


Figure 21.7
Fertilization occurs in the mouth of some female African cichlids. (A) Males of many African cichlids have round spots, termed egg dummies, on their anal fins. During spawning, the female repeatedly deposits a few eggs on the spawning site and then immediately takes them up in her mouth. The male spreads his anal fin against the bottom and the female mouths the egg dummies as the male ejaculates. (B) In some species, females instead mouth "genital tassels", which are elongate, orange lobules that grow from the genital region. (C) Other males have greatly elongate pelvic fins with enlarged, conspicuous tips that reach to the cloaca. All such structures and behaviors may facilitate fertilization, assure paternity, and minimize predation on newly laid eggs. From Fryer and Iles (1972), used with permission.

Substrate-spawning fishes are less likely to form large groups than water column spawners; they also release fewer eggs at each spawning. Males typically set up territories over appropriate spawning substrate, chase away intruding males, and court passing females. Females enter the territory and deposit one or a few adhesive eggs while the male folds his body or fins around her and presses her against the substrate. Sperm release occurs almost immediately, again in part because sneaker and streaker males are always nearby. Paternity can be assured, from the male's point of view, if females facilitate fertilization by taking sperm into the mouth, as happens in many cichlids (Fig. 21.7).

An interesting variation on oral fertilization occurs in callichthyid catfishes of the genus *Corydoras*, the popular armored catfishes of the aquarium trade. In these catfishes, the female places her mouth over the genital opening of the male and drinks his sperm. She then passes the sperm rapidly through her digestive system, extrudes eggs which are held between her pelvic fins, and releases the male's sperm to fertilize the eggs, which are then deposited on the substrate. Sperm drinking could be one way of a female maximizing control over which male fertilizes her eggs. Sperm viability in the female's gut may be facilitated by the specialized nature of the callichthyid intestine, which is modified for air breathing (see Chapter 5, Air-breathing fishes). Callichthyids pass air bubbles rapidly from their mouths to their intestines, perhaps preadapting them for passing sperm through quickly and unharmed (Kohda et al. 1995).

Fishes that spawn on the bottom generally use available structure to protect their eggs. Many eggs are adhesive and stick to plants, rocks, woody debris, shells, or other hard substrates (e.g., herring, silversides, cichlids). Some eggs have tendrils or projections that wrap around plants and debris (e.g., skates, halfbeaks, flyingfishes). Eggs of the Port Jackson Shark (Heterodontidae) have an augerlike whorl around their exterior. Females lay these eggs in cracks and water motion apparently serves to screw the egg deeper into the substrate. California Grunion (*Leuresthes tenuis*, Atherinopsidae) spawn on sandy beaches after high tides on dark nights following a full or new moon (see Fig. 21.6A; Chapter 23, Semilunar and lunar patterns). Capelin (*Mallotus villosus*, Osmeridae) also ride waves up beaches and deposit their eggs in the sand, although subtidal spawning is more common. A few fish species use live invertebrates as a spawning site. Marine snailfishes, *Careproctus* spp. (Liparidae), lay their eggs inside the gill chambers of various crabs. Species of bitterling, *Rhodeus* (Cyprinidae), use freshwater mussels as a spawning site. The male first defends and displays over a particular mussel. The female deposits eggs into the gill chamber of the bivalve using her long ovipositor, after which the male ejaculates over the incurrent siphon of the mussel. Eggs develop inside the mussel and emerge as free-swimming young (Breder & Rosen 1966).

The act of spawning brings together fish that may normally be solitary, territorial, or extremely sensitive to predators, often at locales they seldom frequent. Spawning aggregations are especially common among coral reef species, engaged in by at least 164 species in 26 families, the best known being seabasses, snappers, wrasses, parrotfishes, and surgeonfishes (Claydon 2005). As a possible mechanism to help overcome behaviors that would be counterproductive at this critical moment in a fish's life, many fishes exhibit **spawning stupor**. When in a spawning aggregation or mode, species that are normally difficult to approach or are very active instead move slowly, in an almost trancelike state. They take little or no evasive action when approached by predators or divers. Spawning stupor has been observed in minnows, suckers, mullets, silversides, seabasses, pompanos, and snappers (Johannes 1981; Helfman 1986; Johannes et al. 1999). Most observations are anecdotal, leaving open an excellent opportunity for quantified or manipulative investigations that have grown in importance because aggregating spawners are especially vulnerable to overexploitation (e.g., Fewings & Squire 1999, Sadovy & Cheung 2003).

Parental care

Extent and diversity of care

Parental care is surprisingly common, widespread, and diverse in fishes (Breder & Rosen 1966; Blumer 1979, 1982; Baylis 1981; Potts 1984; Keenleyside 1991; Sargent & Gross 1994, DeMartini & Sikkel 2006). Although most species scatter or abandon eggs upon or after fertilization, approximately 90 of the *c*. 460 families of bony fishes include species that engage in some form of defense or manipulation of eggs and young (Table 21.2; Mank et al. 2005 put the number closer to 30%, or 150 families). Parental care is more necessary for demersal or adhesive eggs that are likely to be found by predators searching along the bottom or among plants or other structure. Hence it is

Table 21.2

A classification of reproductive guilds in teleost fishes, based largely on spawning site and parental care patterns. Specific examples of many groups are given in Table 20.1. From Moyle and Cech (2004) and Wootton (1990, 1999), based on Balon (1975, 1981) with modifications.

I. *Nonguarding species*
- A. Open substrate spawners:
  1. Pelagic spawners
  2. Benthic spawners:
     - a. Spawners on coarse bottoms (rocks, gravel): (i) pelagic free embryo and larvae; (ii) benthic free embryo and larvae
     - b. Spawners on plants: (i) nonobligatory; (ii) obligatory
     - c. Spawners on sandy bottoms
- B. Brood hiders:
  1. Benthic spawners
  2. Cave spawners
  3. Spawners on/in invertebrates
  4. Beach spawners
  5. Annual fishes

II. *Guarders*
- A. Substrate choosers:
  1. Rock spawners
  2. Plant spawners
  3. Terrestrial spawners
  4. Pelagic spawners
- B. Nest spawners:
  1. Rock and gravel nesters
  2. Sand nesters
  3. Plant material nesters:
     - a. Gluemakers
     - b. Non-gluemakers
  4. Bubble nesters
  5. Hole nesters
  6. Miscellaneous materials nesters
  7. Anemone nesters

III. *Bearers*
- A. External bearers:
  1. Transfer brooders
  2. Forehead brooders
  3. Mouth brooders
  4. Gill chamber brooders
  5. Skin brooders
  6. Pouch brooders
- B. Internal bearers:
  1. Ovi-ovoviviparous
  2. Ovoviviparous
  3. Viviparous

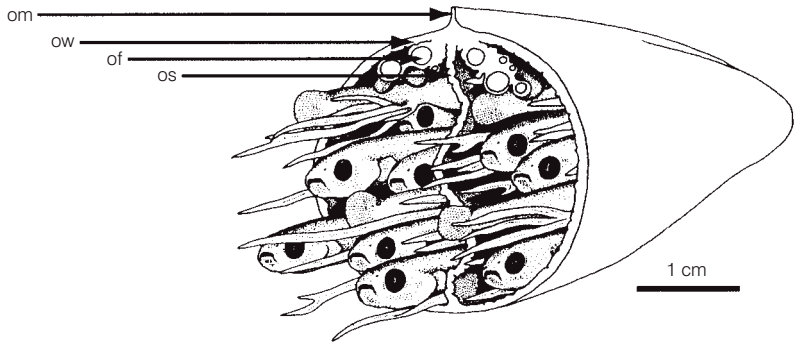


Figure 21.8

Well-developed (near-term) embryos in the ovary of a Mexican goodeid, the Butterfly Splitfin, *Ameca splendens*; 13 embryos are visible. The anterior third of the ovary is not shown. Fingerlike extensions projecting forward from the ovary are trophotaenia, which are epithelial structures that grow from the embryos' anal regions and serve to take up nutrients provided by the mother. Trophotaenia have evolved convergently in goodeids, ophidioids, and embiotocid surfperches. of, oocytes; om, ovarian mesentery; os, ovarian septum, ow, ovarian wall. Regrettably, *A. splendens* is considered to be extinct in the wild, although it is commonly kept and bred in aquaria (IUCN 2006). Drawing by Julian Lombardi, from Wourms et al. (1988), used with permission.

not surprising that few if any species with pelagic, floating eggs provide care for them.

Parental care includes: construction and maintenance of a nest; burying eggs once deposited in the nest; chasing potential egg and fry predators from the nest; fanning or splashing eggs or young with the mouth, fins, or body to provide oxygen and to flush away sediments and metabolic wastes; removal of dead or diseased eggs; cleaning eggs by taking them into the mouth and then returning them to the nest; carrying eggs or young in the mouth or gill chambers, in a ventral brood pouch, or externally on the head, back, or belly; coiling around the egg mass to prevent desiccation; retrieving eggs or young that wander from the nest or aggregation; accompanying foraging young and providing refuge or defense when predators approach; secreting specialized mucus that inhibits pathogen growth or that free-swimming young eat; and provisioning young or aiding them in the capture of food.

Internal gestation of young is a special type of parental care shown by many Chondrichthyes but occurs in only 14 families of bony fishes. Placental connections, common in Chondrichthyes, occur in only one osteichthyan family, the Mexican goodeids (Blumer 1979; Wourms 1988) (Fig. 21.8), although transfer of nutrients directly from mother to developing young (**matrotrophy**) has been demonstrated in poeciliid livebearers and sebastine scorpaenids (Marsh-Matthews et al. 2001; DeMarais & Oldis 2005; DeMartini & Sikkel 2006), and its analog (**patrotrophy**?) is thought to occur in pregnant male seahorses and pipefishes (e.g., Haresign & Shumway 1981; Berglund et al. 1986a, 1986b).

Although much guarding involves simple behavior derived from everyday activities, such as fanning eggs with the pectoral fins to maintain adequate oxygen levels (e.g., Green & McCormick 2005), some parental activities represent surprisingly unique specializations. For example, in many seahorses and pipefishes, females lay their eggs at the entry to brood pouches on the male's belly, a structure that varies in complexity within the family. The pregnant male fertilizes the eggs and retains and protects the eggs and young inside the pouch, helping them osmoregulate and providing them with oxygen and perhaps nutrition until they reach a relatively advanced stage of development (e.g., Wilson et al. 2003a). "Birth" involves contractions and contortions by the male that expel the young from the pouch. In the kurtoid nurseryfishes, an advanced perciform suborder of the southwestern Pacific, males develop a unique, downward-bent, hook on their foreheads to which the eggs are attached and carried until hatching (Fig. 21.9). The hook develops as a modification of the supraoccipital crest of the skull and is covered by highly vascularized, folded skin. Just how the eggs get there is a matter of conjecture (Berra & Humphrey 2002).

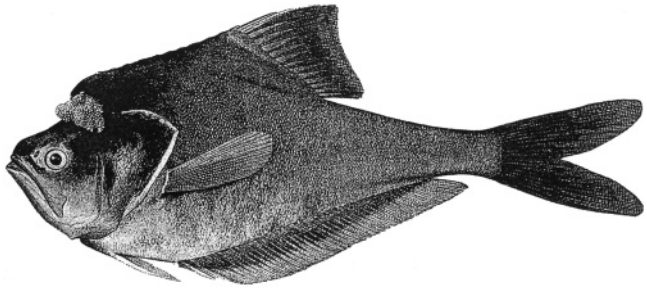


Figure 21.9

A male Nurseryfish, *Kurtus gulliveri*, with eggs attached to his occipital crest. Length about 15 cm. Drawing originally in Weber (1913), reproduced in Berra (2001).

One of the most unusual parental patterns is shown by the Spraying Characin (*Copella*, Lebiasinidae), which deposits its eggs out of water. The male and female line up under a leaf and leap together as much as 10 cm into the

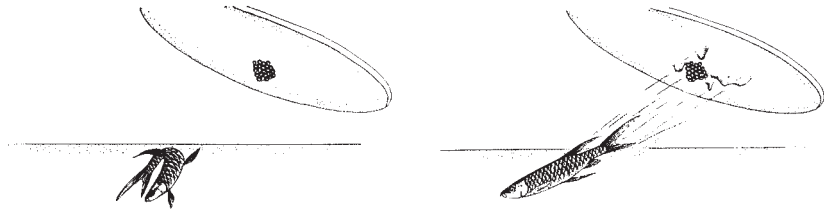


Figure 21.10
Parental care in the Spraying Characin, *Copella* sp. Eggs in this species are deposited on the undersides of overhanging vegetation, out of the water. The male guards the eggs, splashing them periodically with his tail to keep them moist. From Krekorian and Dunham (1972), used with permission.

air, turning upside down and adhering to the leaf's underside momentarily. In this manner, a dozen or so fertilized eggs are stuck repeatedly to the leaf. Over the next 2–3 days, the male moistens the egg mass by splashing it at 1 min intervals with flips of his tail, correcting for refraction at the water's surface (Fig. 21.10). Newly hatched young fall into the water (Krekorian & Dunham 1972).

Preventing desiccation of eggs exposed to air also explains unusual parental care in intertidal species. Several small, elongate intertidal fishes coil their bodies around the egg mass as the tide goes out, thus trapping a small pool of water in which the eggs sit. This behavior has been recorded for pricklebacks, gunnels, and wolf-eels (Blumer 1982). Other fishes that spawn in the intertidal, such as temperate wrasses and sculpins, cover the eggs with algae, thus controlling desiccation during low tides (Potts 1984). Rockhopper Blennies, *Andamia tetradactyla*, spawn in supralittoral nests in crevices that are above the high water mark for about 12 h daily, the male remaining with the eggs throughout the day (Shimizu et al. 2006). Depositing eggs above the intertidal – covered with algae, deposited among rocks, or buried in sand – has many surprising advantages, once desiccation is prevented. Higher incubation temperatures, higher oxygen concentrations, and reduced predation are among the considered benefits (e.g., DeMartini 1999).

A few fishes provide food for their young via epidermal secretions. Such **trophic provisioning** has been observed in bagrid catfishes and in several cichlids, including discus (*Symphysodon*), Midas Cichlid, as well as members of the genera *Aequidens*, *Etroplus*, and *Oreochromis* (Fig. 21.11A). This form of parental care is suspected in numerous other cichlids, and in a bonytongue and a damselfish. Thickened scales and increased mucus production have been identified in the adults of provisioning species. The importance of provisioning relative to other food sources of the young is unclear (Noakes 1979). Many sharks, and perhaps the living coelacanths, produce trophic eggs that are eaten by developing embryos prior to hatching (Wourms 1981; Heemstra & Greenwood 1992; see Chapter 12). One bagrid catfish in Lake Malawi, Africa, feeds trophic eggs to free-living juveniles. *Bagrus meridionalis* young position themselves under the vent of the guarding female and apparently ingest eggs as they are extruded by the mother; 40% of the young in a nest may have such eggs in their stomachs. Circumstantial evidence indicates that the parental male also helps feed the young by uncovering invertebrates present in the nest or even by spitting out invertebrates captured elsewhere into the nest (LoVullo et al. 1992).

Epidermal secretions serve additional, care-giving functions. Recent studies have shown that guarding males have specialized regions of their bodies that produce mucus with antimicrobial functions that directly benefit developing young. Nest-guarding male Fringed Darters, *Etheostoma crossopterum*, have a mucus-cell-rich region on the top of their heads. Lab tests showed that the mucus had both antibacterial and antifungal activity, and egg clutches with a guarding male present had lower mortality and significantly reduced rates of fungal and bacterial infection (Knouft et al. 2003). Earlier observations suggested that the male actively coats the eggs with mucus. Male Redlip Blennies, *Ophioblennius atlanticus*, and Peacock Blennies, *Salaria pavo*, produce a mucus enriched with antimicrobial substances from their specialized, sexually dimorphic, anal glands (Giacomello et al. 2006). When tending eggs, the males frequently rub their anal region over the nest surface, which could serve to transfer mucus to the eggs. Antimicrobial activity is turning up increasingly as different taxa are explored, and a new class of antibiotic peptides called **piscidins** has been isolated in fish mucus (Noga & Silphaduang 2003). It is a short adaptive jump from producing mucus to using such mucus to aid the survival of developing young, and it would not be surprising to find such parental specializations in other species.

The bottom of the ocean, lake, or a stream is a relatively hazardous environment for defenseless eggs, and many species carry the eggs rather than leave them deposited on the substrate. Mouth or oral brooding is the most common form of egg-carrying, having been documented in at least six families (sea catfishes, lumpfishes, cardinalfishes, cichlids, jawfishes, gouramis); gill chamber brooding occurs in North American blind cavefishes. Eggs are picked up, usually by the male, shortly after fertilization. In the case of some cichlids, eggs are fertilized in the female's mouth, where they are retained (see Fig. 21.7). In cichlids, oral brooding extends well beyond hatching. Free-swimming young forage as part of a shoal near the female. When predators approach, the female signals the young by backing slowly with the head down. The young swim towards her head and she sucks them into her mouth (Fig. 21.11B). Some predatory cichlids will ram the head region of females that are carrying young, forcing them to spit a few out, which are then engulfed by the predator (McKaye & Kocher

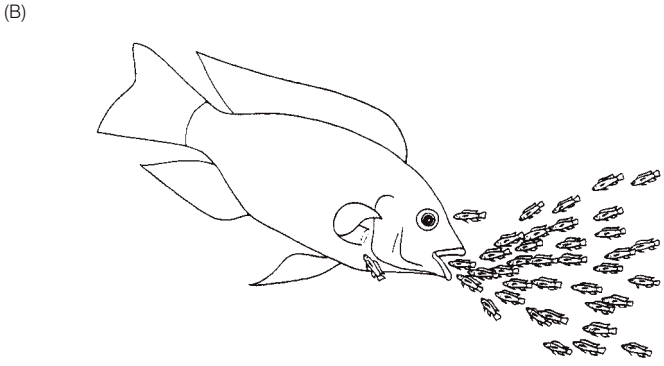


Figure 21.11

Parental care in cichlid fishes. Two of the more striking forms of parental care exhibited by members of the diverse cichlid family are shown. (A) Provisioning young. Few fishes with external fertilization actually provide nutrition for their young. Many cichlids are suspected of provisioning, but the behavior is best known in the discus, *Symphysodon*. A pair of discus is shown, with the young feeding on the mucus secretions of the female. (B) Mouth-brooding. A female opens her mouth after signaling danger to a shoal of young. Mouth-brooding of eggs is fairly widespread in fishes, but brooding of free-swimming young is relatively rare. (A) from Herald (1961), used with permission; (B) from Fryer and Iles (1972), used with permission.

1983). Other forms of external carrying include attachment of eggs to the male's lower lip (suckermouth armored catfishes) or head (nurseryfishes), or the belly of either parent (bagrid and banjo catfishes) (Breder & Rosen 1966; Balon 1975a; Blumer 1982; Berra & Humphrey 2002).

The gender of care-givers

The most common care-giver in fishes is the male. Males alone or in combination with females (= biparental care) account for approximately 80% of 77 families in which the sex of the care-giver is known; males alone care for young in 36–39 families (Blumer 1979, 1982; Mank et al. 2005). The predominance of male parental care in fishes contrasts markedly with its occurrence in other vertebrates, where care by females (amphibians, mammals) or both parents (birds) is more common (post-hatching care is uncommon in reptiles). Male guarding may be explainable as an evolutionary result of external fertilization and a male's way of assuring he alone fertilizes a batch of eggs (= **paternity assurance**) (Ah-King et al. 2005). To accomplish this, a male should: (i) provide a suitable locale where females will lay eggs to be fertilized; and (ii) guard the eggs so that no other male can fertilize them.

Paternity assurance was the likely driving force behind the evolution of brood pouches in pipefishes and seahorses. The female deposits eggs in the male's abdominal pouch, where only his sperm are likely to reach the eggs. In most species, extending care beyond the fertilization stage greatly increases the probability of successful hatching and dispersal, thereby increasing the likelihood that offspring will live to reproduce. Egg and larval predators are common in all environments, as are fungal infections. A guarding male can chase off fishes and invertebrates that might eat the eggs, and can remove diseased or dead eggs, thus slowing the spread of fungi and other infectious pathogens.

Males may care for young longer because females are more likely to spawn with males that already have eggs or young in the nest (e.g., Fathead Minnow, Three-spined Stickleback, Painted Greenling, River Bullhead, Tessellated

Darter, Browncheek Blenny). An unexpected outcome of a female preference for males with eggs is **nest and egg usurpation** (also known as **allopaternal** or **alloparental** care). Male sticklebacks will raid other males' nests, steal eggs, and deposit these eggs in their own nest. Male Fathead Minnows evict males from existing nests and then guard the acquired eggs. In **brood piracy**, a large male may usurp the nest of another male, spawn, and then abandon the nest to be guarded by the original territory holder (Van den Berghe 1988; Magnhagen 1992).

A related phenomenon is interspecific **brood parasitism** or **egg dumping**, where one species spawns in a nest constructed by and guarded by another species. Several species, including gars and minnows, spawn in nests guarded by male sunfishes, and Golden Shiner are known to spawn in nests of Bowfin and Largemouth Bass (Katula & Page 1998). Small minnows also spawn over the mound nests built by larger minnows, such as Bluehead Chub (see above); the eggs are guarded by the large male chub. The chub may benefit by a dilution effect whereby predators are likely to eat the more numerous minnow eggs, whereas the minnow eggs receive the protection of a nest guarded by a large male. A dilution effect probably explains why bagrid catfish tolerate and guard cichlid young in their nests. Mistaken identity cannot be invoked, since the guarding catfish parents selectively chase cichlid young to the periphery of the nest, exposing the cichlids to higher predation rates and decreasing mortality in the catfish young. The young cichlids benefit from the protection of two large catfish plus the mother cichlid that remains nearby (McKaye 1981b; Unger & Sargent 1988; McKaye et al. 1992).

Other examples of brood parasitism include the mochokid Cuckoo Catfish, *Synodontis multipunctatus*, of Lake Tanganyika, which parasitizes broods of several mouth-brooding cichlids by laying its eggs on the substrate as the female cichlid is picking up her own fertilized eggs. The young catfishes eventually eat the cichlid larvae (Sato 1986; Barlow 2000) (Fig. 21.12). Clariid catfishes in Lake Tanganyika are known to dump eggs in nests of auchenoglanidid catfishes (Ochi et al. 2001), and mixed species brooding has been observed in Lake Baikal sculpins (Munehara et al. 2002).

Brood parasitism carries obvious potential costs, as evidenced by the Cuckoo Catfish example, so it is not surprising that some species have tactics that apparently counteract such parasites. A Japanese fish, the taxonomically uncertain Aucha Perch, *Siniperca* (or *Coreoperca*) *kawamebari* (Percichthyidae?), is parasitized by a native minnow with a shorter spawning season; egg dumping leads to higher predation rates on perch eggs. Female Aucha Perch, which normally prefer to spawn in nests with more eggs, avoid perch nests with high numbers of eggs during the minnow's spawning season (Baba & Karino 1998).

If male care evolved to insure that no other males fertilized the eggs, then males would not be expected to provide care in 21 teleostean families with internal fertilization (e.g., Mank et al. 2005). This is almost universally true and even applies to species that are exceptional relative to the familial norm. For example, most sculpins have external fertilization and male parental care. In *Clinocottus analis* and *Oligocottus* spp., fertilization is internal and male parental care is absent (Perrone & Zaret 1979). A cardinalfish, *Apogon*

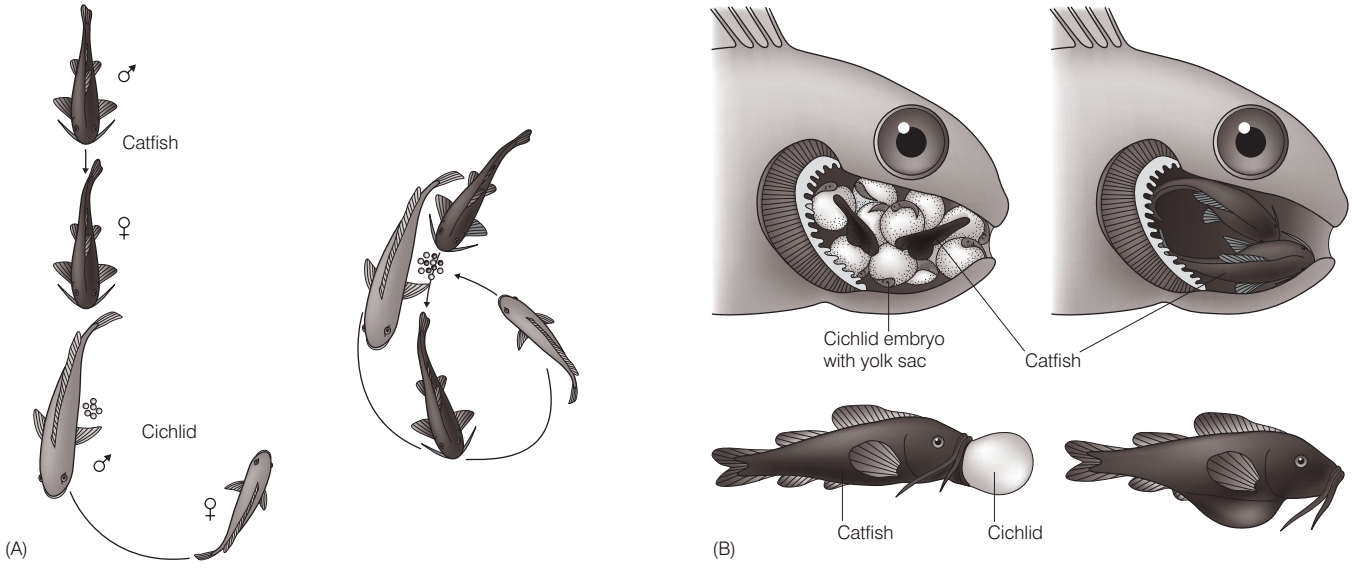


Figure 21.12

(A) Cuckoo Catfish pairs (darker fish) follow close behind spawning, mouth-brooding cichlids, laying their eggs amongst the fertilized cichlid eggs. The female cichlid picks up the catfish eggs along with her own. (B) In the mouth of the mother cichlid, catfish young hatch earlier and develop faster than cichlids, eating first the yolk sacs and eventually entire cichlid larvae. After Sato (1986) and Barlow (2000).

imberbis, is the only known species with internal fertilization and male care. Spawning occurs repeatedly over an extended 5-day period, the male chases off other males, and he also picks up eggs in his mouth immediately after they are laid, all actions that would minimize the opportunity for other males to fertilize the eggs (Blumer 1979).

A final category of care deserving attention is the phenomenon of **cooperative breeding** or **helpers at the nest**. Nonparental care-givers, usually young from a previous breeding episode, remain with the parents and feed and defend new young or defend and maintain the territory. Such helpers occur in over 150 bird and 25 mammal species and in at least 19 species of Lake Tanganyika cichlids (Taborsky 1984; Heg & Bachar 2006). Two of the best-studied Tanganyika species are *Neolamprologus pulcher* and *Lamprologus brichardi* (e.g., Stiver et al. 2006). In *L. brichardi*, helpers remain for about a year through two to three subsequent breeding cycles. They clean and fan eggs, larvae, and fry, remove sand and snails from the breeding hole, and defend the parental territory. Helpers suffer slower growth rates than nonhelping individuals, but receive protection from predators due to territorial shelters and the protective activities of larger family members. Females with helpers produce more fry.

Helping generally imposes a cost because helpers do not reproduce directly while remaining with their parents. However, helpers may promote their fitness (contribution of genes to future generations) more by raising siblings to whom they are closely related than by attempting to breed on their own. Helping is thus an example where kin selection explains an apparently altruistic activity. It is somewhat remarkable that cooperative breeding in fishes has as yet only been observed in related cichlids in Lake Tanganyika (helpers among anemonefishes are suspected but to date been found lacking, e.g., Buston 2004). Cooperative breeding among cichlids is additional evidence of the tremendous ecological and evolutionary plasticity of that family (Kawanabe et al. 1997; see Box 15.2).

The costs of care

As with foraging (see Chapter 19), caring for offspring by parents creates a series of potential trade-offs. A guarding parent often has reduced opportunity to feed, which may reduce later gamete production (e.g., in salmons, ricefishes, and livebearers; Blumer 1979). Male Smallmouth Bass, *Micropterus dolomieu*, fan their nests 24 h a day when they have eggs and young there and rarely leave the nest to feed; mortality among males during their first breeding season can exceed 90% in some lakes (Wiegmann & Baylis (1995). Gillooly and Baylis (1999) measured change in the whole-body composition of male Smallmouth Bass in the field across an 8-day parental care period. They found that nest-guarding males lost an average of 3% of lean mass, a potentially significant amount given that breeding occurs shortly after fish come out of the winter starvation period. Other fishes known to suffer energy loss, decreased growth, delayed reproduction, compromised immune function, or higher mortality due to parental care include Three-spined Sticklebacks, cichlids, other centrarchids, cardinalfishes, and gobies (e.g., Chellappa & Huntingford 1989; Lindstrom 2001; Okuda 2001).

Some costs can be overcome in part if the male eats some of the eggs, a phenomenon known as **filial cannibalism** (Fitzgerald 1992; Manica 2002; DeMartini & Sikkel 2006); Smallmouth Bass males, however, do not eat their young. Such cannibalism is known in at least 17 teleost families, with starvation avoidance by the adult the most likely cause (Manica 2002). Feeding while guarding young is relatively rare in mouth-brooding species. Another cost incurred when nest guarding is lost opportunity to spawn, which compromises future reproductive output. The decision of when to abandon current progeny will therefore be influenced by how much a parent's guarding activities can reduce mortality in the current clutch versus what opportunities for breeding exist in the near future (Perrone & Zaret 1979; Sargent & Gross 1994). Short breeding seasons, scarce additional mates, and short lifetimes would favor parental care of existing offspring over searching for additional spawning opportunities. Females can exploit this dilemma by preferring males that are already guarding eggs (see above).

Caring for young also carries predation risks. Brood defense may reduce predation on the young but simultaneously increases the parent's exposure to predators. Guarding parental sticklebacks, Pumpkinseed Sunfishes, and gobies take more risks as their offspring grow, indicating that the value of the brood can increase relative to parental survival during the parental care phase (Colgan & Gross 1977; Pressley 1981; Magnhagen & Vestergaard 1991). Finally, an inverse relationship often exists between degree of care and number of eggs produced. Pelagic egg scatterers produce hundreds of thousands or millions of tiny eggs that they abandon, whereas species that participate in extensive parental care characteristically produce relatively small clutches of dozens to a few hundred larger eggs. High-quality care may only be possible when small numbers of young are produced. The ultimate evolutionary product, however, is how many offspring make it into the next breeding generation. The existence of **alternative tactics** within and among species attests to the fact that no single reproductive system is universally optimal.

Alternative mating systems and tactics

The literature on social and reproductive behavior in fishes has increasingly focused on the variety of tactics that fishes

use, both among and within species. That interspecific differences should arise is not surprising given the different ecologies and evolutionary histories of different lineages. Intraspecific variation is more puzzling, since we tend to think in terms of species characteristics and "species-typical" behavior.

In addition to initial and terminal males in sex-changing wrasses, small alternative males also exist among gonochoristic fishes such as minnows, salmons, midshipmen, sticklebacks, livebearers, topminnows, sunfishes, cichlids, wrasses, blennies, and gobies (Taborsky 1994) (Fig. 21.13). In the Bluegill Sunfish, *Lepomis macrochirus*, larger, older **parental** males (17 cm long, 8.5 years old) construct nests, court females, and then guard the eggs that they fertilize. Two forms of cuckolder males parasitize the parental males. **Satellite** males are intermediate in size and age (9 cm, 4 years old); they mimic female coloration and behavior and hence gain access to a nest, interposing themselves between the parental male and the female during spawning. Smaller, **sneaker** males (7 cm, 3 years old) lurk in nearby vegetation and dart through nests during spawnings, depositing sperm literally on the run. These three options arise from two discrete alternative life histories: parental males that delay maturation, grow large, and begin spawning when they are older than 7 years old versus cuckolder males that mature as small 2-year-olds, acting first as sneakers and then later (when they achieve the size of reproductive females) as satellite males. Cuckoldry becomes a viable alternative only when parental males are abundant because parental males provide the breeding opportunity (Gross 1984).

Pacific salmons of the genus *Oncorhynchus* demonstrate an analogous pattern (Fig. 21.13). Male Coho Salmon, *O. kisutch*, occur as two types in spawning streams. Large (52 cm long, 2.5 years old), colorful **hooknose** males court the females that have dug linear nests (redds) in the gravel bottom. Breeding success is directly related to male size and proximity to females; larger fish fight successfully to be closest and thereby spawn most. A second group of males, called **jacks**, are smaller and younger (34 cm long, 1.5 years old). These males hide in nearby stream debris and dash onto the redd as the hooknoses are spawning with females. Intermediate-size fish are relatively rare, probably because they are too small to fight successfully and too large to hide successfully. Again, sneaking provides a spawning opportunity for small males that otherwise could not compete with large males for access to females (Gross 1984).

In both examples, it is still unknown whether the alternative tactics are brought about by genetic or environmental influences or a combination of the two. Are cuckolders and jacks genetically programmed to behave as such, do they develop in response to immediate environmental conditions – including the density of larger, parental or hooknose fish – or do genes and environment combine to determine proportions of males? A combination of influences is indicated by the salmon data. Jacks develop from fish that grow faster when young. Clearcutting around

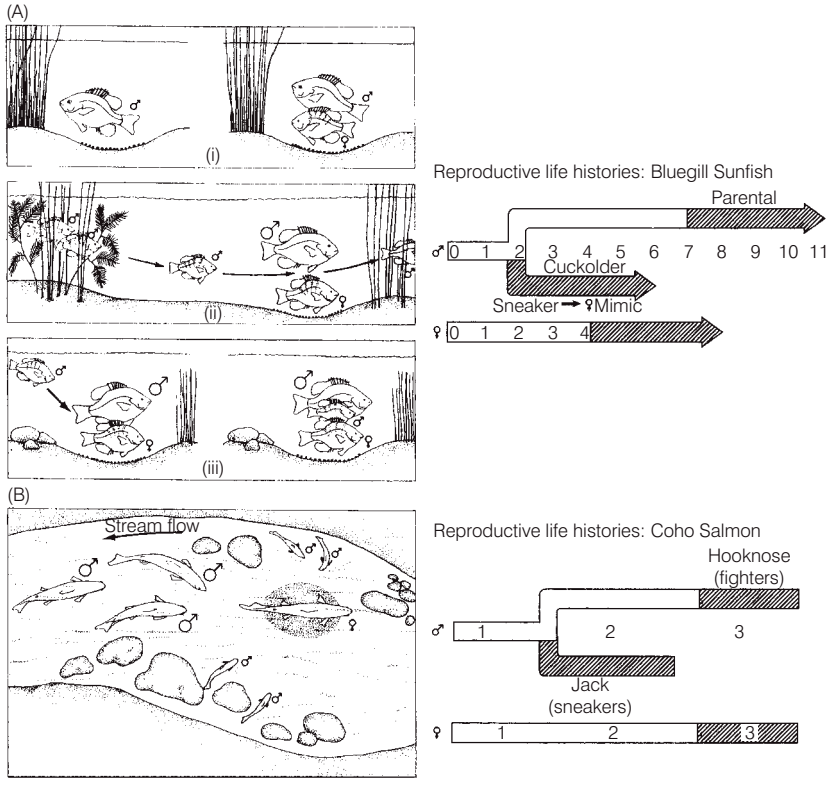


Figure 21.13

Variations in life history and behavior result in alternative mating tactics in male Bluegill Sunfish and Pacific Salmon. Both species are characterized by large, territorial males that court females and fight other males versus smaller males that interject themselves during spawnings by larger males. (A) Bluegill males occur as: (i) large males that dig nests, spawn, and guard eggs; (ii) small sneaker males that hide in vegetation and dart past spawning pairs, quickly depositing sperm; and (iii) intermediate satellite males that mimic female coloration and behavior and thus gain access to spawning pairs. The life history alternatives for male Bluegill are to mature at a young age and small size and adopt a sneaker and then later a female mimic role, or to mature later at a larger size and adopt a courting and parental role. All females mature at an intermediate size and age. (B) Coho Salmon males occur as large, hooknosed males that fight for access to females in midstream, or as smaller jacks that hide near structure or in shallow water and sneak copulations. Life history alternatives for the salmon are to mature at a young age and small size and adopt a sneaker role, or to mature later at a larger size and adopt a fighting role. All females mature at a relatively large size and old age. Modified from Gross (1984, 1991), used with permission.

streams typically raises stream temperatures and increases the amount of debris, promoting faster growth and thereby producing more jacks and more habitat favorable to jacks. Hatcheries favor and produce faster growing fish, and intense fishing pressure also targets the larger fish. Ironically, human activity and exploitation appear to be selecting for less desirable, smaller, "alternative" fish (Gross 1991).

Alternative mating tactics representing variations on the above patterns exist in other fishes (e.g., Fallfish Minnows, cichlids, Peacock Wrasses, blennies, gobies; Ross 1983; Van den Berghe 1988; Barlow 1991; Magnhagen 1992; Henson & Warner 1997; Taborsky 2001; Neat et al. 2003). Why fishes are so labile in mating and life history patterns is problematic. In many instances, the existence of one pattern creates the conditions that favor the development of the other: sneakers depend on territorial males to provide them with breeding opportunities. However, sneaking is negatively frequency dependent in that, because of competition, the advantages of sneaking decrease as the density of sneakers increases. Alternatively, no single strategy may confer a consistently greater selective advantage over others, so each is favored at different times and is consequently maintained at least at low frequencies in a population. Finally, differing reproductive modes may represent nothing more than alternative, equally adaptive responses to similar environmental forces (Fischer & Petersen 1987).

Summary

SUMMARY

1. Reproductive success is the ultimate determinant of adaptations. Factors that characterize the breeding systems of fishes include frequency of mating, number of partners, and gender role of individuals. Not surprisingly, fishes show considerable inter- and intrataxonomic variation in all factors. Most fishes spawn repeatedly, but some (lampreys, eels, salmons) spawn only once during their lives. Most fishes have multiple breeding partners, but examples of polygyny, polyandry, and monogamy are not uncommon.
2. Gender roles in fishes are labile. Although most fishes remain one functional sex throughout their adult lives, sex reversal in either direction is fairly common. Strong influences on the occurrence, timing, and direction of sex reversal include the social environment, in terms of the number of members of each sex, their relative positions in dominance hierarchies, and the relative reproductive contributions of the sexes at different sizes. All-female species of parthenogenetic livebearers use sperm from donor males to activate cell division in eggs, but the male's genes do not contribute to future generations.
3. Sexually selected traits are those that result from intrasexual competition and from the breeding preferences of the opposite sex. Anatomical differences between sexes are called sexual dimorphisms, and include differences in body size, shape, color, dentition, or ornamentation. In most fishes, the male is the "dimorphic" sex (except that females are generally larger). Many fishes develop breeding tubercles or contact organs, again primarily in the males. A major cost of dimorphisms is that the dimorphic sex is more conspicuous to predators.
4. Many fishes spawn in nests that may be simple depressions in the bottom or more elaborate structures made of rocks or vegetation and constructed (usually) by the male, occasionally glued together with body secretions. Truly random mating is rare; some choice of mates is the norm. The spawning act itself often involves elaborate body and fin movements, color change, and chemical and sound production.
5. Once eggs are laid, the male most commonly guards them until they hatch. Internal gestation by females occurs in most elasmobranchs and in a few bony fishes. Mouth-brooding is practiced by many cichlids, some catfishes, cardinalfishes, and a few other families. Eggs may also be carried in male brood pouches or attached to the head (seahorses, nurseryfishes). Some cichlids provide food for young in the form of epidermal secretions. Parental care obviously increases survival of the young but limits the future spawning activities of the parents and exposes them to increased predation. Helpers at the nest, in the form of young from previous broods, are known from a few cichlids.
6. Not all members of a population use the same reproductive tactics. Sneaking is known from many species (salmons, sunfishes, wrasses, gobies) in which generally smaller males lurk on the edge of a spawning area and dash in rapidly while a territorial male is spawning. Whether such alternative tactics are genetically fixed in individuals or represent modifiable responses is unknown.

Supplementary reading

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Chapter **22**

Fishes as social animals: aggregation, aggression, and cooperation

Chapter contents

CHAPTER CONTENTS

Fishes associate during non-mating periods to help or hinder one another. Social interactions, involving aggression or cooperation, occur between individuals of the same species (**intraspecific** interactions) as well as between different species (**interspecific** interactions). Nonreproductive social patterns in fishes involve solitary or territorial individuals, pairs, loose aggregations, and relatively permanent schools or colonies that may change daily, seasonally, and ontogenetically. Fishes keep apart or together through highly evolved transfers of information (communication) that may involve several sensory modes. Our object in this chapter is to review examples of non-mating social interactions in fishes, particularly the influence that communication has on patterns of aggregation, spacing, aggression, and cooperation, to show the diversity of evolved solutions to problems of survival and, ultimately, reproduction. Reproduction and predator–prey interactions are sufficiently influential in fishes to warrant separate chapters (see Chapters 19–21).

Communication

Communication involves the transfer of information between individuals during which at least the signal sender derives some adaptive benefit (Myrberg 1981). To send information, the signal sender must **contrast** with (stand out from) the background. Although this is most obvious (to us) in a visual context – where bright objects are most easily seen against dark backgrounds and dark objects against bright backgrounds – the contrast principle applies to all sensory modes. Background noise, be it visual, acoustic, chemical, tactile, or electric, will mask a signal. Information is transmitted when the signal exceeds the noise; conversely, an animal becomes cryptic if it blends in with the background. The message sent usually results in repulsion or attraction or may inform the signal receiver about the physiological state or behavioral motivation of the sender. Frequently, signals from several modes are combined to enhance the message and reduce ambiguity.

Visual communication

Vision plays a critical role in fish communication in most environments (see Chapter 6). Coloration is dependent on **hue** (wavelength mixtures), **saturation** (wavelength purity), and **brightness** (light intensity) (Hailman 1977; Levine et al. 1980). Coloration is incorporated into scales, skin, fins, and eyes as the product of pigments, achromatic elements, or structural colors. Pigmented cells (chromatophores) in the dermis contain carotenoids and other compounds and

reflect yellow, orange, and red. Achromatics are black and white. Black coloration results from the movement of melanin granules within melanophores; dispersed melanin darkens a fish, whereas melanin concentrated in the melanophores makes the fish appear lighter in color. White coloration comes from light reflected by guanine crystals in leucophores and iridophores. Greens, blues, and violets are generally structural colors produced by light refracted and reflected by layers of skin and scales; the color depends on the thickness of the layers relative to the wavelength of the light (Lythgoe 1979; Levine et al. 1980).

The diversity of color in fishes is essentially unlimited, ranging from uniformly dark black or red in many deepsea forms, to silvery in pelagic and water column fishes, to countershaded in nearshore fishes of most littoral communities, to the strikingly contrasted colors of tropical freshwater and marine fishes (Box 22.1). Visibility (and invisibility) depends on a combination of **fish color**, the **transmission qualities** of water in specific habitats, **background** characteristics, and the **visual physiology of the eye**, especially the retina (Losey et al. 2003; Marshall et al. 2003a, 2003b).

Melanin and guanine reflect light across the entire visible spectrum and are therefore "available" for use in almost all habitats. Black and white are among the most commonly used colors in fishes (e.g., minnows, characins, catfishes, sunfishes, damselfishes, butterflyfishes, grunts, drums, cichlids, gobies, triggerfishes). In the clear waters of a coral reef or tropical lake, yellow and its complement indigo blue are most visible; these are the colors commonly found on butterflyfishes, angelfishes, grunts, damselfishes, parrotfishes, and wrasses on reefs and on characins, minnows, Guppies, rainbowfishes, and cichlids in tropical waters. Nearshore temperate habitats, particularly in fresh water, tend to be stained with organic compounds that give them a yellowish tinge. Red and its complement blue-green are more visible under these conditions and it is not surprising that the breeding colors of minnows, salmonids, sticklebacks, darters, and sunfishes often incorporate these (Lythgoe 1979).

Colors on a fish's body may be used in **static** or **dynamic displays**. Static coloration is generally an identification badge that informs about the species, sex, reproductive condition, or age of a fish. Species identification is achieved through a combination of body form and color; ichthyologists as well as fishes use this combination in determining a species' identification (Thresher 1976). In the myctophid lanternfishes, the number and pattern of photophores (light organs) is species specific and probably aids in schooling and as a sexual isolating mechanism. The taxonomic skills of many fishes are quite good; the Beau Gregory Damselfish can apparently distinguish among approximately 50 different species of reef fishes that intrude on its territory (Ebersole 1977).

Sexual dimorphism in coloration and body morphology is common in fishes, occurring as a permanent distinction in many tropical species or more seasonally in temperate fishes; generally males are the dimorphic or more distinctive sex (see Chapter 21). Ontogenetically distinctive coloration may aid in the identification of potential schoolmates, augmenting the tendency of fishes to aggregate with members of equal size (see below). In at least 18 coral reef families, juveniles differ from adults in color pattern (Thresher 1984) (Box 22.1). As French grunts (Haemulidae) settle from the plankton and take up residence on a coral reef, they develop at least four distinctive color phases associated with changes in habitat and behavior (McFarland 1980).

Dynamic displays involve either rapid exposure of colored, previously hidden structures or changes in color. Dynamic displays include movements of the body, fins, operculae, and mouth. Often fin erection or gill-cover flaring exposes patches of color that contrast sharply with surrounding structures. Grunts open their mouths in head-to-head encounters to expose a bright red mouth lining. Many fishes flare their gill covers during aggressive, head-on encounters; gills and gill margins often contrast with the rest of the body (salmonids, centrarchid sunfishes, cichlids, labrids, Siamese Fighting Fishes). Fin erection and coloration play a dominant role in visual displays, probably because the movement associated with their erection is particularly eye catching. As a result, differential coloration of fins (inclusion of spots and stripes) is common. Fin flicking serves in calling young to parents, as a schooling signal, and during **agonistic** interactions ("agonistic" refers to aggressive and submissive activities, as in the verb "to agonize").

A special case of dynamic display involves the flashing of bacterially produced light by ponyfishes (Leiiognathidae), in which males "shine" their light inward toward a reflective coating of the swim bladder (Fig. 22.1). The light then passes outward through transparent skin and a moveable, muscular shutter in the body wall. Males in schools

Figure 22.1

A nighttime photograph of a male ponyfish, *Leiognathus elongatus*, emitting light from its specialized circumesophageal light organ. The light display is the bright rectangular area just posterior of the pectoral fin. Light emission involves a complex series of structures and behaviors including bacterial light production, internal reflection, and transmission through a muscular shutter in a transparent section of the body wall. Four different light displays have been described in which duration and intensity of light emission are varied. From Sasaki et al. (2003), used with permission.

sometimes coordinate light flashing in spectacular, synchronized displays (Woodland et al. 2002; Sasaki et al. 2003).

Changeable colors serve primarily to advertise alterations in the behavioral state of a fish, or to conceal a fish from aggressors or predators. During agonistic, predator–prey, and breeding interactions, individuals will blanch or darken and develop bars or spots on a moment to moment basis (minnows, dolphinfishes, rudderfishes, cichlids, damselfishes, surgeonfishes, tunas, flatfishes). One can often predict the winner of a territorial encounter by observing differences in body shading. On a circadian basis (see Chapter 23), even the most colorful fishes by day turn relatively dull or blotchy at night. For example, neon and cardinal tetras (*Paracheirodon*, Characidae), which are brilliant blue-green and red by day, assume an inconspicuous pinkish tinge as they rest on the bottom at night (Lythgoe & Shand 1983). Such changes suggest that many visually mediated agonistic interactions cease with nightfall, but that many piscivorous fishes are still capable of locating prey at night using visual cues (Helfman 1993).

Short-term color change is primarily under the immediate control of the nervous system, whereas longer term ontogenetic and seasonal changes are more likely controlled by hormone levels. Seasonal color change is most often associated with the onset of breeding activity, when territorial males develop bright, contrasting coloration (see Chapter 21). In the spring, North American minnows and darters assume color patterns that rival those in any tropical reef or river assemblage. Females in many of these species undergo less dramatic seasonal changes. Interesting ontogenetic changes occur in migratory salmonids and anguillids. Many juvenile salmonids live in streams and combine countershading with vertically oblong, dark "parr" marks that may be disruptive in function. These fish migrate to the open ocean as smolts and develop a silvery coloration that is more effective camouflage in open water, pelagic situations. Upon returning to their natal (birth) stream, many species assume a bright, boldly contrasting breeding coloration that is the antithesis of camouflage. Anguillid eels change from transparent pelagic larvae to countershaded stream- and lake-dwelling juveniles, to bronze or silvery oceanic, reproducing adults.

Visual agonistic displays often involve highly **stereotyped** movements. Combat may involve lateral displays, where two fish swim in place with fins spread, oriented either parallel or antiparallel (head to tail) (Fig. 22.2). As an interaction escalates, fish may begin body beating, a vigorous swimming-in-place that pushes water at an opponent and that may indicate the relative strengths of the combatants. Hence tactile and acoustic, near-field information may be added to the visual display. Antiparallel fish may strike one another with the pectoral fins (as in the anemonefish, *Amphiprion*) or may "carousel", swimming in tight circles around one another. Carouseling can lead to biting of caudal fins or chasing. Color changes frequently accompany lateral displays, and "color fights" occur in some species as different color phases indicate different levels of aggression (e.g., the nandid, *Badis badis*; Barlow 1963). Frontal displays, sometimes with fish facing each other head on and even grabbing each other's mouth, are also common (e.g., in grunts, Corkwing Wrasse, Kissing Gouramis).

Ritualized combat can decide the outcome of an interaction without actual physical fighting. It is in the best interests of both opponents to settle a dispute without incurring injury. The potential for such injury obviously varies among species, but can be considerable, as has been discovered by scuba divers who ignored the distinctive, ritualized, head-swinging displays of apparently territorial Gray Reef Sharks (Johnson & Nelson 1973) (Fig. 22.3). White Sharks also engage in apparently ritualized, agonistic displays toward other White Sharks, including parallel swimming and slapping the tail on the surface in the direction of another White Shark during a feeding bout (Klimley et al. 1996).

A particularly nice example of the multiple functions of visual displays involves the Flashlight Fish, *Photoblepharon palpebratus* (Anomalopidae; Morin et al. 1975). This 6 cm long, nocturnally active fish lives in the shallow waters of

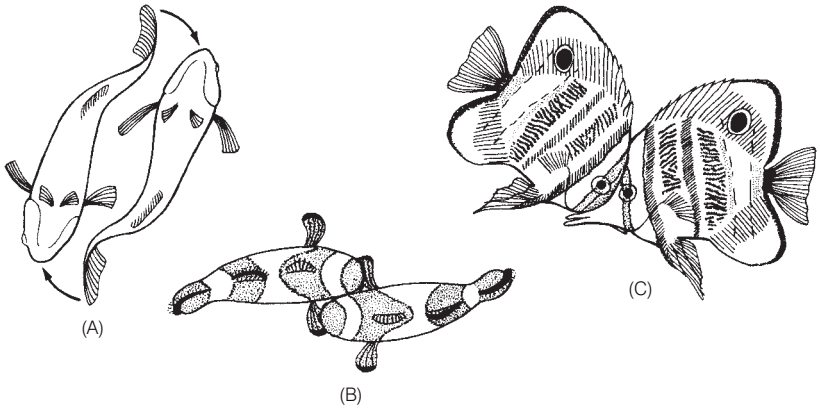


Figure 22.2

Lateral and frontal displays in fishes. During agonistic interactions, fish may line up parallel, antiparallel, or head-to-head and remain stationary, spread fins or operculae, change colors, and swim in place or circle one another. (A) Typical swimming-in-place lateral display when water currents (arrows) are directed at the head of the opponent, as happens in many cichlids. (B) Lateral display in the clownfish, *Amphiprion*, during which individuals strike each other with their pectoral fins. (C) Head-to-head pushing in the butterflyfish, *Chelmon rostratus*. (A) after Chiszar (1978); (B, C) after Eibl-Eibesfeldt (1970).

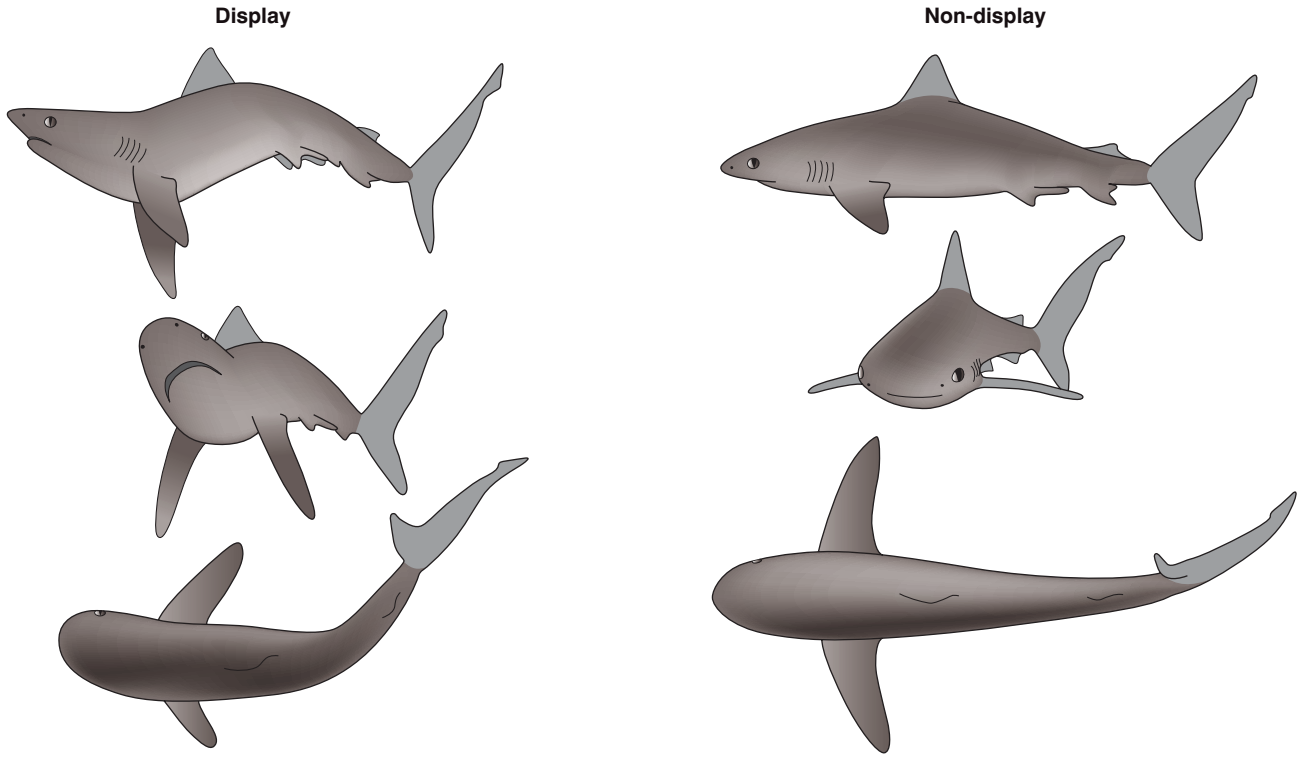
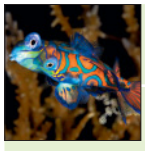


Figure 22.3

Exaggerated swimming display of the Gray Reef Shark, *Carcharhinus amblyrhynchos*. When approached by a diver or another shark or a small submarine, or when competing for food, Gray Sharks lift the snout, arch the back, lower the pectoral fins, and swim in a tense, exaggerated manner (exaggerated postures shown on left, comparatively normal swimming postures on right). If the intrusion continues, the displaying shark may attack the intruder. Similar displays, without attacks, have been observed in Galàpagos, Silky, Lemon, and Bonnethead sharks, and a Bull Shark performed exaggerated S-turn swimming before attacking a small boat that had been following it (S. Gruber, pers. comm.). After Johnson and Nelson (1973), used with permission.



Box 22.1

BOX 22.1

The function(s) of coloration in coral reef fishes

No single topic has dominated the literature on coloration in fishes more than the question of why many coral reef species are so brightly and boldly ornamented. Numerous coral reef families contain spectacularly colored members, including seabasses, grunts, drums, butterflyfishes, angelfishes, Moorish Idols, hawkfishes, damselfishes, wrasses, parrotfishes, dragonets, gobies, surgeonfishes, rabbitfishes, triggerfishes, and filefishes. Even normally drab families such as nurse sharks and moray eels have coral reef representatives with bold coloration.

Discounting speculation that bright coloration in reef fishes is nonadaptive, most hypotheses have focused on coloration serving an **informational** or **anti-informational** function. Anti-informational, camouflage functions were favored by earlier workers who felt that bright coloration served as protective resemblance when a fish was compared with the brightly colored background of corals, sponges, tunicates, and algae on the reef (Longley 1917). However, background matching (aside from countershading) more often characterizes benthic animals that are relatively immobile. Active reef fishes would continually change the background against which they were viewed, often making them a contrasting, conspicuous target.

Crypsis may be more effectively achieved via **disruptive coloration** (Cott 1957; see Chapter 20, Camouflage). Many reef fishes contain large patches of dark and light or adjacent contrasting colors. Boldly contrasting dark and light areas that do not follow the outlines of the body tend to break up that profile. Visually hunting predators recognize objects in part by their shape, and a disrupted body outline

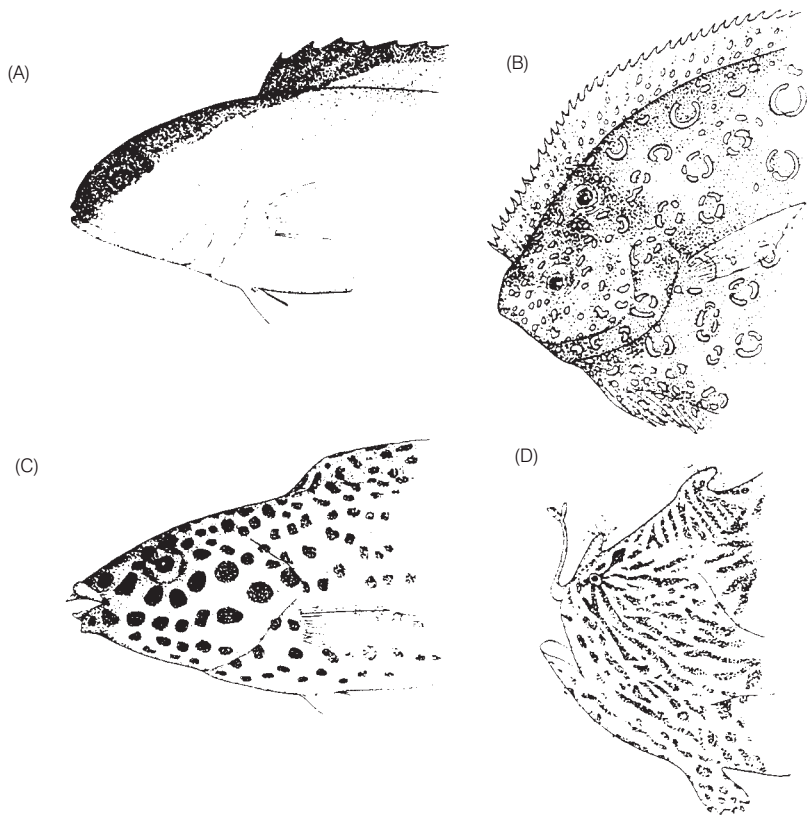


Figure 22.4
Color patterns that camouflage the eye in reef fishes. Predators and prey alike focus on the eyes of other fishes, and many fishes have color patterns that tend to mask the eye or call attention away from it. (A) A Blackcap Basslet (Serranidae): the dark eye is contained in a dark area. (B) A Peacock Flounder (Bothidae) and (C) a wrasse (Labridae): numerous false eyes call attention away from the real eye. (D) A frogfish (Antennariidae): a small eye is subsumed in a series of radiating patterns that converge on different points. From Barlow (1972), used with permission.

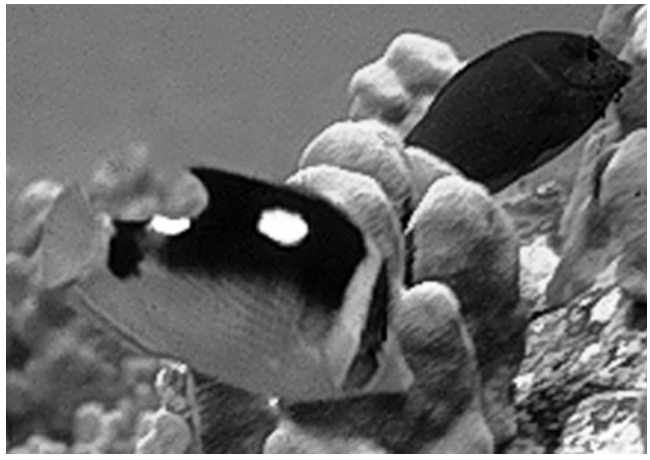
is more difficult to identify. Barlow (1967) suggested that the split-head coloration of many reef piscivores that lurk for or sneak up on prey (e.g., groupers, triplefins) was a disruptive pattern.

Another visual cue used by predators and prey alike is the eye itself. Animals notice and watch the eyes of other animals. When spearfishing, experienced hunters avoid looking directly at their prey and can thereby move closer. In many reef fishes, real eyes are often concealed and false eyes are created. This is accomplished via dark head coloration around a dark eye, or reticulated or mottled body coloration that may include numerous circular patterns (Fig. 22.4). These patterns make the eye blend into the head. Additionally, a prominent dark line that conforms to the profile of the head may pass through the eye. This line is usually a lateral stripe in elongate fishes or a vertical bar in deep-bodied fishes (Barlow 1972). False eyespots, consisting of concentric, contrasting colors and termed **ocelli**, may also occur on or near the caudal peduncle (butterflyfishes, snappers, juvenile damselfishes and angelfishes, bothid flounders, also Bowfin, Red Drum, and several New World cichlids) or on the soft dorsal fin (damselfishes, plesiopids, also notopterid featherfins, centrarchid fliers, mastacembelid eels). Such ocelli may draw attention away from the animal's real and presumably vulnerable eye, may intimidate or disorient a predator that is about to strike, or may function as a head mimic and reduce damage from fin-biting predators (Neudecker 1989; Winemiller 1990a; Meadows 1993) (Fig. 22.5). Ocelli may also serve as shoaling signals to maintain group cohesion.

The alternative interpretation of reef fish coloration is that it serves an information-providing function. Many reef fishes are highly social, interacting both intra- and interspecifically. The clear waters of the reef offer an opportunity for visual signals to evolve. Reef fishes have been referred to as **poster colored** to emphasize their conspicuousness and the possible advertising function of their color patterns (Lorenz 1962; see also Breder 1949). The species-specific nature of color patterns also argues for their role in helping individuals tell species apart during mating, aggregating, or territorial encounters (e.g., Harrington 1993). Color patterns often differ among individuals, allowing **individual recognition** of territorial neighbors or of partners as a pair moves across the reef (Reese 1981; Wilson et al. 2006c). The placement of yellow, red, and black patches posteriorly may help the trailing member of a pair maintain visual contact in the complex reef environment (Kelley & Hourigan 1983). Some angelfishes and surgeonfishes are colorful and territorial as juveniles, but both color and aggressiveness fade later in life. Such an ontogenetic correlation between agonism and poster coloration is additional support for an informational function of reef fish coloration

Figure 22.5

A Fourspot Butterflyfish, *Chaetodon quadrimaculatus*, in the field that has suffered an obvious wound in the region of its posterior ocellus or eye spot. Rare photos such as this one are indirect evidence that ocelli serve as deflective marks that direct the attacks of predators away from more vulnerable head regions. Photo by P. Motta, used with permission.



(Thresher 1984). Also, the eye of many reef fishes is if anything exaggerated and highlighted, sitting at the convergence of radiating lines or outlined in bright, contrasting colors (e.g., some seabasses, angelfishes, damselfishes, wrasses, jawfishes, clinids, surgeonfishes; also some centrarchid basses and cichlids).

Undisturbed reef systems contain an abundance of large, visually hunting predators (lizardfishes, trumpetfishes, cornetfishes, scorpionfishes, flatheads, groupers, hawkfishes, jacks, snappers, emperors, barracuda, flatfishes; Hobson 1994). How can small reef fishes afford to be conspicuous? The answer may lie partly in the reef structure itself. Few other habitats contain the variety and number of hiding places of a healthy coral reef. With adequate refuge sites available, the coloration of fishes that live close to the reef is less constrained by predators than in related, non-reef species. Such correlations hold well for families like damselfishes, wrasses, parrotfishes, rabbitfishes, dragonets, and gobies in which water column-, sand-, or grassbed-dwelling species are often countershaded or drab whereas near-reef species are more boldly colored.

Water clarity can also work against predators, whose activities are conspicuous to potential prey at considerable distances. Diurnally active prey fishes typically have eyes containing dense arrays of small cones that are ideal motion detectors during bright illumination (see Chapter 6, Vision). Any predatory movements will be detected at great distances, allowing prey to take flight or cover long before an attack occurs. Not surprisingly, nocturnally active fishes are not typically poster colored but instead possess relatively uniform coloration. Diurnal fishes seek shelter at night and assume subdued colors that include blotchy, presumably disruptive, camouflage hues. Bright illumination, clear water, and abundant refuges have apparently served to liberate coloration in diurnal reef fishes from its usual anti-informational, cryptic function to an informational, communicative function (Thresher 1977). An analogous pattern holds for African cichlids, where small species that live over and take refuge in complex substrates (rocks, snail shells) tend to be much more boldly colored than larger relatives that live over sand or in the water column (Barlow 1991).

Are reef fishes cryptically or conspicuously colored? In all likelihood, they are both (Marshall et al. 2003b). Many early treatments attempted to explain reef fish coloration from dead specimens or from photographs of live individuals taken with unnaturally powerful lights striking fish at unnatural angles. Behavioral observations may provide the best answers. Agonistic encounters occur between neighboring fishes, whereas predatory encounters occur over larger distances. The bright and contrasting colors that many reef species use in their signals and displays may not be visible over the distances at which predator–prey interactions occur because red, orange, and yellow wavelengths are attenuated much more quickly in clear water than are blues and greens (e.g., Marshall 2000). With the brighter colors "gone", such patterns as countershading may conceal a potential prey individual from a searching predator.

In addition, reef fish color is not static. Butterflyfishes are among the most colorful of the reef fishes. They and many other boldly colored reef fishes are also countershaded. During aggressive intraspecific encounters in the Raccoon Butterflyfish, *Chaetodon lunula*, the countershading fades and the yellow coloration intensifies. Intensification of species-specific coloration occurs in many other reef fishes as well as in temperate marine and freshwater species during mating and agonistic encounters (Thresher 1984). A reef fish can mask its poster colors to hide from a predator or to appease a competitor, or it can intensify coloration to intimidate the competition. One can only conclude that reef fish coloration is dynamic and multifunctional (Hamilton & Peterman 1971; Ehrlich et al. 1977; Marshall et al. 2003a, 2003b).

the Red Sea. It possesses a semicircular luminous organ just below each eye that contains continuously emitting bioluminescent bacteria. The light can be turned on and off by means of a muscular lid. The Flashlight Fish is unique in that it forms shoals at night and uses its light for feeding, predator avoidance, and in behavioral interactions. The light is turned on to attract zooplankton prey and then to illuminate prey. If approached by a predator, the Flashlight Fish swims with the light on and then turns it off and changes direction. The fish thus moves to a place that was unpredictable from its former direction of movement. In a social context, shoals form at night when small groups swim close enough to see each other's lights. Male–female pairs hold territories over the reef. If an intruding *Photoblepharon* approaches, the female swims up to it with her light off and then turns the light on literally in the face of the intruder, causing it to depart (Morin et al. 1975).

A final category of visual signals and reception has caught the attention of fish biologists in just the past decade. This is the topic of **ultraviolet (UV) reflectance** and **detection** (Siebeck et al. 2006). The spectrum of human-visible light falls between 400 and 700 nm, perceived as violet to red colors. UV-A radiation lies between 320 and 400 nm and is invisible to humans. However, many marine as well as freshwater fishes, from elasmobranchs to higher teleosts, have eyes that do not block UV light and that possess retinal pigments with maximal absorption characteristics well in the UV range (Losey et al. 2003). Hence "many teleost fishes may be adapted for vision in the UV range" (Losey et al. 1999a, p. 921).

Although UV light is scattered rapidly in water, biologically useful amounts of UV light penetrate clear aquatic environments to at least 100 m depth. UV light can be especially useful for detecting zooplankton against an open water background (e.g., Jordan et al. 2004). In a social context, the rapid scattering of UV light means that skin pigments that reflect UV, which have been found on the fins, head, and bodies in at least 21 families of reef fishes, will be visible only over short distances. This creates an ideal condition for social signaling at short range while minimizing eavesdropping by other species such as predators (e.g., Cummings et al. 2003; Losey 2003). UV reflection and detection is increasingly proving to play a role in fish social behavior, including mate choice in Guppies and Three-spined Sticklebacks (Smith et al. 2002; Rick et al. 2006), shoaling decisions in sticklebacks (Modarressie et al. 2006), and territorial encounters in damselfishes (Siebeck 2004). UV detection may be important in the ability of fishes to detect **polarized light**, providing additional opportunities for target discrimination in foraging and social signaling as well as affecting orientation ability (Mussi et al. 2005). The visual world of fishes may be very different from ours, and our attempts at interpreting visual and other signals require capitalizing on developing technologies and keeping an open mind.

Acoustic communication

Sound production occurs in well over 50 families of cartilaginous and bony fishes (Myrberg 1981, 2002; Hawkins & Myrberg 1983; Hawkins 1993; Ladich & Fine 2006). Sound production most commonly involves: (i) prey responses to being startled or handled by predators ("stay away" and "release" signals); (ii) mate attraction, arousal, approach, or coordination sounds; (iii) agonistic interactions with competitors for mates and resources ("stay away" signals); and (iv) attraction of shoal mates.

Startle and **release calls** occur in families as different as eagle rays, herring, characins, catfishes (of many families), cods, squirrelfishes, sea robins, grunts, and porcupinefishes. They are elicited when a fish is grabbed, poked, or even surprised. A sudden grunt, croak, or drumbeat might distract a predator, perhaps causing it to release its grip on the prey or hesitate in its attack long enough for the prey to escape. A release call could also attract additional predators, including predators on the individual holding the signaler. A small predator with prey in its mouth could be handicapped in its own efforts to evade a larger predator and might abandon its meal rather than risk becoming one (Mathis et al. 1995). Release sounds could also function as alarm calls (see Chapter 20, Discouraging capture and handling) that notify conspecifics of a predator's presence and activity. The caller would have to have close relatives nearby that could benefit from the sound to offset fitness losses to the signaler from being eaten.

Sound is an integral part of the **courtship and spawning** behavior of many fishes (see Chapter 21). Some sounds produced by male damselfishes (Pomacentridae) and European croakers (Sciaenidae) drive off intruding males. Territorial males also produce vocalizations to bring females closer during courtship (e.g., toadfishes, centrarchid sunfishes, gobies). Signaling rate frequently increases as a female draws nearer, or during the spawning act itself (cods, serranids), suggesting that acoustic communication synchronizes activities between members of a pair. In at least one species of an African mouth-breeding cichlid, male vocalizations stimulate gonadal activity in females, paralleling a widely observed phenomenon in seasonally breeding birds (Myrberg 1981; Lobel 1992).

During **agonistic encounters** associated with territorial behavior, sounds are usually produced by an aggressive or dominant animal; the response of the submissive animal is usually to retreat from the signal sender. Sound production during agonistic interactions occurs in many teleosts, including sea catfishes (Ariidae), loaches (Cobitidae), squirrelfishes (Holocentridae), butterflyfishes (Chaetodontidae), damselfishes (Pomacentridae), gouramis (Osphronemidae), and triggerfishes (Balistidae). Unique structures and behaviors associated with sound production and reception have been found in butterflyfishes, a family previously thought not to produce sounds. Improvements in sound recording

devices have shown that sounds are produced during territorial and pair maintenance interactions, including low-frequency pulses <100 Hz, sounds with peak energy between 100 and 500 Hz, and a high-frequency click at 3.6 kHz (Tricas et al. 2006). A novel chaetodontid swim bladder–lateral line connection, termed the laterophysic connection, is formed from extensions of the anterior swim bladder that connect with the lateral line and even project towards the inner ear (Webb 1998; Webb et al. 2006). The laterophysic connections probably aid in detection of agonistic vocalizations. A unique sound-producing structure found in anemonefishes and other pomacentrids is the "sonic ligament", a connection between the hyoid bar (ceratohyal) and the inner part of the mandible that helps the fish close its mouth rapidly, bringing its teeth together and producing popping sounds (Parmentier et al. 2007). The catalog of sound-producing fishes and interesting acoustic adaptations will undoubtedly grow as more studies are conducted.

Submissive animals also produce sounds that may reduce aggression in an opponent, as recorded from anemonefishes (*Amphiprion*, Pomacentridae) (Myrberg 1981; Hawkins 1993). The importance of sound production during territoriality is evident in the loach, *Botia horae* (Cobitidae), which vocalizes and displays visually to repel intruders of shelter sites. When experimentally muted, residents are unable to repel intruders, whereas sham-operated and intact animals defend their territories successfully (Valinsky & Rigley 1981).

Sound production also functions during **shoal formation and maintenance**. Most group maintenance sounds are produced by vibrating the swim bladder or stridulating of teeth, bones, and fin spines (see Rice & Lobel 2004; Amorim 2006). However, other mechanisms exist. Pacific and Atlantic Herring, *Clupea pallasii* and *C. harengus*, emit trains of pulsed sounds, termed **fast repetitive ticks** (FRTs) that last up to 7 s. These sounds are accompanied by the expulsion of small bubbles from the anal duct and are probably produced in the gut or swim bladder. FRTs are emitted more often at night and FRT frequency increases as school size increases, suggesting that they serve to maintain contact between schoolmates (Wilson et al. 2003b).

Other group maintenance sounds result from water displacement by fins and bodies during swimming and are detected via the lateral line of neighboring fish. Such water displacement informs aggregating fishes of their location relative to schoolmates, serving as a minor repulsive force that combines with visual input to maintain distance between individuals. When pollack (Gadidae) are experimentally blinded, they swim slightly further from schoolmates than when intact. In unblinded fish in which the lateral line nerve is severed and acoustic information therefore eliminated, they swim closer than normal to schoolmates (Pitcher et al. 1976). Interestingly, more actively schooling species within a family (e.g., among cods and damselfishes) are relatively quiet, and sound production in group-spawning fishes is not as common as it is in solitary, territorial species. Whether this silence helps prevent detection by predators or results from other factors is unknown (Hawkins & Myrberg 1983; Hawkins 1993).

Eavesdropping by predators may be a significant cost of sound production. Many predatory fishes (sharks, groupers, snappers, black basses, jacks, barracuda, tunas) are attracted to the incidental, low-frequency sounds produced by feeding or injured fishes. Bottlenose dolphins (*Tursiops truncatus*) include a disproportionate number of sound-producing fishes (e.g., croakers, grunts, toadfishes) in their diet (Barros & Myrberg 1987). Interception of signals, whether by predators, competitors, or potential prey, is always a potential cost affecting the evolution and use of communication signals by a species.

Chemical communication

Exchanges involving chemicals primarily involve the release and reception of **pheromones**, which are chemicals secreted by one fish and detected by conspecifics and that produce a particular behavioral or developmental response in the receiving individual (Hara 1982, 1993; Liley 1982). Chemicals are sensed by both **gustation** (taste) and **olfaction** (smell) in fishes. Sensory receptors are often located not only in the mouth and nostrils, but also on the barbels or even the body surface in many fishes (see Chapter 6, Chemoreception), or on filamentous, muscularized pelvic fins (e.g., gouramis, Osphronemidae).

Chemicals play an important role in food finding and predator avoidance (see Chapters 19, 20), mating (Chapter 21), migration (Chapter 23), parental care, species and individual recognition, aggregation, and aggression in fishes. Parents of several cichlid species recognize their young via chemical signals, and young recognize their own parents in the same way (Myrberg 1975). In salmonids, skin mucus contains species-specific amino acids that are used for individual and sexual recognition. Species recognition in other species is also mediated by chemicals in skin mucus (Hara 1993). Bullhead catfishes (Ictaluridae) and European Minnows (*Phoxinus phoxinus*) can recognize individual conspecifics based on odor. Several schooling species (herring, minnows, plotosid catfish, young salmonids) show an attraction response to water that has contained conspecifics (Pfeiffer 1982).

Chemically mediated agonistic interactions include scent marking of territories or shelters, which takes advantage of the persistence of chemical signals relative to other sensory modes (Hara 1993). Members of sexual pairs of Blind Gobies, *Typhlogobius californiensis*, defend a burrow against individuals of the same sex. Recognition of burrow mates and of intruders is based on chemical cues. Yellow Bullhead Catfishes develop dominant–subordinate relationships that are mediated by chemical secretions. Experimen-

tally blinded fish can discriminate between odors produced by different individuals. If a dominant fish is removed and then returned to a tank the next day, a blinded subordinate still treats it as dominant. If the dominant is returned after losing an agonistic encounter with a third fish, the previous subordinate will attack it, again based on chemicals apparently produced in the skin mucus. Bullheads also produce an aggression-inhibiting pheromone when living in groups. Fighting by aggressive individuals even decreases when they are exposed to water in which a communal group was living. In Siamese Fighting Fishes, *Betta splendens* (Osphronemidae), males display more actively in front of mirrors when placed in water that had contained another male (Todd et al. 1967; Hara 1993).

Tactile communication

Tactile information is transmitted at close range, when fish are in contact. Accurate information about the relative strength of combatants can be exchanged during pushing matches or when fishes lock jaws during mouth fighting. Many fights escalate into and end in biting. Anemonefish strike each other with their pectoral fins during antiparallel lateral displays (see Fig. 22.2). Fish frequently touch each other with tactile sensors, such as barbels in catfishes, loaches, and goatfishes, but also with long, filamentous pelvic fins (e.g., gouramis); searobins (Triglidae) have touch receptors in their separated anterior pectoral fin rays. Nuptial tubercles, epidermal bumps on the body and fins of many fishes (see Chapter 21), are used to stimulate potential mates and maintain contact between a pair during breeding. Courtship and copulation in many sharks involves biting of the female by the male; the male often holds onto the female's fins or body for prolonged periods (Pratt & Carrier 2001).

Touching between fishes is fairly uncommon, except during extreme fights, mating, and parent–offspring interactions. In parental species, young frequently contact the parent, usually using the mouth to feed on parental tissue or mucus. Such behavior also serves to maintain cohesion between parent and young, to promote parental behavior (perhaps by stimulating the production of parental behavior-inducing hormones), and to communicate the behavioral state of the young, such as fear or hunger. Parent-touching behavior occurs in bonytongues (Osteoglossidae), catfishes (Bagridae), damselfishes, and more than 20 species of cichlids (Noakes 1979).

Electrical communication

Fishes are unique in that some species both produce and receive electrical information based on very weak electrical output (see Chapter 6, Electrical communication). The **electric organ discharge** (EOD) is species and often sex specific in South American gymnotiform knifefishes and African mormyriform elephantfishes (the German common name, *tapirfische*, likens the latter family more to tapirs and is actually more descriptive). A fish can modify amplitude, frequency, pulse length, or interpulse length of its discharge, or alter parts of its EOD such as the fundamental frequency or peak power frequency. Fish can thus exchange information about species, sex, size, maturational and motivational state, location, distance, and individual identification. Electric discharges are used commonly during agonistic interactions (Bullock et al. 1972; Westby 1979; Hagedorn 1986; Hopkins 1986).

Much research has been conducted on the social context and function of EODs during courtship and territorial encounters in both groups (Møller 2006). Most but not all species have sexually dimorphic EODs. In apteronotid knifefishes, the male emits at a higher frequency in some species but in others it is the female that has a higher frequency discharge (Zhou & Smith 2006). Isolation of male hypopomid knifefish, *Brachyhypopomus pinnicaudatus*, leads to a gradual decrease in the sexually dimorphic component of the duration and amplitude of its waveform. The differences are restored when a second fish is introduced to the test animal, suggesting that maintaining sexual differences in EOD comes at some cost, perhaps explaining why sexual dimorphism is not universal (Franchina et al. 2001). If two knifefish are emitting at the same frequency, the overlap can cause interference (= jamming). A **jamming avoidance response** (see Chapter 6) is well known in gymnotids, whereby fish avoid jamming by shifting their EOD frequency away from that of nearby conspecifics. What has been shown more recently, however, is that the Brown Ghost Knifefish, *Apteronotus leptorhynchus*, actively jams the output of others during competitive interactions (Tallarovic & Zakon 2005). Both male and female Brown Ghosts presented with actual or simulated (via electrical playback) intruders with a higher EOD frequency than their own raise their EOD frequencies to within potential jamming range.

In mormyriform fishes, shifts in EOD duration and phase amplitudes occur during agonistic encounters in juvenile as well as adult fishes, regardless of gender. EODs are used during interactions in combination with other display modes, utilizing multisensory communication systems that enhance signal transmission and reception (Schuster 2006). Interacting fish will head butt one another and also swim parallel and in place, which could push water and sound waves at the other fish as well as providing visual and tactile cues (Terlaph & Møller 2003; Terlaph 2004).

Agonistic interactions

Aggressive interactions usually result from competition or potential competition for valuable resources. Defendable resources include food and feeding areas, refuge and resting sites, mates and mating grounds, eggs, and young. Defense

can produce dominance hierarchies in aggregating fishes or territoriality in more solitary species. In addition, a hierarchy can exist among neighboring territory holders, and dominant–subordinate relationships often exist when solitary fish meet.

Behavioral hierarchies

Dominance hierarchies ("peck orders") are either linear or despotic. In **linear** hierarchies, an alpha animal dominates all others, a beta animal is subordinate to the alpha but dominates lower ranked individuals, etc., down to the last, or omega, individual. Such a hierarchy exists in harems of the sex-changing Cleaner Wrasse, *Labroides dimidiatus* (see Chapter 21). A single male dominates up to six females, which in turn have their own linear hierarchy. Linear hierarchies also exist in salmonids, several livebearers, and centrarchid sunfishes (Gorlick 1976). In **despotic** situations, a single individual, the despot, is dominant over all other individuals, while subordinate animals have approximately equal ranks. In captive anguillid eels, a single large individual can monopolize 95% of a 300 L aquarium, relegating 25 other individuals to the remaining area where they mass together in continual contact. Despotic hierarchies have also been observed in Coho Salmon, *Oncorhynchus kisutch*, and bullhead catfishes, *Ameiurus* spp. (Paszkowski & Olla 1985).

Dominance can be determined by size, sex, age, prior residency, and previous experience. In general, large fish dominate over smaller, older over younger, and residents over intruders. In many species, males usually dominate females, whereas in others, such as Guppies, females dominate males. Previous experience, in terms of recent wins and losses, often determines the outcome of future interactions; victorious fish tend to be aggressive and defeated fish submissive. Dominant fish typically occupy the most favorable microhabitats, relegating subordinates to suboptimal sites with respect to cover availability, current velocity, or prey densities. As a consequence, dominant individuals will have higher feeding rates, which ultimately lead to faster growth, better condition, and higher fitness (e.g., salmonids; Bachman 1984; Gotceitas & Godin 1992). Dominance hierarchies have also been observed in requiem and hammerhead sharks, minnows, ictalurid catfishes, amblyopsid cavefishes, cods, ricefishes (Oryziidae), topminnows, livebearers, centrarchid sunfishes, cichlids, labrids, blennies, and boxfishes (Ostraciidae).

Territoriality

Territoriality implies a defended space, either the **personal space** around an individual (= individual distance) or a bounded area around some resource (e.g., Grant 1997). A territory may encompass several resources, as in male pomacentrid damselfishes in which the territory provides food (algae), a spawning site and the eggs spawned there, and refuge holes from predators where the territory holder also rests at night. Territories are often subunits of the larger **home range** occupied by an individual (see next section).

Territoriality is widespread in fishes, occurring in such diverse groups as anguillid eels, cyprinids, ictalurid catfishes, gymnotid knifefishes, salmonids (affecting stocking programs and the effects of introduced species), frogfishes, sticklebacks, pupfishes, rockfishes, sculpins, sunfishes and black basses, butterflyfishes, cichlids, damselfishes, wrasses, barracuda, blennies, gobies, surgeonfishes, and anabantids. Territoriality has not been observed in agnathans or elasmobranchs, although the threat responses of Gray Reef Sharks (see Fig. 22.3) may represent defense of personal space.

Territorial defense often involves displays such as fin and gill spreading, lateral displays and exaggerated swimming in place, vocalizations, chasing, and finally biting. Prolonged exchanges of displays frequently occur at territorial boundaries. When territories are being established or contested (as opposed to temporary trespassing), priority of ownership, previous experience, and individual size usually determine the outcome of a dispute. Again, territory holders win over intruders, previous winners defeat previous losers, and large fish win over small fish. Territories near one another can create "territorial mosaics" of several contiguous territories (e.g., salmonids, pomacentrids, mudskippers, blennies; Keenleyside 1979).

The costs of territorial defense – energy and time expended, exposure to predators, resource loss to competitors while defending distant portions of a territory – increase with increasing territory size. Food production affects territory size because a territorial animal must often meet its daily energy requirements from the resources available within its territory. As would be expected, increased food density leads to a decrease in territory size (e.g., in Rainbow Trout; rockfishes, Scorpaenidae; surfperch, Embiotocidae; several damselfishes; Hixon 1980a, 1980b). Interestingly, in Beau Gregory Damselfish, males decrease territory size with increasing food but females respond by increasing territory size. Larger females can produce more eggs and hence increased energy intake apparently overcomes the costs of defending a larger territory (Ebersole 1980).

Territoriality is often flexible. Territorial boundaries and intensity of defense can vary as a function of the relative impacts of different intruders. Herbivorous damselfishes defend a larger space against large competitors such as parrotfishes and surgeonfishes than against small damselfishes; damselfishes also tolerate large competitors for shorter times inside the territory, attacking them more aggressively. The strongest attacks are directed at potential egg predators, which have the greatest relative impact on the reproductive success of the damselfish. Juvenile Coho Salmon also defend a larger territory against larger conspecific intruders. Butterflyfishes chase species with which they overlap in diet but tolerate the presence of non-competitors

(Myrberg & Thresher 1974; Reese 1975; Ebersole 1977; Dill 1978).

Territoriality may also vary over time at several levels. Juvenile grunts (Haemulidae) form daytime resting shoals over coral heads. Individuals stake out small territories of about 0.04 m^2 within the shoal; the territories often contain refuge sites from predators. These territories are defended vigorously with open mouth displays, chases, and biting. In the evening, the shoal becomes a polarized school that moves from the reef to adjacent grassbeds to feed. No agonism is seen during the migratory period, as such behavior would negate the antipredator function of the school when moving across the dangerous reef edge. Once in the grassbeds, the shoals break up and the fish occur as widely spaced, foraging individuals, implying space-enforcing behaviors (McFarland & Hillis 1982). Territoriality changes with age in many species. Young Atlantic Salmon are territorial in streams. As they grow and their food requirements shift to larger prey, they move into deeper water and join foraging groups that have dominance hierarchies rather than territories (Wankowski & Thorpe 1979). In some species, agonistic interactions occur during the breeding season, with fish aggregating peaceably at other times (e.g., codfishes).

Home ranges

Territories are usually a spatial subset of the larger area that a fish uses in its daily activities. Such **home ranges** or activity spaces are common in fishes, which move over the same parts of the habitat at fairly predictable intervals, often daily but also at other timescales (Lowe & Bray 2006). Home range is dependent on fish size and species. Larger species and individuals generally move over larger ranges, although range size may decrease with growth in an individual (e.g., Bocaccio Rockfish, *Sebastes paucispinis*, Starr et al. 2002; Greasy Grouper, *Epinephelus tauvina*, Kaunda-Arara & Rose 2004). Home range may be very restricted, as in the few square meters around a coral head (e.g., gobies, damselfishes) or contained in a tide pool (e.g., pricklebacks) (Sale 1971; Horn & Gibson 1988; Kroon et al. 2000). Some benthic stream fishes may have ranges of 50–100 m^2 (Hill & Grossman 1987) whereas others may range over hundreds of meters (e.g., Albanese et al. 2004). Intermediate ranges of a few hundred square meters characterize many lake, riverine, kelpbed, and reef species, although many large coral reef fishes are relatively sedentary, utilizing concentrated reef resources. Home ranges of many large species such as groupers and snappers may not exceed 0.1 km^2 (Pittman & McAlpine 2003). Pelagic predators such as tunas, salmons, large sharks, and billfishes cross entire oceans seasonally or repeatedly. But even these oceanic wanderers show evidence of periodic residence in certain areas on a seasonal basis (see Chapter 23, Annual and supra-annual patterns: migrations).

Although a fish may spend 90% of its time each day within its home range, it is common to encounter individuals many meters or even kilometers away from their usual activity space. Such movements characterize fishes in most habitats (e.g., Fausch et al. 2002). These periodic excursions imply a well-developed **homing ability** in many species. Numerous studies, involving experimental displacements of tagged individuals, have repeatedly shown a strong tendency to return to home sites in many fishes. The Tidepool Sculpin, *Oligocottus maculosus*, can be displaced as far as 100 m from its home tide pool and will find its way back, using either visual or chemical cues. Older fish can still remember the way home after 6 months in captivity. Younger fish have shorter memory spans and require both visual and chemical cues to find home successfully, whereas older individuals do not require both types of information (Horn & Gibson 1988). In some species, adults find their way around the home range by identifying landmarks, creating a **cognitive map** of the locale (Reese 1989). In general, older fish have a stronger homing tendency and often occupy smaller home ranges than younger individuals. Since juveniles are the colonists that most often invade recently vacated or newly created habitat, this generalization is not surprising (Gibson 1993).

The use of a home range is affected by several components of a fish's biology. Normal ranges are often deserted during the breeding season. This may involve no more than a female damselfish having to leave her territory to lay eggs in the adjacent territory of a male, but can also involve long-distance movements of 100 km or more to traditional group-spawning areas, such as occurs in many seabasses on coral reefs. Colorado Pikeminnows, *Ptychocheilus lucius* (Cyprinidae), make annual round-trip movements of as much as 400 km between traditional spawning and normal home range areas. The home range also interacts with shoaling behavior in some species and can differ among individuals within a species. Yellow Perch, *Perca flavescens*, form loose shoals (see next section) of many individuals that forage in the shallow regions of North American lakes. Home range size is directly correlated with the amount of time individuals spend in shoals. Individuals with strong shoaling tendencies also have larger home ranges. As a shoal enters the residence area of an individual, the resident fish joins the shoal until the shoal moves to the boundary of the home range. Home ranges and fidelity to particular sites have probably arisen because intimate knowledge of an area increases an individual's ability to relocate productive feeding areas or effective refuge and resting sites, reducing the amount of energy expended and risk incurred while searching for such locales (Helfman 1984; Tyus 1985; Shapiro et al. 1993).

Knowledge of home range size has important implications for fish conservation, especially with regard to the creation of reserves and protected areas. Reserves must be large enough to encompass the home ranges of both sed-

entary and mobile species; without specific knowledge of daily, seasonal, and ontogenetic movements, a reserve might fail to encompass the range of habitats or the actual areal expanse needed to protect most species and most life history stages (Kramer & Chapman 1999; Cooke et al. 2005; Sale et al. 2005). The likelihood of spillover of individuals into adjacent areas, an anticipated benefit of reserve creation, also depends on movement and will vary in relation to reserve design and species behavior. Relationships between home range size and reserve design have been examined in tropical and temperate locales involving taxa as diverse as seabasses, sparids, goatfishes, wrasses, and surgeonfishes, to name a few (Meyer et al. 2000; Egli & Babcock 2004; Meyer & Holland 2005; Popple & Hunte 2005; Topping et al. 2005).

Aggregations

Shoaling

The most obvious form of social behavior in fishes is the formation of groups, either unorganized **shoals** or organized, polarized **schools** (Fig. 22.6). By convention, some social attraction among individuals is required for a group to be considered a shoal or a school, whereas fish that are mutually attracted to food or other resources are an **aggregation** (e.g., Freeman & Grossman 1992). Shoals involve social attraction, coordination, and numbers. Two fish are not a shoal because one fish often leads and the other follows. However, when three or more fish co-occur, each fish reacts to the movements of all adjacent fish. The group becomes the leader and the fish become the followers. Operationally defined, a shoal is a group of three or more fish in which each member constantly adjusts its speed and direction in response to other group members; if the behavior is highly synchronized and fish swim parallel, the group is a school (Partridge 1982).

As many as half of all fish species may form aggregations at some time in their life. Aggregations can serve several purposes concurrently (see Parrish & Hamner 1997). The chief functions are to reduce the success of predators (see Chapter 20), increase foraging success (Chapter 19), synchronize breeding behavior (Chapter 21), and increase hydrodynamic efficiency. Some species shoal throughout their lives (e.g., many herrings, anchovies, minnows, silversides), others only as juveniles (Bowfin, plotosid catfishes, surgeonfishes, pufferfishes). Some species aggregate when young, disband as juveniles or adults, and reaggregate to spawn, either in groups or as pairs (many salmonids, seabasses). Foraging aggregations may turn into breeding aggregations as fishes migrate to traditional spawning locations and are joined by members of other aggregations (Yellow Perch, grunts, rabbitfishes). Normally solitary adults may congregate during the winter and such aggregations probably remain together through a spring spawning season (e.g., carp).

Within a species, schooling tendency may change with predation intensity. Guppies in predator-dense habitats school throughout their lives, but only juveniles school where predators are rare. European Minnows that co-occur with predators inherit a stronger schooling tendency than do minnows without predators (Magurran 1990). The intense predation pressure that small fishes experience and the prevalence of shoaling behavior particularly among juveniles and small species attests to the antipredator func-

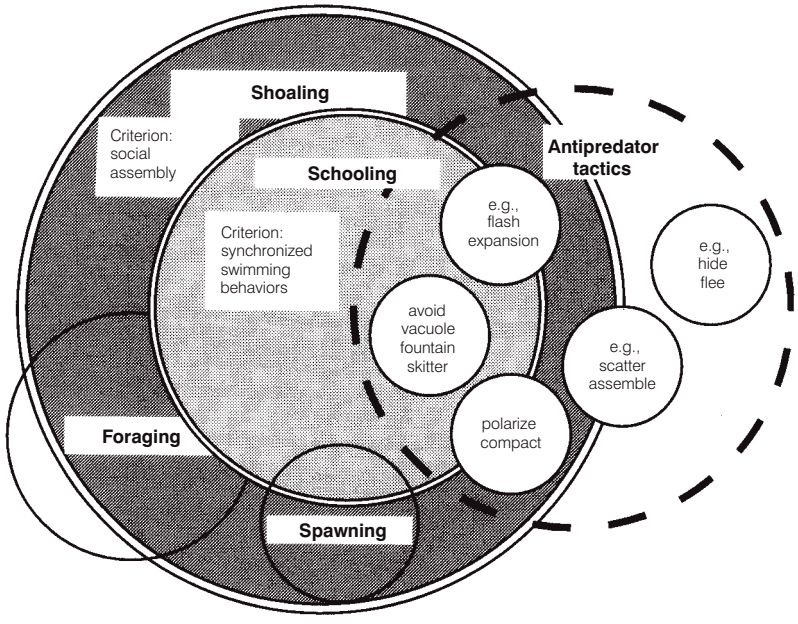


Figure 22.6
Types and activities of fish aggregations. Shoals contain fish attracted to one another but whose activities are only loosely coordinated. In schools, behavior is synchronized: fish often swim parallel, in the same direction, with fairly uniform spacing (the "polarized school" of many authors). Foraging and spawning groups generally form shoals, whereas predator avoidance often results in highly synchronized schooling activities. In this figure, five common antipredator actions and their relationship to grouping behavior are shown in the smallest circles (see also Chapter 20, Responses of aggregated prey). After Pitcher (1983), used by permission of the publisher Academic Press Ltd, London.

tion of most aggregations (Shaw 1970, 1978; Magurran 1990; Pitcher & Parrish 1993; see Chapter 20).

Regardless of function, most fish shoals are relatively unstable. Few fishes, at least in inshore locales, maintain their groups through an entire 24 h period. Many shoals form each morning, disband at night, and reform the following morning but with different individuals. In fact, available evidence indicates little shoal fidelity in most fishes: dace, minnows, killifish, Yellow Perch, surgeonfishes, parrotfishes, and Bluegill Sunfish join and leave foraging shoals frequently (Freeman & Grossman 1992; Hoare et al. 2000). Climbing Perch, *Anabas testudineus* (Anabantidae), even show a preference for shoaling with unfamiliar individuals, especially if unfamiliar fish are part of a larger group (Binoy & Thomas 2004), and European Minnows, *Phoxinus phoxinus*, will prefer shoals of unfamiliar fish when the unfamiliar fish are in a significantly larger shoal (Barber & Wright 2001). However, advances in molecular genetic techniques are revealing a degree of permanence in the form of **stable kin groups** in some wild fish schools (e.g., Brook Char, *Salvelinus fontinalis*; Fraser et al. 2005; Eurasian Perch, *Perca fluviatilis*, Behrmann-Godel et al. 2006).

Fidelity may also be strong in nocturnal fishes that reaggregate each dawn and form daytime resting schools at fixed refuge locales (e.g., squirrelfishes, grunts, copper sweepers, some bullhead catfishes; Hobson 1973; Helfman 1993). In some nocturnal species, relatively complex social structure and interactions develop that rival the societies of birds and mammals (Box 22.2). Migratory schools (e.g., large tunas, Bluefishes) may also show strong group fidelity, but definitive information is lacking.

Fishes space themselves fairly regularly within fish schools (e.g., Partridge et al. 1983; Abrahams & Colgan 1985). A perfect crystal lattice is the theoretical ideal spatial distribution for school members: neighbors should be 0.3–0.4 body lengths apart, 5 body lengths behind and centered between preceding fish, with neighbors beating their tails in antiphase (opposite directions). Fish could gain a 65% energy saving from the wakes and vortices generated by fish around them (Weihs 1975). However, few if any groups achieve the proposed ideal lattice structure (Pitcher & Parrish 1993; Parrish & Turchin 1997). Regardless, considerable energy savings may accrue in a school because the fish are doing more than simply "drafting" in a region of reduced flow created by the fish ahead of them (Liao et al. 2003). Some fishes contract only anterior body muscles, allowing a passive wave of undulation to propagate posteriorly along the body, much as waves pass down a flag in the wind. A fish thus progressively slaloms between the vortices shed by the fish swimming ahead of it, matching its swimming movements in phase with oncoming drag vortices, rather than expending energy pushing off the vortices (similar energy savings are experienced by fish undulating behind a rock or other object in flowing water).

Earlier authors had proposed that a hydrodynamic advantage may also develop through drag reduction when one fish swims through the mucus produced by fish ahead of it in a school (Breder 1976). However, insufficient mucous is produced, even in schools of a billion fish, to affect drag significantly (Parrish & Kroen 1988). Predation also disrupts spacing because individuals under attack should attempt to place schoolmates between themselves and a predator (the **selfish herd** phenomenon; Hamilton 1971). Again, however, experimental tests call into question whether central locations are in fact safer (Parrish 1989b). Obviously, many factors (size, sensory input to the lateral line, visibility of neighbors, swimming speed, species composition, vulnerability to and behavior of predators, social status) contribute to the exact (and variable) structure of schools.

Colonial fishes form essentially stationary aggregations. Colonies may exist for breeding, as when male sunfishes and cichlids and female triggerfishes aggregate and construct nests or set up display sites. Some damselfishes set up contiguous territories in suitable habitat patches on a coral reef. Three-spot and Bicolor damselfishes will be found in areas of a few square meters, even though adjacent, similar reef areas contain no such fishes (Schmale 1981). Garden eels (Congridae) occupy small burrows a few centimeters apart on sandy regions of coral reefs (Fig. 22.7). Jawfishes (Opisthognathidae), another burrowing coral reef form, tend to form colonies of two to nine individuals on rubble-strewn sandy bottoms (Colin 1973).

Optimal group size

Predatory success decreases as prey group size increases (Neill & Cullen 1974; Landeau & Terborgh 1986). Larger prey groups also experience greater competitive success, foraging efficiency, and hydrodynamic efficiency. Consequently, selection should favor prey fish that join and maintain large shoals. But above some group size, benefits are offset by competition for food and mates, by interference between individuals in avoiding predators (e.g., confusion among group members due to collisions, indecisiveness, or obstructed views), and increased conspicuousness of large versus small groups (Pitcher & Wyche 1983; Abrahams & Colgan 1985; Parrish 1988). Oxygen consumption in large groups may also leave trailing members in regions of depleted oxygen (McFarland & Moss 1967). Given these costs and benefits, can an optimal group size be determined? Do fish tend to form or join optimally sized shoals?

Optimal group size is complicated because antipredator functions probably favor larger optima than do feeding groups. If dominance hierarchies exist, dominant individuals, with their preferential access to resources, may have a larger optimum than would subordinate members. Subordinate animals must decide between sustaining the costs of

Figure 22.7
Garden eels (Congridae) live in colonies of several hundred individuals on sand bottoms near coral reefs. Individuals feed on zooplankton during the day, often extending just the anterior portion of their bodies out of burrows, the sides of which are cemented with mucus produced by the fish's skin. Withdrawal of one individual into its burrow stimulates withdrawal of all other members of the colony. Photo by G. Helfman.

Box 22.2

BOX 22.2

Social transmission of cultural traditions in fishes

Traditions are social behaviors maintained across generations, either by inheritance or by learning, as when young individuals are taught by or observe and copy the actions of older individuals. **Culture**, to biologists, is not the refinement of tastes and artistic judgment but rather involves the behavioral transmission of information. By watching and copying the activities of other, usually older individuals, young chimpanzees learn how to use grass stems to "fish" termites out of mounds, young antelope learn the locations of communal display (lekking) grounds, and young oystercatchers learn how to open bivalves; fishing, lekking, and bivalve opening are hence cultural activities (Bonner 1980).

Fishes also exhibit a number of behavioral traditions, and the number of examples of **social learning** increases as studies expand (Brown & Laland 2003). The same breeding locales are frequently used year after year in both marine and freshwater fishes. Although part of this continued use relates to site-specific, appropriate conditions for spawning, dispersing, or caring for larvae, seemingly adequate, nearby sites are ignored while the traditional site continues to be used. Traditional breeding locales have been found in numerous fish species (e.g., herring, groupers, snappers, surgeonfishes, rabbitfishes, parrotfishes, wrasses, mullets; Loiselle & Barlow 1978; Johannes 1981; Thresher 1984; Turner 1993); the return of salmon to their natal stream to spawn is not included because information is obtained through individual imprinting and memory and may have a hereditary component (McIsaac & Quinn 1988).

The process by which traditions are established and maintained has been investigated with respect to breeding sites in wrasses and twilight migration routes in grunts. Bluehead Wrasses, *Thalassoma bifasciatum*, have a mating system where many females mate with solitary large males that hold territories. The locations of these territorial mating sites may remain stable for more than 12 years, encompassing four wrasse generations. Adjacent, seemingly appropriate sites (downcurrent edges of a reef that include vertical projections) are not used. Female choice of sites, rather than choice of males, determines where males establish territories. To test whether traditions were maintained by a genetic response or through social transmission, Warner (1988, 1990) removed entire populations from reefs and replaced them with naive individuals. He found that breeding sites chosen by transplanted groups were a random sample of the available locales and that newly used territories eventually became traditional breeding sites. Hence former traditional sites were in fact maintained by social convention. Interestingly, if an additional removal/replacement manipulation was performed on the same reefs, the second group of transplants tended to prefer the same sites as the first transplanted group. This suggests

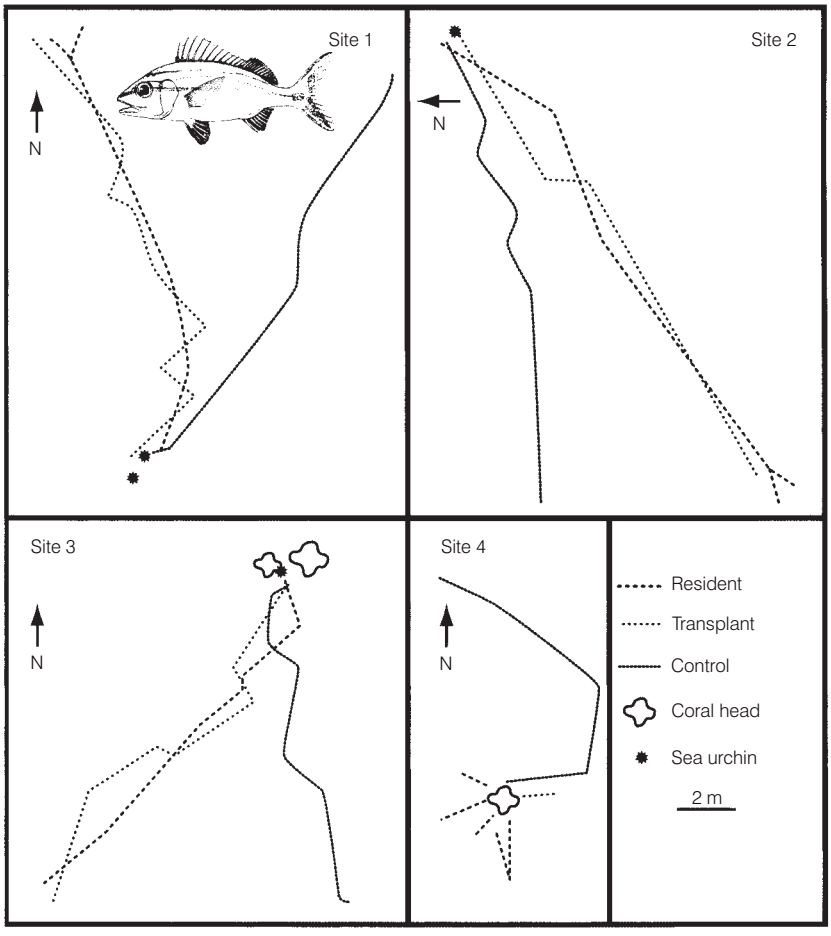


Figure 22.8
Testing for social learning in juvenile grunts. The twilight migration routes at four experimental sites are shown. "Resident" fish are those with an established migration route. "Transplants" were brought from another location and allowed to follow resident fish. "Control" fish were also transplanted but were released at the resident site after resident fish were removed, hence controls had no opportunity to learn the routes. At sites 1 through 3, transplants adopted the resident route and used it even when residents were absent. Controls never used the resident route. At site 4, residents did not migrate but instead drifted away in different directions. Transplants also drifted away from the resting site, whereas controls underwent a distinctive migration. Adapted from Helfman and Schultz (1984), used with permission; grunt drawing from Gilligan (1989).

that the fish assessed site quality and had definite preferences, which did not necessarily include the original, traditionally used spawning locales. Hence tradition is powerful enough that a breeding locale may continue to be used even though that locale may not be the best available in the habitat.

Juvenile grunts (*Haemulon*), as well as many other nocturnal reef fishes, undergo a remarkably predictable migration at dawn and dusk each day that probably thwarts the success of twilight predators (McFarland et al. 1979). Grunts feed on invertebrates at night in the grassbeds that adjoin patch and fringing reefs. By day, they form resting schools over coral heads. The locations of such schools and the routes taken by the school resident over a coral head represent traditional activities. Over more than a 3-year period, a school will take the same approximate route to and from the grassbed, even though no individual grunt in the school is more than 2 years old. How do younger fish know the correct route between resting site and grassbed?

To test for the relative influences of genetic and social transmission, Helfman and Schultz (1984) transplanted individuals between schools of juvenile French Grunts. After mapping established migratory routes, members of distant groups were added to resident schools. Transplanted fish (identified by small injected paint marks) were allowed to follow residents for four twilights. Then all residents were removed and the migration of the transplanted fish was observed. The route was similar to the one taken previously by the residents (Fig. 22.8). To test for a possibly innate response (i.e., given the terrain, any grunt at this locale would take the same route regardless of experience), new transplants were given no opportunity to observe migrating fish. These control fish migrated in a variety of directions. Hence, the social traditions of resting site locale and twilight migration route in grunts are established via **cultural transmission**. Learning through cultural transmission of information has been shown in several other contexts in several other fish species (Brown & Laland 2003; Kelley & Magurran 2003; Griffin 2004).

a large group versus being alone. The conflicting needs of group members may make attainment of an optimum impossible. Minimal group size should be easier to determine than maximal size. Prey should avoid being alone or joining very small groups. When Fathead Minnows were allowed to choose between shoals of different sizes, they consistently chose the larger of the two shoals, particularly when one shoal was relatively small (less than eight fish) and a predator was present. Zebra Danio, *Danio rerio*, females also consistently chose a larger shoal, although male Danios showed no such preference. Banded Killifish, *Fundulus diaphanous*, chose larger shoals when under predatory threat but smaller shoals when feeding cues were present. These findings indicate that fishes alter their decisions with respect to shoal size in response to changes in the social and ecological context of shoaling (Hager & Helfman 1991; Hoare et al. 2004; Ruhl & McRobert 2005).

Interspecific relations: symbioses

Symbiosis is the living together of two unrelated organisms. In **parasitism** one member of a pair benefits and the other suffers a reduction in fitness, in **mutualism** both members of a pair benefit, and in **commensalism** one benefits and the other is neither harmed nor helped. Mutualistic relationships are the most interesting because they indicate a relatively long period of co-evolution between pair members. Fishes form mutualistic relationships with other fishes and with a variety of invertebrate species.

Parasitism

The abundance and diversity of external and internal parasites of fishes is tremendous and beyond the scope of this discussion (e.g., Dogiel et al. 1961; Sinderman 1990; Gabda 1991; Bush et al. 2001; Benz & Bullard 2004). Three families of fishes – synaphobranchid eels, trichomycterid catfishes, and carapid pearlfishes – include members that are internal parasites on fishes and other animals (carapids are discussed below under Mutualism and commensalism). The Snubnose Parasitic Eel, *Simenchelys parasiticus* (Synaphobranchidae), burrows into the flesh of bottom-living fishes such as halibut and has even been found in the heart of Mako Sharks (see Chapter 14, Subdivision Elopomorpha). The trichomycterids are particularly insidious because, in addition to feeding on tissue and blood in a host's gill cavity, the diminutive, eel-like Candiru (*Vandellia*, 2.5 cm) of South America occasionally enters the urethra of human bathers and wedges itself there with its opercular spines, requiring surgical removal (Spotte 2002; see Chapter 14, Subdivision Otocephala, Superorder Ostariophysi).

Many fishes, including marine catfishes, characins, tiger-perches (Theraponidae), carangids, sea chubs (Kyphosidae), sparids, cichlids, blennies, and spikefishes (Triacanthodidae) fall into a category somewhere between parasitism and predation by removing scales or taking pieces out of fins of other fishes (Losey 1978; Noakes 1979; Zander et al. 1999). Populations of scale-eating cichlids from Lake Tanganyika (*Perissodus*) contain even numbers of individuals whose mouths twist left or right, facilitating scale removal from the right or left sides of their prey, respectively (Hori 1993). Cookie cutter sharks, *Isistius* spp. (Squalidae), remove plugs of flesh and blubber from tunas and cetaceans, and lampreys rasp through the skin of numerous fishes and feed on tissues and body fluids (see Chapters 12, 13). At least two species, the Cutlips Minnow, *Exoglossum maxilingua*, of North America, and the Eyebiter Cichlid, *Dimidiochromis compressiceps*, of Lake Malawi, commonly remove eyeballs from unsuspecting prey (although neither species' behavior has been studied adequately). Access to food sources for many of these **partial consumers** depends on deceit; small piranhas resemble and school with other characins and then bite the tails off their schoolmates; several juvenile carangids (e.g., *Scomberoides*, *Oligoplites*) resemble their silverside and anchovy schoolmates, whose scales they remove; sabretooth blennies mimic cleanerfishes (see below); and cookie cutter sharks may mimic bioluminescent invertebrates that live in the deep scattering layer of the mesopelagic region (Losey 1978; Sazima & Machado 1990; see Chapter 18, The deep sea).

Mutualism and commensalism

Some of the best studied mutualistic interactions involve fishes that pick external parasites from other fishes. **Cleaning** behavior exists in almost all aquatic environments and involves dozens of shrimp and more than 111 fish species in 29 families (Sulak 1975; DeMartini & Coyer 1981; Lucas & Benkert 1983; Tassell et al. 1994; Côté 2001; Zander & Sotje 2002). As many as 18 different species of nearshore, primarily kelpbed species in California are known to clean other fishes (McCosker 2006). Mutualistic, co-evolved relationships are most obvious on coral reefs (Limbaugh 1961; Feder 1966; Losey 1987; Losey et al. 1999b). Juveniles of a number of wrasse, butterflyfish, damselfish, and angelfish species clean other fishes, but cleaning specialists occur only among the cleaner wrasses (*Labroides*) of the Pacific and the neon gobies (*Gobiosoma*) of the Caribbean (Fig. 22.9). Cleaners are usually territorial, occupying well-defined and often prominent coral heads or other locales referred to as **cleaning stations**. Communication between host and cleaner is obvious and stereotyped. Host fishes of numerous species approach these stations and pose, frequently assuming head-up or head-down positions while hovering in the water column, blanching

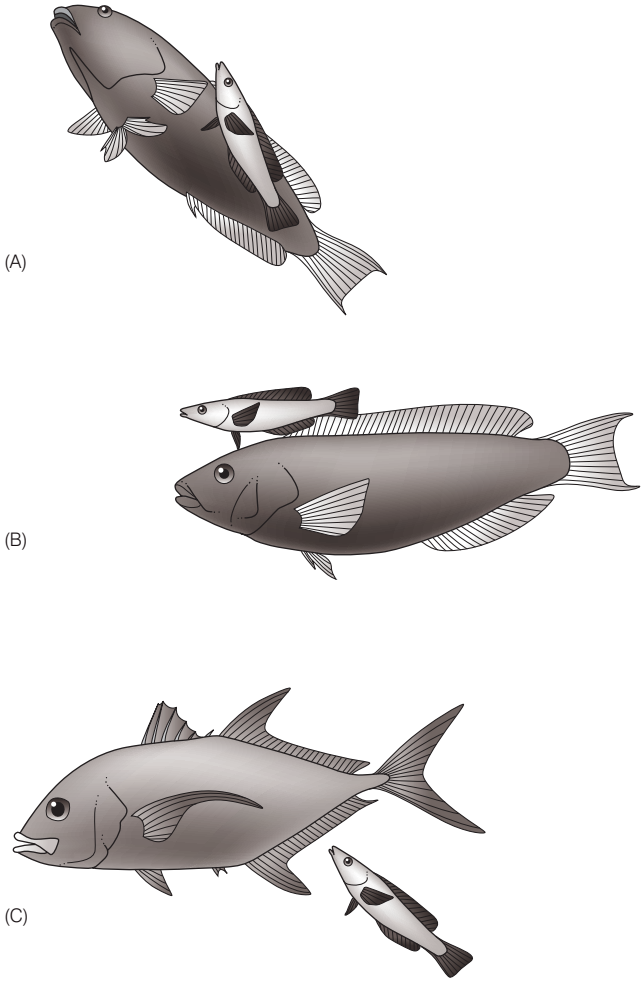


Figure 22.9

Typical cleaning activities of a cleaner wrasse, *Labroides* sp., from the tropical Pacific. Cleanerfishes exist in almost all habitats, but only in tropical seas are species relatively specialized for this role. (A) A large wrasse poses in a head-up position while the smaller cleaner inspects it for parasites and necrotic tissue, contacting the host with its pelvic, anal, and caudal fins. (B) The cleaner solicits posing from a potential host by riding it while flicking the host with its pelvic fins. (C) The cleaner is about to remove a parasite or necrotic tissue from the anal fin of a carangid. After Losey (1987).

in color, spreading their fins, and opening their mouths. Cleaners approach in a bouncing or tail wagging manner, frequently contacting a host during this dance, and then pick over the host's body surface, often entering the mouth or gill covers of herbivores and piscivores alike (Grutter 2004).

Parasites, particularly copepods, are removed, as are mucus and pieces of tissue around wounds; parasite loads are rapidly reduced following cleaning bouts (Grutter 1999; Sikkel et al. 2004; Cheney & Côté 2005). Since hosts without parasites or wounds will solicit cleaning, tactile stimulation alone by the cleaner must attract some fishes (Losey 1979; Bshary & Wurth 2001), and hosts that are parasite-free may allow cleaners to pick them over and feed on mucus as a means of maintaining a relationship that is more valuable at other times. A cleaning bout is terminated when the cleaner leaves or the host fish shudders or snaps its mouth closed and open. Cleaning relationships have been exploited by humans, who use the European Corkwing Wrasse, *Symphodus melops*, among other temperate labrids to help reduce external parasite infestations on Atlantic Salmon kept at extremely high densities in aquaculture pens (Sayer et al. 1996).

Many cleaners have converged on coloration patterns involving bold stripes, and a dark median lateral stripe appears to be important for host fish recognition of the cleaner guild (Stummer et al. 2004; Arnal et al. 2006). Both cleanerfishes and shrimp appear to be largely immune to predation and consequently service such predators as moray eels, seabasses, snappers, and barracuda (Côté 2001). In the Indo-Pacific, at least one wrasse species, *Diproctacanthus xanthurus*, cleans damselfishes that do not leave their territories and hence cannot take advantage of cleaning stations (Randall & Helfman 1972). Two species of sabre-toothed blennies, *Aspidontus taeniatus* and *Plagiotremus rhinorhynchus*, mimic the coloration and behavior of *Labroides* spp. to gain access to posing hosts from which they take pieces of fins and body tissue. The deception is most successful with young hosts.

The importance of cleanerfishes in reef fish dynamics may differ at different locales. The experimental removal of cleaners from a Caribbean reef led to a decrease in host fish density and an increase in parasitic infections, whereas a similar removal in Hawaii led to no such changes (Losey 1978; Gorlick et al. 1987). A more extensive, multireef, 6-month removal experiment on the Great Barrier Reef of Australia also found no detectable effect on total fish abundance or on fish species diversity (Grutter 1997). However, a survey and removal/addition investigation of *Labroides dimidiatus* in the Red Sea found little short-term impact after removal but a significant decline in fish diversity after 4–20 months; immigration or experimental addition of cleaners also resulted in a significant increase in fish diversity within the first few weeks (Bshary 2003). Additionally, an 18-month study that excluded *L. dimidiatus* cleaners from small Australian reefs showed that exclusion reefs had half the species diversity and one-fourth the abundance of fishes of reference reefs (Grutter et al. 2003). The strongest impact in both long-term studies was on large, mobile species – the same species that are likely to affect other reef organisms via predation and grazing. Hence cleanerfishes, although small and relatively rare, can act as **keystone** species, affecting the "movement patterns, habitat choice, activity, and local diversity and abundance of a wide variety of reef fish species" (Grutter et al. 2003, p. 64).

Some interspecific associations involve exploitation of one species' feeding habits to the benefit of another species. Fishes that dig in the substrate, such as stingrays, goatfishes (Mullidae), suckers (Catostomidae), and Yellow Perch are commonly followed by other fishes that feed on invertebrates disturbed by the digger's activities (termed "**scroungers and producers**" in the behavioral literature). Such following and scrounging has also been observed among European wrasses, the producer species being much larger than the scrounger (Zander & Nieder 1997). The purportedly commensal relationship between shark-sucking remoras (Echeneidae) and large hosts such as sharks and rays is probably of this nature, involving feeding by the remora on leftovers following a host's meal. However, actual interactions between host and hitchiker are seldom observed. Some remoras may clean parasites off their hosts, which would be mutualistic, whereas others may create a hydrodynamic burden, particularly when attached to relatively small hosts, creating a parasitic situation. Certain postural changes seen in sharks suggest they are trying to get a remora to move to a less sensitive part of the shark's body (Ritter 2002), although other observations suggest that sharks and rays that accelerate or jump clear of the water may be attempting to dislodge remoras (e.g., Brunnschweiler 2006).

Symbiotic interactions with non-fish species generally involve the use of invertebrates as spawning substrates, as predator refuges, to avoid extreme climatic environmental conditions (e.g., protection from desiccation or wave action), and as shoal mates. The Bitterling, a European cyprinid, lays eggs in the mantle cavity of a freshwater mussel. These eggs hatch after a month and are expelled in the excurrent flow from the mussel. The mussel benefits in that its own larvae are parasitic on the gills of adult bitterlings. The proximity that bitterlings maintain to the mussels, with males establishing territories over the mussels and females inserting their ovipositors into the bivalves, undoubtedly facilitates attachment of the mussel larvae to the fish host (Breder & Rosen 1966).

The use of an invertebrate as a structural refuge against predators is common. Shrimpfish (Centriscidae), clingfishes (Gobieosocidae), cardinalfishes (Apogonidae), and juvenile grunts hover among the spines of long-spined sea urchins or rest beneath the urchins. Such fishes are usually clear or white with black stripes. Some fishes seek shelter inside living invertebrates, a habit called **inquilinism** or **endoecism**. The Caribbean conchfish, *Astrapogon stellatus* (Apogonidae), lives by day in the mantle cavity of a queen conch, a large gastropod. Individual conchfish forage at night on small crustaceans and enter the siphon canal of a live conch an hour before sunrise. Other cardinalfishes live with crown-of-thorns starfish, sea anemones, and sea urchins. Members of the elongate pearlfish family, Carapidae, similarly live by day inside mollusks (see Fig. 14.25) and various echinoderms such as sea cucumbers and pincushion starfish, which they enter via the anus; as many as 15 individual pearlfish have been found in a single sea cucumber host. Pearlfishes, the more primitive species of which are free-living, are also nocturnal foragers on small invertebrates but cross the line from commensalism to parasitism by consuming the viscera of their host (Thresher 1980, 1984; Parmentier & Vandewalle 2005). Dependence on finding a host can be costly to settling larvae, as indicated by the large number of pearlfish tenuis larvae that have been found in the stomachs of adult pearlfishes (Tyler et al. 1992). Other inquiline species include liparid snailfishes (e.g., *Liparis inquilinus*) and Red Hake, *Urophycis chuss* (Phycidae), that inhabit sea scallops and can be found together in a single scallop (Luczkovich et al. 1991).

Many gobies live among sponges and corals, sea whips, and brain corals or share burrows created by worms or various shrimplike crustaceans (e.g., Arrow Goby, *Clevelandia ios*; Blind Goby, *Typhlogobius californiensis*; McCosker 2006). Truly mutualistic partnerships occur in tropical gobies that co-habit with alpheid shrimp, the goby serving as a sentry while the prawn digs and maintains the burrow. Communication between partners is primarily tactile: the essentially blind shrimp maintains antennal contact with the goby's tail and senses tail flicks executed by the goby when predators approach (Preston 1978; Karplus 1979) (Fig. 22.10).

Symbioses between fishes and cnidarians are common, including fish that live on soft and hard corals (various gobies), or among the tentacles of jellyfish and Portuguese men-of-war (e.g., the Man-of-war Fish, *Nomeus gronovii*, Nomeidae). Although many fishes associate with sea anemones (Randall & Fautin 2002), including eastern Pacific Painted Greenlings *Oxylebias pictus* (Elliott 1992), the most highly evolved relationships are between pomacentrid anemonefishes and large sea anemones in the tropical Pacific and Indian oceans (Fig. 22.11). Approximately 30

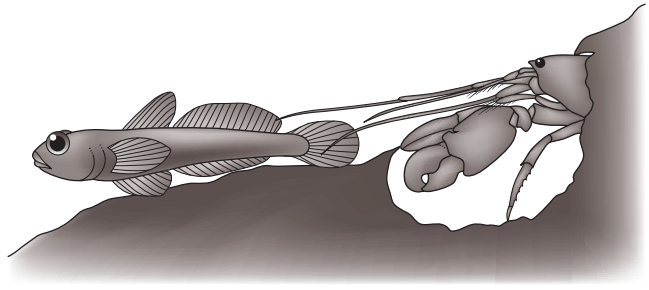


Figure 22.10

Goby–shrimp symbiosis. Several tropical goby species in the Pacific, Indian, and Atlantic oceans live with burrowing alpheid shrimps. The goby stands guard at the burrow entrance while the shrimp excavates and repairs the burrow. The shrimp, which is often functionally blind, maintains contact with the goby via its antennae. If the goby is removed, shrimp will often seal up the burrow entrance and not emerge until the goby is replaced. After Losey (1978).

Figure 22.11
Anemonefish, *Amphiprion bicinctus*, move among the tentacles of an anemone. Stinging cells in the anemone's tentacles would paralyze other fishes but are not discharged when contacted by a resident anemonefish. Photo by H. Fricke.

fish species in the genera *Amphiprion* and *Premnas* and 10 species of anemones are involved. Details differ among species of fishes and anemones, but basically any other fish that touches the anemone's tentacles is likely to be stung by nematocysts (stinging cells), paralyzed, and consumed, whereas anemonefish frequently contact the tentacles and are not stung. Although the exact mechanism that protects anemonefishes from the nematocysts remains unclear, mucus secretion, presumably by the fish, plays an integral role in an acclimation process that is aided by differing degrees of innate protection from anemone stings (Elliott & Mariscal 1997).

An anemonefish's intimacy with its host is considerable. Embryonic anemonefish imprint on the smell of host anemone species prior to dispersing as larvae, which influences their choice of settlement sites after the planktonic period (Arvedlund et al. 1999). Most individuals seldom move more than a few meters from their host, and adults remain with a single host for life. The relationship is considered mutualistic because the fish gains protection from predators on both itself and its eggs (which are laid on coral rock under the anemone) and also consumes other anemone symbionts and even the anemone itself. In turn, anemonefish chase away predatory butterflyfishes that eat anemones. The fish may also remove feces and debris from the anemone's upper surface, may drop food onto the anemone, may consume anemone parasites, and the fish's excreted waste products may stimulate the growth of symbiotic algae (zooxanthellae) within the anemone (Mariscal 1970; Allen 1975; Fautin 1991). The combined benefits of these activities to the anemone are substantial: anemones that harbor anemonefishes have faster growth rates, higher asexual reproduction (fission) rates, and lower mortality rates than anemones that lack the symbionts (Holbrook & Schmitt 2005).

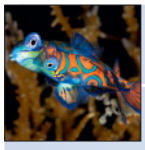
For fishes that use invertebrates as protection, such as gobies in invertebrate burrows and clownfishes in anemones, refuges may be in short supply and territorial defense of the structure is fairly common (e.g., Grossman 1980). This is the probable explanation for the complex social system, territorial defense, and sex reversal of anemonefishes (see Chapter 21), populations of which appear to be limited by the number of available anemones.

Interspecific shoaling

Many fish aggregations contain members of more than one species, forming **heterospecific shoals**. In monospecific aggregations, most fishes are of similar sizes (Pitcher 1983). This level of conformity is necessary because unusual appearing individuals contrast with the background of the more common fish and are preferentially selected by attacking predators. In a school, a perfectly healthy and normally swimming individual will be conspicuous to a predator if it is a different size or coloration from the majority of its schoolmates. Additionally, most schools cruise at efficient speeds and escape predators at high speeds that are both dependent on body length. A relatively large or small fish is likely to have different optimal swimming speeds than different-sized schoolmates; a relatively small fish will find itself trailing the school after a fast acceleration. Stragglers, like odd fish, are preferentially attacked by predators. When several abundant, morphologically similar species school together, they tend to segregate by species, either associating with conspecifics more closely or even creating horizontal layers that are relatively monospecific. Hence each fish gains the added benefit of being in a large school but avoids the risk of being the odd individual among another species (Allan 1986; Parrish 1988, 1989a).

Hydrodynamics and predator avoidance dictate uniformity across a school. However, fishes that aggregate for foraging reasons are not as constrained by the need to be similar. For example, foraging schools of parrotfishes and surgeonfishes in the Caribbean frequently include other parrotfishes and surgeonfishes, as well as trumpetfishes, hamlets, butterflyfishes, goatfishes, and wrasses. Surgeonfishes and parrotfishes both feed on algae and thus benefit from the large numbers that overwhelm territorial herbivorous damselfishes. Carnivorous species may consume invertebrates flushed by the activities of the herbivores or may also capitalize on territorial swamping and feed on invertebrates that live in algal mats of the territory or on the eggs of the damselfish. Larger predators, such as trumpetfish, may use the school or its members as moving blinds that conceal the predator and allow it to feed on the damselfish itself (trumpetfish will change color to match that of large or abundant school members). The presumed costs that small carnivores might suffer due to increased conspicuousness in a heterospecific shoal are apparently outweighed by gaining access to otherwise defended resources. The trade-off is underscored by the evasive maneuvers that minority fish take when a mixed species shoal is threatened. Rather than flee with the school, odd fish abandon the school and seek nearby shelter (Robertson et al. 1976; Aronson 1983; Wolf 1985).

Finally, fishes also form shoals with non-fish species. For reasons that remain puzzling, many tunas school with or below various dolphin species in the tropical Pacific. Fishing boats seek out the dolphin schools and surround them with large purse seine nets as the tuna remain below the mammals; the dolphins unfortunately become bycatch and frequently drown. On a less grand scale, postlarval French grunts school with dense clouds of mysid shrimps shortly after the grunts settle from the plankton and onto coral reefs. Both species are similar in size (8–13 mm) and appearance, but the mysids greatly outnumber the grunts. Grunts benefit from the antipredation function of the schools, affording them a degree of protection probably related to the number of mysids in a school. As the grunts grow, they school more on the periphery of the mysid aggregation and feed on the mysids. What began as a commensal or mutualistic relationship turns into a predator–prey interaction (McFarland & Kotchian 1982).



Summary

SUMMARY

1. Social aggregations, except where fish incidentally converge on a resource, require communication to be maintained; territorial defense similarly requires communication. Fishes use all six senses to communicate with one another. Static and dynamic visual displays, using colors and movement of fins or gill covers or turning on and off photophores, are common. The multiple functions of bright coloration in reef fishes have been long debated. They may have evolved in part because clear water makes predators detectable at a distance and the reef provides many places to hide from predators, thus eliminating a major cost of being colorful.
2. Fishes use sound when grasped by a predator, when spawning, defending territories, and in maintaining shoals. Sounds are produced by vibrating swim bladders, by rubbing bones or teeth together, and by the movement of the fish through the water. Eavesdropping by predators may be a significant cost of sound production.
3. Chemical production and detection functions during food finding, predator avoidance, mating, migration, parental care, territoriality, individual recognition, and aggregation. Pheromones are chemicals produced for intraspecific communication. Shoaling species are attracted to water that has contained conspecifics, and aggression can be reduced by production of specific chemicals in catfishes. Tactile communication is limited primarily to mating, parent–offspring activities, and during extreme fights. Electrical communication is used extensively in families that have evolved the ability to produce and detect weak electric fields (South American knifefishes, elephantfishes); electrical output is often species, sex, and size specific.
4. Agonistic interactions involve aggression and submission, usually between conspecifics interacting in dominance hierarchies or during territorial encounters. Territoriality is common in fishes, which defend feeding, breeding, resting, and predator refuge territories.
5. Activity in fishes is often limited to a fairly defined area, termed a home range. Home ranges may be as small as a few square meters or as large as many square kilometers; larger species and individuals generally move over larger ranges. Individuals have an internal map of their range and a highly developed ability and

strong tendency to return to their home range when experimentally displaced.

6 Fishes aggregate in loosely organized shoals or tightly organized schools. Aggregations function to increase food finding ability, for reproduction, to save energy, and chiefly to decrease the success of predators. Most aggregations form and break up repeatedly, but some have long-term stability that may even exceed the life span of individual members and are thus traditional.

7 Symbiotic relationships between species include parasitism, mutualism, and commensalism. Three fish families are known internal parasites (cutthroat eels, candiru catfishes, and pearlfishes). Mutualistic relationships include the many species that pick external parasites off other fishes, clownfish–anemone associations, and shrimp–goby pairs. Commensal relationships usually involve a fish living in association with an invertebrate, and may include sharksuckers attached to large elasmobranchs.

Supplementary reading

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Chapter 23

Cycles of activity and behavior

Chapter contents

CHAPTER CONTENTS

A fundamental characteristic of biological systems is their cyclical nature. Physiological and behavioral cycles exist at numerous temporal scales. Hearts beat and nerves discharge spontaneously on a regular rhythm, producing such predictable cycles as brain "waves". Hormone production, respiration, locomotor activity, and photomechanical movements within the eye show distinct cycles. Such processes are usually driven by a neural pacemaker or are linked to external cues. Hence the rising and setting of the sun, the phases of the moon, and the annual orbit of the earth around the sun create periodic physical stimuli such as illumination, climatic, and tidal cycles that in turn determine the onset, timing, and periodicity of many activities in fishes. The commonness of such cycles is not surprising; evolutionary adaptation is facilitated by constant or at least predictable selection pressures, and the external cues for such cycles as day length, tides, and seasonal climate have been distinct and relatively predictable (Schwassmann 1980), at least prior to human-induced climate disruptions. Our object in this chapter is to review some pronounced biological cycles in fishes that are driven by internal (endogenous) clocks, by external (exogenous) cues, and by a combination of factors. We will focus on daily, semilunar or biweekly, monthly or lunar, seasonal, and annual patterns of activity, particularly those that involve foraging, migration, and reproduction.

Diel patterns

The 24 h, **diel**, or daily periodicity of the earth's rotation creates a predictable pattern of light and darkness that has a profound effect on the biology of almost all animals and plants. Organisms are cued externally by sunrise and sunset; by day, night, or twilight length; or their activities are determined by an internal clock with a roughly 24 h period that may be reset by some external light cue.

Light-induced activity patterns

Activity patterns in fishes generally represent a direct response to changing light levels, but are also affected by the activity patterns of their predators and prey (McFarland et al. 1999). In most environments, fishes are **diurnal** and tend to feed primarily during the day or are **nocturnal** and feed by night, while some feed primarily during **crepuscular** periods of twilight and fewer still show no periodicity (Table 23.1). On average, about one-half to two-thirds of the species in an assemblage will be diurnal, one-quarter to one-third are nocturnal, and about 10% are crepuscular (e.g., Helfman 1993; Lowe & Bray 2006) (Fig. 23.1).

These distinctions are sharpest at tropical latitudes, where families can often be characterized as diurnal, nocturnal, or crepuscular (Hobson 1991; Helfman 1993). On **coral reefs**, herbivorous fishes are almost exclusively diurnal, for reasons that remain unclear but may relate to the need to visually identify edible and inedible algae. Parrotfishes, surgeonfishes, rabbitfishes, and sea chubs roam the reef, often in large shoals. They feed on algae and seagrass, some of which is defended by territorial damselfishes, parrotfishes, and blennies. Fishes that feed primarily on encrusting sponges, tunicates, corals, and hydrozoans are also largely diurnal; this group includes angelfishes, butterflyfishes, pufferfishes, and triggerfishes. Many wrasses, butterflyfishes, goatfishes, mojarras, and small seabasses eat

Table 23.1

Diel activity patterns – defined as when fishes feed – of better known groups and families of teleostean fishes. For many families, activity patterns are only known for a few species. Some large families appear under more than one heading because of intrafamilial variability. From Helfman (1993) and other sources, especially Lowe and Bray (2006).

All or most species diurnal Acanthuridae (surgeonfishes), Ammodytidae (sandeels), Anthiinae (anthiine seabasses), Atherinopsidae (surfsmelts), Chaetodontidae (butterflyfishes), Characoidei (characins), Cichlidae (cichlids), Cirrhitidae (hawkfishes), Cyprinodontidae (killifishes), Embiotocidae (surfperches, except Walleye and Rubberlip), Esocidae (pikes), Gasterosteidae (sticklebacks), Gobiidae (gobies), Kyphosidae (sea chubs), Labridae (wrasses), Mugillidae (mullets), Mullidae (goatfishes), Percidae (perches, darters, except pikeperches), Pomacanthidae (angelfishes), Pomacentridae (damselfishes), Scaridae (parrotfishes), Siganidae (rabbitfishes), Synodontidae (lizardfishes)
All or most species nocturnal Anguilliformes (most true eels, some morays, and congers are diurnal), Anomalopidae (flashlight fishes), Apogonidae (cardinalfishes), Batrachoididae (toadfishes), Clupeidae (herrings), Diodontidae (porcupinefishes), Grammistidae (soapfishes), Gymnotoidei (South American knifefishes), Haemulidae (grunts), Holocentridae (squirrelfishes), Kuhliidae (aholeholes), Lutjanidae (snappers), Mormyridae (elephantfishes), Ophidiidae (cusk-eels), Pempheridae (sweepers), Priacanthidae (glasseye snappers), Sciaenidae (drums), Siluriformes (catfishes)
Both diurnal and nocturnal species Carangidae (jacks), Catostomidae (suckers), Centrarchidae (sunfishes), Congridae (conger eels), Cyprinidae (minnows), Gadoidei (cods), Leiognathidae (ponyfishes), Mullidae (goatfishes), Pleuronectiformes (flatfishes), Salmonidae (salmon, trout), Scorpaenidae (rockfishes: diurnal juveniles, nocturnal adults), Serranidae (groupers), Sphyraenidae (barracudas)
Several crepuscular species[a] Carangidae (jacks), Elopidae (tarpons), Fistulariidae (cornetfishes), Gadoidei (cods), Lutjanidae (snappers), Serranidae (groupers)
Several species without distinct activity periods Aulostomidae (trumpetfishes), Muraenidae (moray eels), Pleuronectiformes (flatfishes), Scombridae (mackerels, tunas), Scorpaenidae (scorpionfishes, rockfishes), Serrandiae (groupers)

[a] Also active at other times.

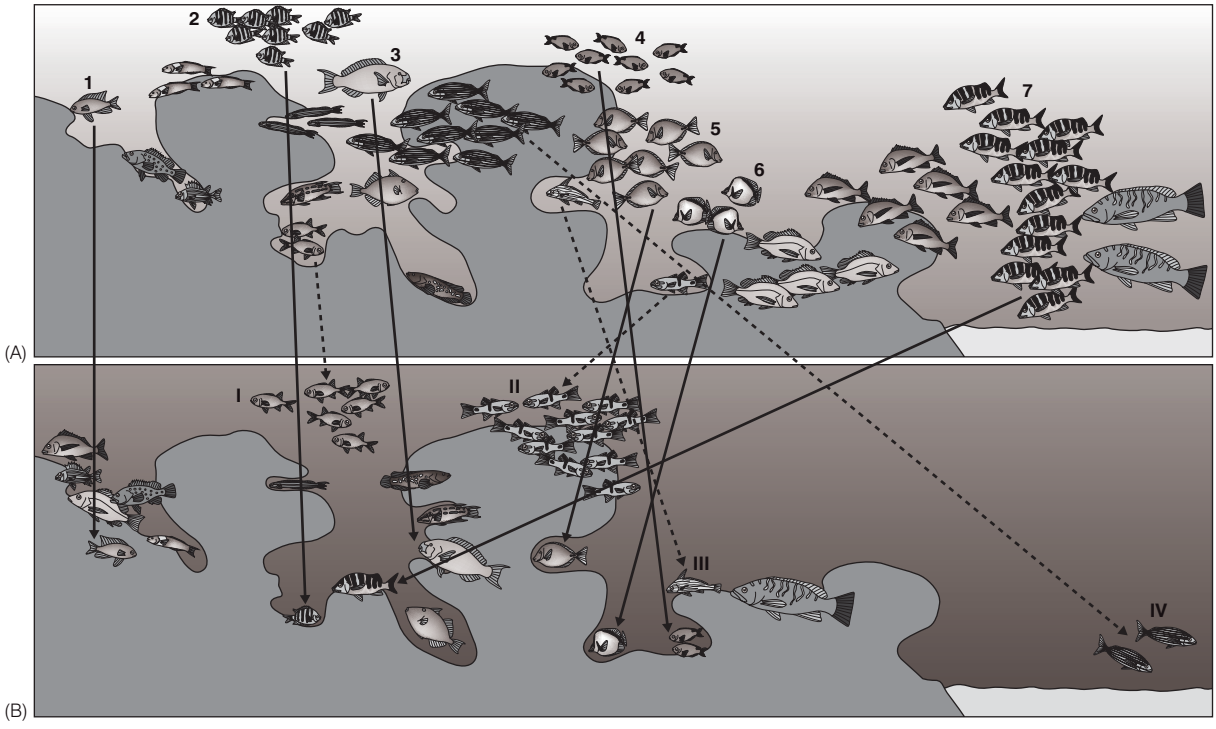


Figure 23.1

Day (A) versus night (B) distribution of families in a rocky reef area, Baja California, Mexico. Solid lines show habitat differences of diurnal fishes, dashed lines of nocturnal groups. Diurnal species: 1, benthic damselfishes; 2, Sergeant Major damselfishes; 3, parrotfishes; 4, zooplanktivorous damselfishes; 5, surgeonfishes; 6, butterflyfishes. Nocturnal species: I, squirrelfishes; II, cardinalfishes; III, drums; IV, grunts. After Lowe and Bray (2006), based on Hobson (1968).

mobile or buried invertebrates (e.g., small crustaceans and polychaete worms) and are also diurnal.

Zooplanktivores are particularly abundant and conspicuous during the day, including anthiine seabasses, damselfishes, wrasses, fusiliers, and butterflyfishes. Zooplanktivores also form large shoals, but these aggregations often remain over a particular section of the reef and wait for currents to bring planktonic prey to them; congrid garden eels similarly "aggregate" their burrows and feed on passing zooplankters (see Fig. 22.7). A small group of piscivores, including lizardfishes, trumpetfishes, cornetfishes, scorpionfishes, jacks, hawkfishes, barracuda, and flatfishes, are active primarily during daylight. Cleaning fishes that pick external parasites from other fishes (wrasses, gobies, and juvenile angelfishes and butterflyfishes) are active by day (see Chapter 22, Interspecific relations: symbioses). However, some of the largest shoals of fishes encountered by day in tropical waters are nonfeeding, **resting shoals** of nocturnal foragers. Sometimes numbering in the millions, aggregations of zooplanktivorous silversides, anchovies, and herrings frequently hover near structure or in sandy embayments (Parrish 1992). They may be subjected to attacks by roving seabasses, jacks, and tunas. Better protected are the daytime resting shoals of invertebrate-feeding squirrelfishes, copper sweepers, cardinalfishes, and grunts, which occur over coral or in caves (Fig. 23.2).

The prey resources available by day on a coral reef change dramatically at night (Hobson 1991, 2006). Many invertebrates bury themselves in the sand or in small holes in the coral, whereas others come out of hiding and move about the reef and into the water column. The maximum size of zooplankton increases substantially from relatively small (<1 mm long) diurnal forms to larger (>2 mm long) nocturnal animals; these larger invertebrates make up most of the diet of nocturnal zooplanktivores. Almost all nocturnally active fishes are carnivorous, feeding on mobile invertebrates that they locate and engulf with relatively large eyes and large mouths. Grunts, snappers, porgies, and emperors are generally found close to the bottom, whereas zooplanktivorous anchovies, herrings, silversides, squirrelfishes, cardinalfishes, glasseye snappers, and copper sweepers forage higher in the water column. Nocturnal zooplanktivores rely heavily on vision to find their prey and feed successfully even at relatively low light levels (e.g., Holzman & Genin 2003).

Predation pressure on fishes at night compared to day apparently varies as a function of habitat, with near-bottom predation greater but water column predation lessened (e.g., Danilowicz & Sale 1999; but see Sancho et al. 2000a). The piscivores that roam the reef after nightfall include various eels, sharks, squirrelfishes, snappers, groupers, and jacks (e.g., Young & Winn 2003). An apparent reduction in predation in the water column is reflected in the morphology of nocturnal planktivores, which tend to be less streamlined than their diurnal counterparts, and also in a general lack of shoaling behavior at night by either nocturnal or diurnal species.

Successful feeding by piscivores occurs primarily during the transitional periods of **evening and morning twilight**, when diurnal and nocturnal groups essentially replace one another ecologically (see Box 23.1). Crepuscular predators include tarpon, cornetfishes, groupers, snappers, and jacks, but can also include smaller species such as lizardfishes, squirrelfishes, grunts, and pinguipedid sandperches (e.g., Holbrook & Schmitt 2002). Although their activities are concentrated at this time, most of these fishes, and predatory fishes in general, are highly opportunistic and will take prey any time of the day or night.

Figure 23.2

A daytime resting school of juvenile French and White Grunts hover amidst *Diadema* sea urchins. At dusk, grunts move away from coral areas and feed in sand and grassbed regions, returning the next morning to the same daytime locales. Photo by G. Helfman.

Fishes in other habitats and latitudes vary in the predictability of their daily activity cycles. Tantalizingly little is known about tropical freshwater assemblages (Lowe-McConnell 1987). Characins, cyprinids, and cichlids are predominantly diurnal, catfishes nocturnal, but beyond such generalizations our knowledge is relatively limited. Poeciliids as a group are usually considered diurnal, but recent work in Trinidad suggests greater flexibility than that usually portrayed. Guppies in streams that contain predators such as the erythrinid Trahira or Wolffish, *Hoplias malabaricus*, are in fact diurnal feeders, ceasing activity and moving to stream edges at dusk. But where *Hoplias* does not occur, Guppies feed actively at night, show better growth rates, and engage in more courtship (Fraser et al. 2004). Guppies are among the best studied fishes behaviorally, including both field and laboratory manipulations. Perhaps when such manipulations or greater studies are performed on other groups that we view as invariant in their diel activities, we will discover greater plasticity (e.g., Reebs 2002).

At higher latitudes, activity cycles are similar in some respects but notably different in others. In *temperate lakes*, familial distinctions are weaker than on coral reefs. Diurnal zooplanktivores are abundant (minnows, sunfishes, perches) and have nocturnal counterparts among the herrings, minnows, whitefishes, and sunfishes (Helfman 1981b, 1993). Herbivores are relatively rare. Diurnal invertebrate feeders include minnows, suckers, mudminnows, topminnows, sunfishes, and perches. Their nocturnal counterparts include eels, catfishes, trout, sculpins, sunfishes, and drums. Piscivores, which again have an activity peak at twilight, are represented during the day by pickerels, Pike, and black basses and at night by Bowfin, salmonids, Burbot, temperate basses, sunfishes, and pikeperches. Nocturnal fishes rest by day amidst vegetation or other structure or form daytime resting shoals. Diurnal fishes often sink to the bottom and rest in relatively exposed locations at night.

Nearshore California *kelp beds and rocky reefs* also contain diurnal, nocturnal, and crepuscular species, but again familial distinctions are blurred (Ebeling & Hixon 1991; Lowe & Bray 2006). By day, shoaling zooplanktivores are abundant (silversides, seabasses, surfperches, damselfishes, wrasses, scorpionfishes), as are diurnal invertebrate feeders (seabasses, surfperches, clinids, gobies); these groups have nocturnal equivalents among the scorpionfishes, grunts, croakers, and surfperches that feed on relatively large prey both near and above the bottom. Herbivores are relatively rare, although they are more abundant in shallower, intertidal areas (blennies, pricklebacks, gobies; Horn 1989). Piscivores (seabasses, scorpionfishes, greenlings) are active primarily during twilight or nighttime; many scorpaenid rockfishes are diurnal as juveniles but nocturnal as adults (Lowe & Bray 2006). Nocturnal fishes form daytime resting aggregations, and diurnal fishes rest at night either in holes or in exposed locales.

At temperate latitudes, twilight changeover patterns (Box 23.1) are more variable compared to coral reef species. Activity patterns of temperate lake and kelp bed fishes are less precise in that: (i) many species feed both diurnally and nocturnally; (ii) reputedly diurnal and nocturnal species overlap in activity times; (iii) species within a family vary in major periods of activity; and (iv) individuals within a species vary in twilight changeover activities. Such variation could result from longer twilight lengths at higher latitudes, where dark adaptation of a fish's eye keeps pace with the rate of light change and hence diurnal species can maintain activity well into twilight and nocturnal species can commence activity before twilight ends. A latitudinal gradient in twilight length could interact with reduced predation pressure, reduced species diversity, or greater climatic instability to produce the relatively "unstructured" temporal patterns at higher latitudes (Helfman 1993; Lowe & Bray 2006).

The above discussion focuses on active animals. However, inactivity accounts for half the diel cycle in most fishes, which often prompts the question of whether or not fish sleep. **Sleep** occurs when a fish assumes a typical resting posture for a prolonged period, uses some form of shelter, and is relatively insensitive to disturbance (Reebs 1992, 2001, 2002). By this definition, many species sleep, including dasyatid stingrays, minnows, bullhead catfishes, butterflyfishes, cichlids, mullet, wrasses, and surgeonfishes. Croakers apparently do not sleep. Some parrotfishes and wrasses secrete a mucus envelope around themselves at night while sleeping, a behavior that has been subjected to much speculation. The mucus cocoon may thwart roving nocturnal predators such as moray eels by concealing odors or serve as an early warning, given that the parrotfish dashes out of the mucus envelope when it is touched (Videler et al. 1999). It may also have antibacterial or antiparasitic properties (Shephard 1994), or it may be an incidental byproduct of mucus production that occurs throughout the diel cycle but does not accumulate during the day because the fish are continually active (J. E. Randall, pers. comm.). The barrier, however, fails as a deterrent to attacks by snails, such as the dwarf triton *Colubraria*, which pierces the cocoon and the fish with its proboscis and sucks blood from the sleeping parrotfish (Bouchet & Perrine 1996).

The adaptive significance of sleep in fishes remains a matter of debate. One likely function is immobilization during a period when an animal is relatively inefficient at both foraging and predator avoidance. Hence energy is conserved and predators avoided, assuming some refuge is found before a quiescent state is assumed (Reebs 1992).

Vertical migrations

An entirely different daily rhythm of migration that appears largely dependent on light levels is the vertical migration undertaken by numerous fish species in both marine and

Box 23.1

Death in the "Children's Hour": changeover at twilight on coral reefs

Between the dark and the daylight,
When the night is beginning to lower,
Comes a pause in the day's occupations,
That is known as the Children's Hour.
H. W. Longfellow, in Cody (1899)

If one enters the water on a coral reef slightly before sunset and follows the events that occur over the next half hour, a striking **sequence** takes place in the activity and composition of the fishes. This sequence has been observed at several Pacific and Caribbean locales and probably occurs in most coral reef assemblages. Similarities among sites, despite dissimilar species, suggest that common selection pressures are operating, leading to a convergence in the behavior of the fishes. The twilight changeover period involves approximately four different phases of activity (Hobson 1968, 1972, 1991; Collette & Talbot 1972; Helfman 1993):

1. *Migrations of diurnal fishes.* Beginning about an hour before sunset, zooplanktivorous fishes (e.g., anthiine serranids, butterflyfishes, damselfishes) descend from the water column to the reef, and large herbivores (e.g., parrotfishes, surgeonfishes) migrate from daytime feeding locales to nighttime resting locales along predictable paths.
2. *Cover seeking of diurnal fishes.* From just before sunset until about 20 min after sunset, diurnal fishes seek shelter in the reef. Small individuals enter holes and cracks in the reef, whereas larger fish nestle under overhangs and in depressions. A species sequence exists; wrasses are among the first to seek shelter, followed by zooplanktivorous damselfishes, butterflyfishes, larger damselfishes, and parrotfishes. The time at which a species seeks cover is constant, with only a few minutes' variation from one evening to the next. Cover seeking by many diurnal species also occurs during the next phase.
3. *The quiet period: evacuation of the water column.* Beginning about 10–15 min after sunset, the level of activity and number of fishes above the reef drops precipitously. For the next 15–20 min, activity by small fishes in the water column comes to a standstill. Whereas minutes earlier the reef was alive with migrating and feeding fishes, the water column is now empty, leaving an observer with an uneasy feeling of abandonment. Hobson (1972) termed this phase the **quiet period**, when neither diurnal nor nocturnal fishes are moving about. All activity does not cease, however. Predatory fishes, such as groupers, jacks, and snappers, are active at this time, generally swimming close to the bottom and striking up at prey fishes that remain in the water column. This predatory tactic undoubtedly capitalizes on the difficulty prey have seeing dark-colored predators below them against the background of the darkened reef, whereas the predators are striking up at targets that are silhouetted against the lighter evening sky.
4. *Emergence and migration of nocturnal fishes.* The end of the quiet period is marked by the movement of nocturnal fishes up into the water column and along the reef face. Bigeyes, cardinalfishes, and croakers appear over the reef about half an hour after sunset and begin feeding on invertebrates. Grunts, squirrelfishes, and copper sweepers migrate along predictable paths from daytime resting locales to nighttime feeding areas (see Box 22.2). The water column above and around the reef is now occupied by active fishes.

The evening sequence is repeated again in reverse at dawn. Nocturnal fishes migrate back to resting locales and seek shelter, often in the exact same spot they occupied the previous day (e.g., Marnane 2000). A morning quiet period occurs when predators are most active, and then diurnal fishes reoccupy the water column and migrate to their daytime feeding locales. The predictability of times and locales, cued primarily by specific light levels, is striking.

Crepuscular predators are the apparent key to understanding the predictable, convergent nature of events during twilight on coral reefs. Predatory threat results from a combination of environmental, physiological, and behavioral factors unique to crepuscular periods (Fig. 23.3). During twilight, light declines from daytime levels of about 10,000 lux to nighttime levels of about 0.0001 lux. The light-adapted, cone-dominated eyes of many diurnal species cannot dark-adapt quickly enough and thus become ineffective at capturing light in the changing, dimmer conditions of dusk. At the same time, conditions are still too bright for the sensitive, rod-dominated eyes of nocturnal fishes that are highly effective at capturing light.

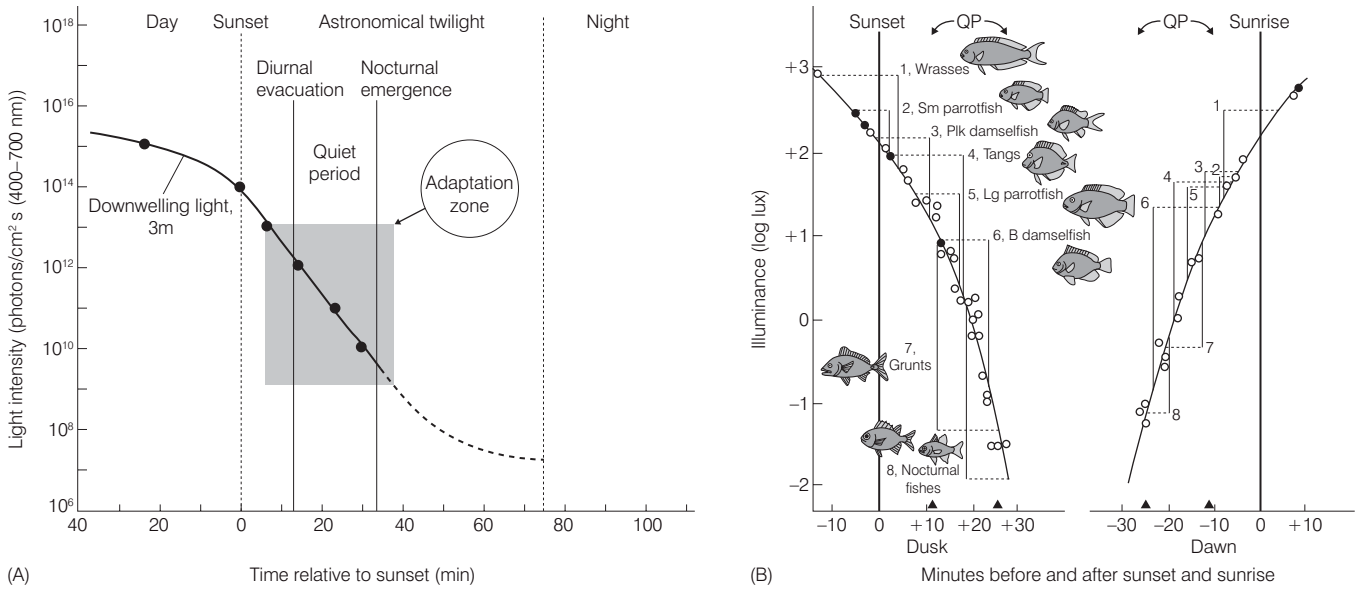


Figure 23.3

Light availability, dark adaptation, species changeover, and predator–prey interactions at evening twilight on a coral reef. (A) Available light (curved line) decreases maximally during the period from 13 to 33 min after sunset. This is the time (stippled area) when (i) diurnal eyes are dark-adapting, (ii) predators are maximally active and successful, and (iii) diurnal and nocturnal prey species abandon the water column, creating the quiet period. Approximate lux values for light units are 10^{14} photons = 10,000 lux, 10^{8} photons = 0.0001 lx. (B) Temporal sequence of cessation of activity of reef families at dusk, and onset at dawn. Families are coded by number. B, benthic; Lg, large; Plk, planktivorous; QP, quiet period; Sm, small. (A) after Munz and McFarland (1973), used with permission; (B) after McFarland et al. (1999), used with permission.

Twilight is therefore a period of intermediate conditions, when cones still function, but not with great efficiency. Many reef predators have fewer but larger cones than are found in diurnal eyes and more but smaller cones than are found in nocturnal eyes. This **intermediate eye** provides less visual acuity than a diurnal eye during the day and is less effective at light capture than a nocturnal eye at night. However, the intermediate eye is relatively better during the changing conditions of twilight, when neither diurnal nor nocturnal eyes function well. The light-capturing photopigments in the retinae of reef fishes also indicate an influence of twilight conditions. Diurnal, nocturnal, and crepuscular fishes have rod pigments that are most sensitive to light in the blue-green portion of the spectrum (about 490 nm), which matches prevailing wavelengths during twilight better than it matches the dominant greener nighttime light at 580 nm. Both diurnal and nocturnal fishes appear to sacrifice nocturnal vision in favor of being able to capture light during the dangerous crepuscular periods.

These anatomical and physiological differences, combined with the predatory tactic of striking up at backlit prey in the water column, helps explain why the post-sunset minutes are so dangerous for potential prey species. The quiet period of inactivity by small diurnal and nocturnal fishes appears to be a direct result of the threat of being eaten by predators at that time, rather than physical limitations involving visibility of their own prey (e.g., Rickel & Genin 2005). Evening and morning twilight may account for only 5% of the 24 h diel cycle, but conditions at twilight have an apparent influence out of proportion to the absolute time involved.

freshwater habitats (see Chapter 18, The deep sea). In most fishes, this movement involves an upward migration at dusk to feed and a downward migration at dawn. For example, Alewives (*Alosa pseudoharengus*, Clupeidae) migrate upwards in lakes in the evening at a rate that parallels the migration of their prey, a mysid shrimp. Zooplankton often migrate to the surface at night to take advantage of reduced visual acuity in visually hunting zooplanktivorous fishes. Predator avoidance could also explain vertical movements in many larval and juvenile fishes (e.g., Sockeye Salmon, Walleye Pollock); by remaining in dark, deep waters by day, vertical migrators can avoid visually orient-

ing, diurnal predators. Vertical migration could also increase a fish's encounter rate with plankton if currents differ at the surface versus at depth. Many oceanic regions are characterized by surface currents that flow in one direction and deeper waters that flow in a different direction, if at all. By swimming down, a fish can remain in relatively stationary, deep waters by day as the surface currents replenish the food supply in the waters above, a scenario analogous to feeding off a moving conveyor belt. It has also been postulated but not demonstrated that fishes could gain an energetic advantage by moving into warm surface waters to feed actively and then returning to cooler, deeper waters to metabolize and grow (McLaren 1974; Janssen & Brandt 1980; McKeown 1984; Nielson & Perry 1990).

Not all diel activity cycles relate only to feeding and predator avoidance. The timing of spawning is quite predictable for many species and even families. Diurnal spawners include many minnows, sunfishes, darters, cichlids, and wrasses. Twilight spawning characterizes some damselfishes (dawn) and butterflyfishes, wrasses, parrotfishes, and bothid flounders (dusk). Nocturnal spawning, not surprisingly, is difficult to observe but is known in the Yellow Perch, which is a strongly diurnal feeder (see below).

Circadian rhythms

A **circadian** rhythm is a pattern of activity governed by an internal clock with a period of roughly 24 h. The actual onset of activity may be shifted each day (the clock may be "reset") by some external stimulus or *Zeitgeber* (German for "time giver") such as sunrise. The need for an external resetting mechanism becomes obvious when one realizes how much day length changes during different seasons. Tides and feeding events can also serve as *Zeitgebers*. Activity rhythms in many teleosts can become established (**entrained**) if a meal is provided at a fixed time each day. Fish then develop an activity rhythm that anticipates the time of feeding, even in the absence of food and in constant light (Spieler 1992). In the absence of a *Zeitgeber*, such as during experimental conditions of constant light or darkness, rhythms are often maintained at slightly more or less than 24 h and are referred to as **free running**.

Free-running rhythms, involving either diurnal activity and nocturnal inactivity or the converse, have been demonstrated in a number of fishes, including hagfishes, swell sharks, anguillid eels, minnows including Goldfish, salmonids, suckers, South American knifefishes, burbots (Gadidae), killifishes, moronid temperate basses, and wrasses (Boujard & Leatherland 1992; Reebs 1992, 2002; Gerkema et al. 2000). Many fishes that show such patterns also exhibit considerable inter- and intraindividual variation in the rhythms (Reebs 2002).

Normally distinct activity cycles can be disrupted by experimental additions of predators or by the removal of resting structure. Distinct cycles also often break down during the breeding season and when fish migrate. Many strongly diurnal reef fish species spawn late into evening twilight (Sancho et al. 2000b), and normally diurnal minnows, Yellow Perch, and gobies spawn at night. The adaptive function of such breakdowns in periodicity is not understood. More obvious is the adaptiveness of a loss of activity rhythms in species that demonstrate parental care. Eggs and larvae must be guarded and fanned throughout the diel cycle, not just when the parents are normally active. Studies of several species, including catfishes, sticklebacks, centrarchid sunfishes, cichlids, and damselfishes indicate that parental care is also provided during the time period when adults would normally be inactive (Reebs 1992, 2001).

Circadian rhythms control many other aspects of fish behavior, morphology, and physiology. Many functions are under neuroendocrine control. The **pineal organ** on the dorsal surface of the brain secretes the hormone **melatonin**, which has a direct effect on the seasonal control of reproduction, sexual maturation, development, and growth, as well as shorter term effects on coloration, locomotor activity, and social behavior (see Chapter 7, The endocrine system). Melatonin is secreted on a circadian basis, maximally at night and minimally during the day. This rhythm, which is entrained by light and temperature detected by the pineal, is maintained even in cultured pineal tissue removed from a fish (Zachman et al. 1992). Photoreceptors sensitive to changing light and involved in circadian regulation also occur in the parapineal organ, parietal eyes, and deep brain (Foster et al. 2006). Secretion of hormones, such as prolactin, estradiol, progesterone, cortisol, testosterone, thyroxine, and triiodothyronine also follow **endogenous** (internally generated) circadian, semilunar, or lunar periodicities that are in turn affected by day length, temperature, and other hormone concentrations. Changing the light or temperature regime, or injecting a fish with hormones or hormone precursors, will cause changes in swimming activity and rest, temperature and salinity selection, reproduction, fat deposition, weight gain, and other aspects of growth. Hence the light–dark cycle can affect the timing of a **neural pacemaker** or **clock**, which in turn determines the timing of neural and hormonal cycles, which then entrain cellular rhythms in tissues, all governing the activity and behavior of the fish (Meier 1992).

The physical location of the clock (or clocks) in fishes remains a mystery. In mammals, a region in the brain, specifically the suprachiasmatic nucleus of the hypothalamus, serves as an endogenous oscillator (master clock). No direct analog of the suprachiasmatic nucleus has been found in fishes, although the hypothalamus has neural connections to light-receiving structures and other features that make it a candidate region for such a role, and the pineal has also been implicated in the control of many circadian rhythms in fishes (Boujard & Leatherland 1992; Holmqvist et al. 1992).

Tidal patterns

Tidal cycles are caused by the gravitational pull of the moon and to a lesser extent the sun on the oceanic water mass. Most coastlines experience a **semidiurnal** tidal regime that involves two high tides and two low tides each day, highs and lows being separated by about 6.2 h. Relatively strong, **spring** and relatively weak, **neap** tides occur at biweekly intervals. Daily tidal ranges can vary from a few centimeters to several meters depending on locale. Any marine animal that lives in the intertidal zone must either move out of the area in anticipation of or with lowering water levels, or face desiccation. Movements in general have to be synchronized with the fall and rise of tides. A drop in hydrostatic water pressure from a smaller overlying water column could serve as an external cue of a falling tide, and flooding of a pool could indicate an incoming tide. However, most intertidal animals, including fishes, appear to anticipate tidal changes via an internal clock that is reset by **exogenous** (external) cues (see above and Fig. 23.4).

Shallow intertidal areas – mud flats, saltmarshes, seagrass beds, mangroves, reef flats, or the rocky intertidal – are among the most productive regions in the sea. Plants grow rapidly in warm, shallow water, resulting in an abundant food base. Shallow depths mean that large aquatic predators are relatively scarce. These conditions create a relative bonanza for fish species that can adapt to the physiological conditions within the intertidal region. Tidal regions are by definition fluctuating environments, except that most fluctuations occur with predictable periodicity. Hence animals can capitalize on the fluctuations, or at least adapt to predictable environmental constraints. Falling tides in particular create numerous problems for fishes, including desiccation, rapid changes in and exposure to extreme temperatures, pH, and salinity, and exposure to terrestrial and aerial predators. Fishes generally follow one of two courses in dealing with low tide conditions: they either abandon shallow water with falling tides, or they remain in the intertidal area and seek shelter in cracks, algae, under rocks, or in pools (Gibson 1992, 1993; Horn & Martin 2006).

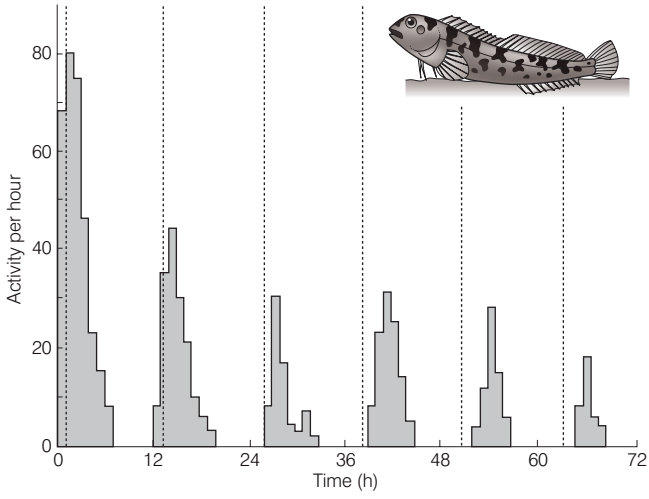


Figure 23.4

Endogenous, circatidal activity rhythm of the Shanny, *Lipophrys pholis*, held in a laboratory under continuous light. Activity is indicated by the darkened histograms, times of high tide where the fish was captured are denoted by the vertical dashed lines. The Shanny is normally active at high tide. In the absence of tidal stimuli, the activity cycle "free runs" with a period of 12.4 h, displacing it slightly from predicted high tides with each cycle. In the field, the fish's clock would be recalibrated (reset) by the hydrostatic pressure of high tide, which would keep the fish's activity synchronized with actual tides. After Gibson (1993), after Northcutt et al. (1990).

The former, termed **visiting** species, migrate in and out with the tides. This is particularly common with the many species that use intertidal areas as nursery grounds or refuges for juvenile fishes. Saltmarsh creeks along the Atlantic coast of North America serve as such nurseries for numerous species of worm eels, herrings, croakers, porgies, mullets, and flatfishes, as well as housing adults of dozens of other species. Approximately 80% of the commercial landings from the US Atlantic and Gulf of Mexico fisheries consists of species that spawn offshore and use saltmarshes for nurseries (Shenker & Dean 1979; Weinstein 1979; Miller et al. 1985). Juvenile fishes slosh in and out of the intertidal zones, being carried out of a marsh creek with the outgoing tide and back in again with the flood tide. Analogous tidal nursery situations exist in many parts of the world, such as mangroves in most tropical areas and the tidal swamps of western and northern Australia, which are used by juveniles of 24 families of fishes (Davis 1988). Adults of coral reef species also show on–off reef movements that correspond with tides. Low tides on hot days can create hot, anoxic conditions over large sections of reef and sandy tidal flats. Such areas are commonly avoided during low tides but reoccupied by fishes that move back onto the reef from the deeper reef face or from channels as cooler, oxygenated water floods the region during incoming tides.

Intertidal **resident** species remain in the intertidal zone at low tide and hide in areas insulated from complete desiccation, or make periodic visits into water or spray zones. Residents show the greatest degree of adaptation to the intertidal environment. Most are relatively small (<20 cm), which allows them to hide in holes and cracks or under piles of vegetation (pricklebacks, gunnels, sculpins, clingfishes, blennioids, gobies), and also presents less surface area to turbulence. Bodies are either thin and elongate (gunnels, pricklebacks, clinids) or depressed (sculpins, clingfishes). Elongate bodies are effective at cramming into tiny places. The intertidal zone is frequently exposed to breaking waves, particularly during high tides, and depressed body morphologies of many species are convergent with

those of fishes that live in other high-energy environments such as river rapids (e.g., Asian hillstream loaches, loach gobies, New Zealand Torrentfish; see Chapter 18, Strong currents and turbulent water). Suction cups, formed by fused pelvic fins, occur convergently in clingfishes, snailfishes, and gobies. Also convergent in fishes dwelling in high-energy and bottom areas is negative buoyancy, achieved through a missing or greatly reduced swim bladder. Some intertidal residents have evolved extreme tolerance to water loss: clingfishes can live up to 4 days out of water if humidity exceeds 90% and can sustain as much as 60% loss of total water content. This tolerance exceeds that of many amphibians. Gobiid mudskippers of the tropical Indo-Pacific spend 80–90% of their time out of water, being submerged and inactive only during high tides (Horn & Gibson 1988; Gibson 1992).

Tidal activity cycles in many fishes have an apparent endogenous basis. European Shanny, *Lipophrys pholis* (Blenniidae) and Goby, *Gobius paganellus* (Gobiidae) held in the laboratory under constant conditions still show an activity pattern that corresponds to a semidiurnal tidal regime (see above). They rest at the local time of low tides and swim actively at the expected times of high tides (see Fig. 23.4). Similar patterns, also known from anguillid eels, Tomcod (Gadidae), clingfishes, killifishes, sculpins, mudskippers, and flatfishes, appear to reflect an internal **circatidal** clock with a period of about 12 h, but one cannot completely rule out the possibility that the fishes are sensing fluctuations in the gravitational pull of the moon and sun. The clock may be reset by changing water depth, which in the field would correlate with fluctuating hydrostatic pressure caused by alterations in the weight of the water column above the fish (Gibson 1982, 1992).

Activity cycles in many intertidal species are constrained by the cyclical nature of oxygen availability. Photosynthesis during the day oxygenates the water, but both plants and animals consume oxygen at night. Hence many intertidal fishes have an ability to breath air (Horn & Martin 2006) and many reduce their activity, and their oxygen consumption, at night (Horn & Gibson 1988). Tides may override normal activity patterns for species that occur in a variety of habitats. American Eels, which are strongly nocturnal in nontidal habitats, travel with **tidal currents** by day and swim against them while foraging at night. Both Eels and killifish capitalize on tidal flooding to gain access to the food resources of the saltmarsh surface, eels by night and killifish by day (Weisberg et al. 1981; Helfman et al. 1983). Conversely, intertidal fishes that live in regions with very minimal tidal ranges, as in the Mediterranean, synchronize their activity patterns with day–night cycles instead of with tides (Gibson 1993).

Utilization of inshore areas by larval and juvenile fishes creates a particular logistic problem related to tidal cycles. Water flow is favorable for entry into such areas during only half of the tidal cycle; for much of the time, small fishes must fight outflowing currents of several knots, impeding or reversing any progress they may have made. Fishes overcome this problem by engaging in **selective tidal stream transport** or modulated drift (e.g., Wippelhauser & McCleave 1987; Forward & Tankersley 2001). Typically, immigrant fishes move up into the water column on incoming tides, but move down close to the bottom on outgoing tides. They are consequently carried inshore with incoming currents, but minimize slipping back offshore by taking advantage of reduced ebb currents as water is slowed by bottom topography and friction. They thus "ratchet" themselves into the estuary. Selective tidal stream transport has been observed in post-larval American eels, spot (Sciaenidae), and flounders. Adult anguillid eels, cod, and flatfishes on spawning migrations use similar transport mechanisms to move along the shore or in open water. Selective tidal stream transport could be adaptive as a directional aid and also reduces the energy and time required to reach a particular locale; the response might be driven by an endogenous circatidal clock, as discussed in the previous section (Miller 1988; Gibson 1992; Forward & Tankersley 2001; Metcalfe et al. 2006; see also Chapter 9, Getting from here to there: larval transport mechanisms).

Semilunar and lunar patterns

One postulated function of cyclical behavior is the opportunity that it affords individuals to **synchronize** their behavior with that of conspecifics. Nowhere is such synchronization more obvious and necessary than in reproduction. Not only must both sexes aggregate at the same locale to release gametes, but preparatory events of gametogenesis (gamete production) and secondary sex character development must also occur with similar timetables that converge on the same small time window. Predictable external cues that occur over biologically appropriate time periods are prime candidates as drivers of such cycles. The monthly orbit of the moon is a particularly common *Zeitgeber* because of its predictability, but also because of the direct links among lunar phase, nocturnal illumination, and tidal and current strength.

An illustrative example of this interrelationship involves the grunion, *Leuresthes tenuis* (Atherinopsidae), that spawn literally on the beaches of southern and Baja California (Fig. 23.5; see also Chapter 21, The spawning act). Grunion spawn after high tides on the three or four dark nights following a full or new moon during the spring and summer, the time when highest tides occur at night (Walker 1952; Martin & Swiderski 2001; Martin et al. 2004). These lunar periods correspond to spring tides, when water is pushed to its maximum height up the beaches. The same wave cover will not occur for at least 2 weeks. Females ride waves

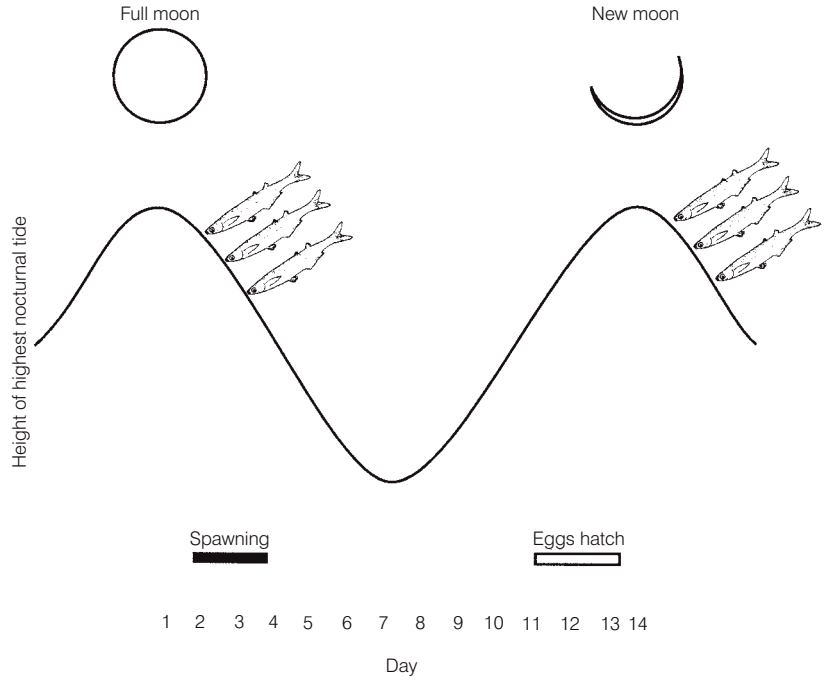


Figure 23.5
Semilunar spawning cycle of the Grunion. Grunion are small (15 cm) atherinopsids that frequent the nearshore waters of Baja and southern California. They spawn every 2 weeks in the summer during spring tides, when waves sweep farthest up the beaches. Adults ride the waves up the beach, dig in the sand, and deposit and fertilize eggs. Spawning occurs shortly after peak tides, insuring that eggs will not be inundated again until the next spring tide, 10–14 days later, when they are ready to hatch. Fish symbols indicate nights of spawning. Redrawn from Alcock (1989), used with permission.

up the beach, dig with their tails into the wet sand, and deposit eggs. Males deposit sperm around the females. The eggs normally develop in the moist sand for about 10 days. They will not hatch until the next spring tides, when waves once again cover the higher portions of the beach and the agitation of the breaking waves stimulates hatching (Griem & Martin 2000). If waves do not reach the eggs, they can delay hatching for an additional 2 weeks (gonad maturation is, however, on an 18-day, not 14-day, cycle). Spring tides promote synchronization of male and female behavior, allow a sufficient 2-week interval for embryogenesis, and facilitate spawning under the cover of darkness which may lessen predation on adults. The eggs are deposited where further wave action will not expose them for 2 weeks, again potentially reducing predation. A second grunion species, *L. sardina*, engages in similar behavior but spawns both day and night. In its Sea of Cortez locale, spawning coincides with the period of highest tides (Clark 1925; Gibson 1978).

Grunion reproduction is an example of **semilunar** periodicity; such cycles usually involve a 14.7-day interval. Synchronization with a period of maximum spring tides is common in fishes with semilunar, lunar, or longer cycles. Two groups with such rhythms are intertidal spawners and coral reef spawners. Intertidal spawners include the grunions as well as a southern hemisphere whitebait, *Galaxias attenuatus*, Surf Smelt (*Hypomesus*), Capelin (*Mallotus*), a stickleback (Gasterosteus), silversides (*Menidia*), killifishes (*Fundulus*), four-eyed fish (*Anableps*), and a Japanese pufferfish (*Fugu*) (Martin & Swiderski 2001). Intertidal spawners deposit eggs during spring high tides on sand or pebble beaches or amidst algal and root mats, leaf axils, and bivalve shells. Spawning often occurs on the days or nights following full or new moons. The eggs are exposed to air sometime during the next 2 weeks before the next spring tides, at which time they hatch. Smelt and killifish eggs actually require aerial incubation and will die if continually immersed, apparently because of relatively low oxygen concentrations in water. A reduction of aquatic predation on the eggs is often postulated as the primary selection pressure favoring intertidal spawning, although predation on puffer eggs is minimal due to their toxicity (Gibson 1978; Taylor 1984, 1990; Leatherland et al. 1992).

Many coral reef fishes exhibit lunar or semilunar synchronization in their spawning activities (Johannes 1978; Gladstone & Westoby 1988; Robertson 1991; Domeier & Colin 1997; Takemura et al. 2004), although some species show no correlation with lunar period (e.g., Sponaugle & Pinkard 2004). Most larger coral reef species that spawn in the water column do so at twilight or at night during new or full moon or both, often on high or ebbing tides. Larger species move to deep water, often to form spawning aggregations at predictable locales. Smaller species rush momentarily into the water column above the reef. Both groups have pelagic eggs and larvae, and larvae return to reefs primarily during spring tides. Johannes (1978) postulated that such behavior serves to move eggs and larvae out of the range of the abundant benthic and demersal predators on the reef, basically exporting the eggs out of the adult habitat but not necessarily out to sea.

Other explanations for the periodicity and timing of coral reef fish spawning either focus on larval or adult biology. Larval hypotheses, in addition to those proposed by Johannes, include maximized dispersal of larvae to distant habitats, swamping or saturation of predators (such as Whale Sharks; Heyman et al. 2001), synchronization of larval production with production of invertebrate larvae on which they feed, reduction of competition among different larval cohorts, nocturnal spawning to minimize ultraviolet damage to floating eggs, and optimization of the timing of larval settlement in appropriate reef habitats. Adult biology hypotheses focus on synchronization of activities among spawners, optimization of the conditions under which adults spawn, and improvement of conditions for egg guarding in species that show parental care.

No single hypothesis explains reproductive timing in all species (Barlow 1981; Taylor 1984; Robertson et al. 1990; Gibson 1992; Sancho et al. 2000b), but larval biology hypotheses may pertain more to water column spawners and adult biology hypotheses may better explain selective forces acting on benthic spawners that guard their eggs. Proof by exception comes from studies of species with unpalatable eggs, larvae, and adults. The Sharpnose Puffer, *Canthigaster valentini*, is protected by noxious chemicals at all life history stages (Gladstone & Westoby 1988). It spawns near the bottom during the day throughout the year, shows no definitive cycling, has an unhurried courtship display, exhibits no parental care, and embryos hatch on incoming tides. Apparent liberation from predation has also removed the selection pressures that induce periodicity and other more usual spawning behaviors in reef fishes. Few direct tests of most hypotheses have been attempted and much exciting work remains to be done on this topic.

A variety of adaptive scenarios can be postulated for lunar cycles synchronized with spring tides in nearshore marine and estuarine fishes. More puzzling are lunar spawning cycles in some freshwater and high seas fishes. For example, two Lake Tanganyika cichlids spawn during full moons, which might minimize diurnal predation on eggs while enabling adults to monitor the activities of their own, nocturnal, catfish predators. An apparent semilunar spawning cycle in an offshore gadoid, *Enchelyopus cimbrius*, is even more puzzling, aside from synchronization of reproductive behavior among adults (Gibson 1978; Taylor 1984; Leatherland et al. 1992).

Lunar cycles have been found in other aspects of the biology of fishes. White Suckers show an endogenous lunar rhythm of temperature preference, selecting relatively high temperatures during the new moon and lower temperatures during the full moon. Guppies show a change in the spectral sensitivity of their retinae that has a lunar periodicity. Semilunar cycles have been found in feeding rate, body mass, body length, scale growth, otolith deposition, RNA/DNA content, and in concentrations of various plasma constituents in fishes. These phenomena may all be interrelated; feeding rate could affect all the other growth and condition parameters. The downstream migration of young salmonids is also cued by lunar events. Newly emerged Coho Salmon fry (*Oncorhynchus kisutch*) move downstream from spawning redds at night during the new moon. Cover of darkness may reduce predation, whereas synchronization could aid in forming shoals and also swamp any predators that were present (see Chapters 20, 22). Older smolts move downstream by day during the new moon, which delivers the migrants at the river mouth during spring low tides, which in turn aids movement out of the river and into the sea. Models explaining smoltification and migration in several salmonids (see Chapter 10) suggest that the full moon initiates a process of morphological, behavioral, and physiological changes (perhaps mediated by thyroid hormones) that prime the animal for eventual downstream migration during the new moon. The new moon is also the primary time of upstream migration by elvers and downstream migration of maturing adults of anguillid eels. Again, the underlying mechanisms and clocks driving these periodicities remain a mystery (Leatherland et al. 1992).

Seasonal patterns

Activity and distribution

The ectothermic nature of fishes makes them affected by and therefore highly responsive to seasonal fluctuations in temperature. At temperate and polar latitudes, food availability, vegetative cover, turbulence, oxygen availability, and water clarity all vary greatly among seasons. Ice cover on high-latitude lakes leads to oxygen depletion and **winterkill** conditions; thermal stratification at lower latitudes creates analogous **summerkill** conditions. Hence fishes in these habitats characteristically move into and out of shallow, nearshore zones with the progression of the seasons.

For example, a typical pattern in a lake in the northeastern United States finds the shallow regions devoid of vegetation and fishes in early spring after ice melt and until the surface water warms above about 10°C. With warming water, minnows, catfishes, pickerel, sunfishes, black basses, killifishes, and Yellow Perch move into nearshore regions. At water temperatures of around 15°C, sunfishes and many others spawn and vegetation growth is apparent. In late spring and early summer, as temperatures exceed 20°C, vegetation is well established and fish are distributed throughout the littoral zone, including deeper portions such as drop-offs down to the thermocline. In late summer and early fall, as temperatures fall below about 15°C and plants begin to die back, fishes first move from the deeper littoral zones to the shallower regions. As temperatures fall below 10°C and vegetation becomes sparse, fishes abandon nearshore regions presumably for deeper water. If periods

of warm weather occur during the fall, fish will reoccupy and then abandon the shallows as the water warms and recools (Hall & Werner 1977; Keast & Harker 1977; Emery 1978; Helfman 1979a).

We know much about fish distribution and activity during spring, summer, and fall. However, winter biology remains poorly understood, although information is growing. In North American *temperate and arctic lakes*, many fishes feed actively despite thick ice cover; smelt, numerous salmonids, esocids (Northern Pike, Chain Pickerel), percids (Yellow Perch, Walleye, Sauger), and centrarchid sunfishes all feed actively. Where many lake fishes go in winter remains a mystery. Deeper water is a logical choice because vegetation, which provides shelter for both fishes and their prey during warm months, disappears from the shallows in winter. Also, winter storms make shallow regions unstable before ice cover develops, and cause ice grinding when ice breaks up. Small and large temperate North American lakes experience a net decrease in both diversity and abundance of fishes in shallow waters during the winter. Centrarchids as a group move into deeper water. Large Carp and Bigmouth Buffalo (*Ictiobus cyprinellus*) in Lake Mendota, Wisconsin move to two traditional winter aggregation areas in relatively deep (5–7 m) water. Gill netting in those areas during one winter caught 43,000 kg of Carp and 3000 kg of Bigmouth Buffalo whereas nets set at other locales caught nothing. Northern Pike show a tendency to occupy deeper water and to swim farther offshore under ice.

Some species remain in the shallows or move into them from deeper water. Minnows remain in the littoral zone of lakes and occupy piles of twigs, small cracks in rocks and logs, or even bury themselves 0.5 m down in gravelly bottoms. Salmon and trout, whitefishes, Burbot, and sculpin occupy deeper water by summer but move into shallower water to feed under the ice. In the Laurentian Great Lakes, fishes abandon the shallows in fall and early winter, but some (whitefishes, herrings, salmonids, Troutperch, sculpins, and suckers) return after the ice cover develops and filamentous algae appear. Again, early winter storms make the shallows down to about 10 m depth a turbulent and unstable habitat. At very high, Arctic latitudes, little day/night or summer/winter differences are shown by the relatively depauperate fish faunas of lakes (Diana et al. 1977; Johnsen & Hasler 1977; Emery 1978; Helfman 1979a).

The extreme conditions that develop during winter in ponds and small lakes lead to different behavior patterns. As ice and snow cover develop, deoxygenation occurs, beginning at the lake bottom and moving up through the water column. At very low oxygen tension levels (e.g., <0.5 mg/L), lake species that are most resistant to winterkill mortality (e.g., Mudminnows, Umbridae; Pike; Yellow Perch) engage in behaviors that enhance their survival. They move up in the water column and take up positions immediately under the ice where it is thinnest and where oxygen concentrations are greatest, with their noses in contact with the ice. They seek out gas bubbles and inhale water from around the bubbles. Mudminnows will even engulf bubbles (air bubbles are squeezed out of ice as it freezes or are exhaled by aquatic mammals such as beavers and muskrats). Sunfishes, such as the Bluegill, swim throughout the water column and frequently encounter deoxygenated water; they are the first to die under winterkill conditions (Petrosky & Magnuson 1973; Klinger et al. 1982).

Among *stream fishes*, salmonids are as usual the best studied with regard to winter behavior. Several species (especially juvenile Sockeye and Atlantic salmon and Rainbow, Brown, Cutthroat, and Bull trout) remain active but switch from constant activity or diurnal foraging and nocturnal refuging to nocturnal foraging and resting by day (e.g., Thurow 1997; Valdimarsson & Metcalfe 1998; Bremset 2000; Jakober et al. 2000; Steinhart & Wurtsbaugh 2003). Daytime shelter use often entails settling under boulders or in the spaces between boulders and cobbles, thus saving energy by resting in areas of low current flow, protecting fish from physical damage from ice moving in the water column, and probably also concealing them from predators. Suitable refuge habitats – either cobbles or slow-flowing water – may be limiting, and inter- and intraspecific competition for appropriate refuge sites is reflected in territorial combat between fishes when they move into shelters at dawn (Harwood et al. 2001, 2002). Overwinter survival of Rainbow and Cutthroat trout and Chinook and Coho salmon is higher in stream sections that contain cobbles or large woody debris (e.g., Solazzi et al. 2000). Minnows also switch from diurnal to nocturnal activity as temperatures drop, occupying cobble substrates during diurnal resting periods (Cunjak 1996; Greenwood & Metcalfe 1998). These observations underscore the importance of maintaining high habitat diversity – especially clean, complex bottoms with cobble or woody debris but also of pools and backwater areas – as a means of improving year-round survival of a variety of stream fishes (Cunjak 1996; Jakober et al. 1998; Brown et al. 2001).

Temperate marine fishes also exhibit cycles of small-scale, seasonal movements that relate to temperature and climatic changes (longer migrations are discussed below). Many fishes abandon shallower waters when large algae die back in winter. In central Californian kelp beds, juvenile fishes inhabit understory kelp during spring and summer, using it for shelter and eating the invertebrates that live there. Juveniles disappear each fall and winter as the understory dies back or is reduced by periodic storms. Adults of resident species, particularly surfperches (Embiotocidae) and predatory Kelp Bass (*Paralabrax*, Serranidae) tend to remain in the area year round but undergo changes in diet and foraging locale as the resource base shifts. Southern Californian bays and estuaries undergo a marked cycle of species richness and individual abundance, both of which

peak in summer and are lowest in winter. The fauna contains resident (topsmelts, surfperches, gobies, flatfishes) and seasonal (anchovies, mullets) species. Seasonal movements in and out of the bays are strongly linked to changes in temperature, salinity, and the productivity of macroalgae. In Puget Sound, Washington, which is relatively protected from winter storms, rockfishes (*Sebastes*, Scorpaenidae) school in midwater and move down a few meters to slightly deeper water in the winter. Benthic species remain in kelp bed and reef areas year round (Ebeling & Laur 1985; Horn & Allen 1985; Ebeling & Hixon 1991; Stephens et al. 2006).

On the Atlantic coast of North America, common names imply seasonal cycles of movement and abundance. Summer Flounder (*Paralichthys dentatus*, Bothidae) spend warmer months nearshore along the coastline and in bays. They migrate offshore in the fall to deeper (30–200 m) water to spawn. In contrast, Winter Flounder (*Pleuronectes americanus*, Pleuronectidae) migrate to deeper water in the summer and then return to bays as the water cools; they also spawn in winter. Other species undergo seasonal movements that differ by individual age. Adult Tautog (*Tautoga onitis*, Labridae) move offshore in the fall as water temperatures drop below about 10°C, while young Tautog and Cunner (*Tautogolabrus adspersus*) move from grass and algal beds that are dying back to other shallow habitats that provide greater shelter before these fishes enter a winter torpid state. A pattern in many temperate marine environments is a dependence on algae as a refuge or as an indirect or direct food source. As colder months approach and algal beds cease productivity and lose their "above-ground" parts, many species abandon these regions for deeper waters or waters that will provide cover during months of low food production (Bigelow & Schroeder 1953b; Olla et al. 1979; Rogers & Van Den Avyle 1982).

Reproductive seasonality

The most notably seasonal activity in fishes and most other organisms is reproduction. Successful reproduction requires careful synchrony in physiology, anatomy, and behavior of both sexes. Spawning occurs when both sexes have completed gametogenesis, gamete maturation, secondary sex character development, and spawning readiness and arrive at the proper spawning locale at the same time. A series of environmental cues are likely to trigger each stage of a reproductive cycle. Seasonally dependable cues, particularly ones that may insure survival of larvae (plankton blooms, sea temperature changes, alterations in currents) are the most likely cues to be used and are usually associated with seasonal, cyclical climatic events such as monsoonal rains, oceanic surface and upwelling currents (e.g., El Niños), and temperature cycles. Although environmental cues influence timing, flatfishes and seabass held under constant laboratory conditions still show predictable seasonality in their gonadal cycles, indicating an endogenous basis to reproductive cycles (Bye 1990).

Seasonal cycles occur in most families, but "seasons" are defined differently in temperate versus tropical habitats. Most species in temperate latitudes spawn in spring or summer, a few in fall and winter. Conditions favoring larval growth and survival appear to be primary determinants of the phasing of reproduction. In temperate locales, spring and summer are times of maximal food productivity, and are also periods when protective vegetation is maximally available. Although many fishes in tropical and even subtropical regions breed year round (e.g., livebearers, numerous reef species), even these species show periods of peak reproductive activity that occur at relatively predictable times of the year.

Temperate freshwater fishes undergo reproductive cycles that are influenced strongly by **changing photoperiod** (day length) and **temperature**. Because gametogenesis is a complicated and lengthy process (see Chapter 9), environmental conditions at the time of initiation of gametogenesis will be different from those in effect when spawning occurs. Hence different cues are used at different phases in the cycle. In salmonids, spawning time is heritable, occurring at the same time each year over a period of 2–6 weeks in a particular genetic strain (Scott 1990). However, timing may differ among stocks in geographically nearby rivers or even in different streams flowing into the same river, reflecting **locally adapted genotypes** (e.g., NRC 1996b; Stewart et al. 2002) (Fig. 23.6). The rhythm is circa-annual, endogenous, and entrained by environmental cues, primarily photoperiod, but can be modified by temperature. Salmonids

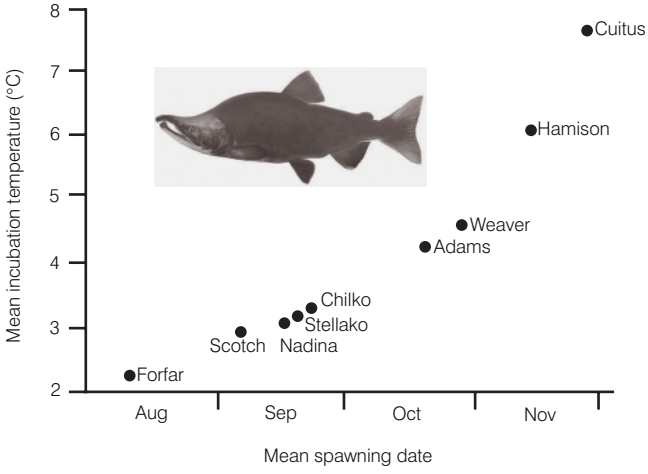


Figure 23.6

Genetically based, local adaptation in Fraser River Sockeye Salmon. Among stocks (named dots), fish spawn on different dates, and eggs are incubated at different mean temperatures. These differences lead to emergence dates favorable to juvenile feeding. Different spawning dates also help to coordinate migrations among smolts originating at different distances from the sea. After Brannon (1987); sockeye drawing from USDA Forest Service, www.fs.fed.us.

are generally divided into fall (September to December) and winter (January to March) spawners. Most species are fall spawners, including Brown Trout, Brook Trout, Lake Trout, and Atlantic Salmon; among Pacific *Oncorhynchus* species, spawning occurs in late summer through early winter, with much latitudinal variation (e.g., Groot & Margolis 1991; Augerot 2005; Quinn 2005). Rainbow Trout are generally late winter spawners. In both groups, the reproductive cycle is initiated during the previous springtime in response to increasing day length.

Temperate cyprinids, such as the Golden Shiner (*Notemigonus crysoleucas*), Goldfish (*Carassius auratus*), Humpback Chub (*Gila cypha*), and Lake Chub (*Couesius plumbeus*), all spawn in late spring and early summer. Gametogenesis begins in the fall in response to decreasing temperature and shortening day length, advances slowly during the winter, and then accelerates and is completed in spring in response to increasing day length and rising temperature. Sticklebacks have a similar cycle, as do most spring/early summer spawning fishes in temperate locales. Carp (*Cyprinus carpio*) show a variant cycle, involving gonad development in late summer, quiescence in winter, and then final maturation of oocytes and spawning in the spring. The European Tench, *Tinca tinca*, is unusual in that it spawns in the fall. Late fall, winter, and early spring in temperate lakes are too unproductive for the small larvae of most species and consequently spawning does not normally occur during those seasons. The exceptionally large size of eggs and physiological tolerance of cold temperatures in salmonids may explain their fall–winter spawning and success at high latitudes (Baggerman 1990; Hontela & Stacey 1990).

Temperate fishes, as well as many other animals and plants, use **photoperiod** as a proximate environmental indicator of current and future climate. Typically, long days (e.g., >13 h light) and warm temperature cause gonadal **recrudescence** (resumption of gametogenic activity), whereas short days inhibit recrudescence, regardless of temperature. Available evidence suggests that many temperate fish species have an endogenous, circa-annual clock that drives reproductive activities, and that this clock is affected by another, circadian clock of photosensitivity. A critical piece of information is day length; days shorter than some minimum cause both initiation and cessation of reproductive behavior. The circadian clock can tell a fish if day length is increasing, but the fish must be most sensitive to light at a time of the day when daylight would indicate increasing day length (Fig. 23.7). Daylight during the first 8–10 h after sunrise could occur at just about any time of year, but daylight 10–12 h or more after sunrise will not occur during winter. Hence fish have a clock that tells them how many hours have passed since sunrise, and they tend to be insensitive to light during the first 10 h or so after sunrise. Light encountered after that period, during the "photoinducible phase" of photosensitivity, has a strong influence on gonad development. The existence of a photoinducible phase and a photosensitive circadian rhythm was discovered by exposing fish to 2 h pulses of light at different times of the day. Sticklebacks exposed to light 14–16 h after sunrise showed greater rates of sexual maturation than fish experiencing light at other times of a light–dark cycle. The position and length of the photoinducible phase change with season and temperature (Baggerman 1990; Taylor 1990).

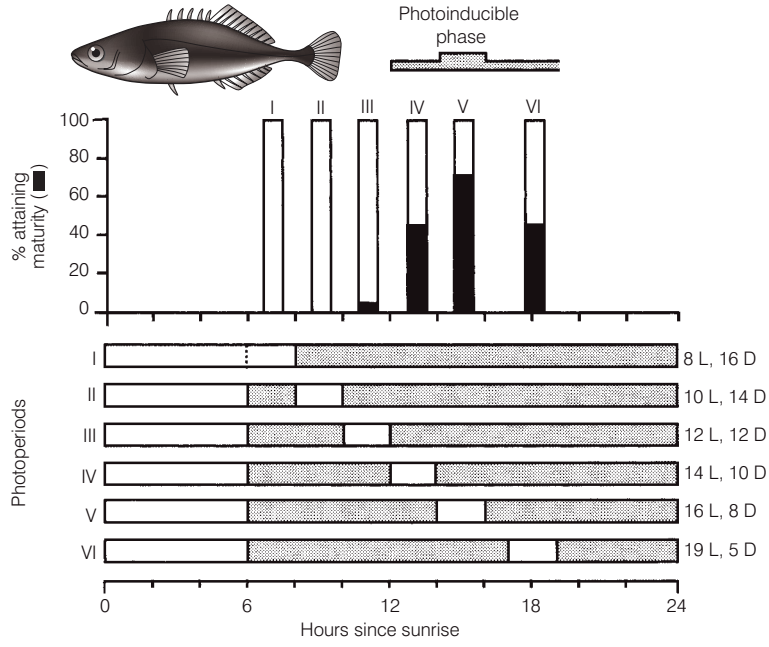
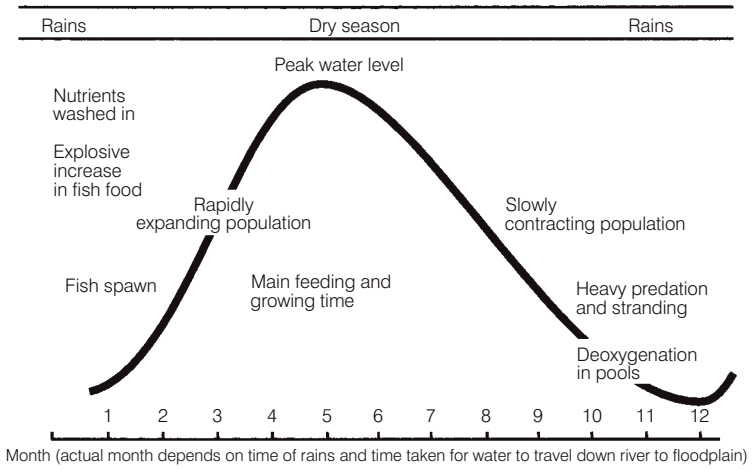


Figure 23.7

Sticklebacks have a daily rhythm of photosensitivity that is maximal about 14–16 h after sunrise. During this maximally sensitive period, exposure to light induces sexual maturation. The photoinducible phase helps the fish determine if day length is increasing, as would happen during spring and summer. Experimental manipulations of daily light/dark cycles can pinpoint the existence and position of the photoinducible phase by providing a 2 h pulse of light at different times after sunrise. The open bars at the bottom indicate when lights were on, the darkened portions when lights were off (0 = sunrise). Light 14–16 h after sunrise would be naturally experienced when days consisted of 16 h of light (L) and 8 h of dark (D), as would happen during summer. Maximum levels of sexual maturity (bar V) are found in this light regime. From Baggerman (1985), used with permission; stickleback drawing from www.seagrant.wisc.edu.



Fish movements	Up river	Disperse on floodplain	Back to river	Confined to pools
Fish biomass	Production of young	Very rapid growth	Heavy losses	Much reduced
Fishing	Of upstream migrants (destructive)	Diffcult: fish dispersed, much cover	Intensive as fish move back to river	In pools (dry season refuges)

Figure 23.8

The seasonal progression of events for many fishes in large tropical rivers. The dark curved line indicates relative water levels. Seasonal flooding of highly productive gallery forests and swamps opens these areas up to lateral migration, feeding, and spawning by fishes. Many regions show two rainy seasons and both result in lateral migrations. Fat stores increase as fishes capitalize on the food abundance in flooded regions. From Lowe-McConnell (1987), used with permission.

Seasonality among freshwater fishes at *tropical* latitudes (between 30°N and 30°S latitude) is defined more by rainfall than by temperature (Goulding 1980; Lowe-McConnell 1987; Munro 1990a; Winemiller & Jepsen 1998) (Fig. 23.8). Regions between 15° north and south of the equator generally have two rainy seasons per year, whereas higher tropical latitudes have one rainy and one dry season. The floodplains, lakes, and seasonal swamps created by a rising river are common spawning and nursery grounds in many locales, and many riverine fishes have reproductive cycles that coincide with seasonal inundation of gallery forests and swamps, perhaps cued by rainfall or rising water levels (Lim et al. 1999; Agostinho et al. 2004; de Lima & Araujo-Lima 2004). Newly inundated areas are advantageous spawning locales because: (i) accumulated nutrients are released, which creates plankton blooms and food for progeny; and (ii) predation is minimized by abundant vegetation for refuging and because large flooded expanses minimize contact with predators. In contrast, receding water and reduced habitat space during the dry season means that predators and competitors are concentrated, which also leads to deoxygenated water. Dry season and aseasonal spawners often provide extensive parental care, including provisioning of young, and/or possess secondary breathing structures (e.g., lungfishes, bagrid catfishes, cichlids, anabantoids).

Adults of many tropical freshwater species, including osteoglossid arapaima, mormyrids, large characins, cyprinids, many catfishes, and gymnotid knifefishes, migrate up tributaries and onto flooded plains to spawn (Fig. 23.8); many such migrations cover much more than 100 km (Munro 1990a; Lucas & Baras 2001; Welcomme 2003). Lake-dwelling species and populations in these families move into tributary streams, whereas lacustrine herrings, silversides, and percomorphs often spawn within the lake itself. Seasonality in other riverine species involves migrations upriver to headwater regions in anticipation of seasonal rains (e.g., large characins, catfishes). Many small characins, killifishes, livebearers, and cichlids reproduce year round, although peaks in recruitment often correspond with high water.

Worldwide, predatory species often spawn earlier than their prey, thus assuring a food source for young predators. For example, the South American characin, *Hoplias malabaricus*, is predatory throughout life and breeds earlier than most other species. In contrast, juvenile piranhas are omnivorous and adults breed along with other nonpredatory species, although predatory species that used to be restricted to seasonal spawning in inundated floodplains now regularly find favorable spawning habitat behind dams (e.g., Haddad & Sazima 2003; see Chapter 26, Dam building). Regardless, spawning migrations upriver or onto flooded areas must be preceded by gonadal recrudescence that anticipates seasonal rainfall by several months. The cues that stimulate gonadal growth and gametogenesis are poorly understood, but may include photoperiod and temperature changes (particularly at higher latitudes in the tropics), social interactions, food availability and energy stores, as well as endogenously controlled rhythms, perhaps entrained by previous spawning itself (Munro 1990a).

Temperate marine teleosts have restricted spawning periods that vary by species, locale, and genetic stock (Bye

1990). At any particular locale, however, a stock is likely to have a fairly short and predictable time period during which most spawning occurs. Typically, pelagic species spawn over a 4-month period, with a shorter period of maximal activity. For example, Cod in the North Sea off the northeast coast of England spawn between January and May, with 70% of eggs produced during 6 weeks of that period. Peak spawning of European Plaice (*Pleuronectes platessa*) in the Southern Bight of the North Sea occurred within 1 week of January 19 over the 39-year period between 1911 and 1950.

The locale of spawning is also fairly predictable and defined by oceanic phenomena such as thermoclines or frontal areas, which are transition regions between differing water masses. American and European eels migrate to spawn in a region of the Sargasso Sea where a persistent frontal zone, defined by marked horizontal differences in temperature, salinity, and water density, exists every spring (McCleave et al. 1987). Inshore, temperate marine species are strongly seasonal. Coastal California species spawn mostly in the spring and summer (e.g., Grunion, surfperches, halibut, Sheephead, Blacksmith, croakers, seabasses, pricklebacks), some spawn in winter or early spring (rockfishes, starry flounder, lingcod), and a few spawn in the fall (greenlings, cabezon). Predominantly spring and summer spawning also typifies Atlantic temperate fishes (halibut, killifishes, most flatfishes, seabasses, porgies, many croakers, wrasses), with a few winter spawners (Summer and Winter flounder, sculpins, some croakers) (Ferraro 1980; Holt et al. 1985).

Coral reefs experience less extreme seasonal variation than temperate habitats and are less subject to the vagaries of rainfall than tropical freshwater systems. As a consequence, many coral reef fishes spawn through most or all of the year, particularly at low latitudes (e.g., many damselfishes, wrasses, parrotfishes, grunts, surgeonfishes). Nevertheless, seasonal reproduction is also common among many families, including groupers, snappers, damselfishes, rabbitfishes, gobies, and pufferfishes. Seasonal spawning peaks have been found in most tropical locales, including sites in the Indian Ocean, South China Sea, and tropical Atlantic and Pacific oceans. "Springtime" peaks are most common, followed next by two periods of major spawning activity in the spring and fall. The most common environmental correlate of these peaks is that they occur when major currents around islands are weakest. Spawning during slack current periods would minimize the long-distance dispersal of larvae away from home reefs (Johannes 1978; Sale 1978; Robertson 1991).

Recruitment of larvae to the reef is also cyclical and seasonal. Even species that breed throughout the year show seasonal peaks in the arrival of larvae and **episodic pulses** of larval arrival. French Grunts, *Haemulon flavolineatum*, in the Caribbean breed year round. Larvae arrive in semilunar pulses over an 8-month period, with greatest recruitment in May, June, and November. Damselfishes in the southern Great Barrier Reef breed during a 5-month, summertime period and larvae are recruited in pulses, with one or a few major pulses accounting for most arrivals. Larvae arrive on a lunar cycle, the major feature being that little recruitment occurs around the time of the full moon. Most settlement of fish larvae on coral reefs occurs at night, suggesting a strong influence of visual predators. Avoidance of full moon periods would have a similar function. From the above, it is evident that spawning and recruitment do not necessarily follow the same timetables. Larvae can be produced, but conditions for settling after the larval period of a month or two may not be favorable. In fact, abundance of larvae offshore and settlement of larvae on the reef do not necessarily coincide. For example, Nassau Grouper, *Epinephelus striatus*, larvae can be found along the Bahamas Bank of the western Atlantic over a 2–3-month period, but actual larval settlement occurs almost entirely over a 4–6-night period when storm-driven currents push water and larvae into shore (McFarland et al. 1985; Doherty & Williams 1988; Doherty 1991; Shenker et al. 1993).

Seasonal reproduction: proximate and ultimate factors

Munro (1990b) has proposed a classification of the proximate cues that determine the occurrence of different portions of the reproductive cycle. He recognizes four factors that control the development and synchrony of breeding cycles.

1. **Predictive cues** are general periodic environmental events that a fish can use to predict that the spawning season is approaching. Changing day length and temperature are predictive cues that are likely to trigger the onset of gametogenesis and secondary sex character development. Gametogenesis may have an endogenous circa-annual rhythm that is entrained by some predictive environmental cue (e.g., heteropneustid catfish, Rainbow Trout, sticklebacks).
2. **Synchronizing cues** signal the arrival of spawning conditions. Typically, the presence of a suitably appearing and behaving mate, perhaps releasing pheromones, may serve as such a cue, causing final gamete maturation and release. The pheromone may even be produced by another species, as in the case of minnows that are nest associates of other species and spawn only in the presence of the host species (Rakes et al. 1999; see Chapter 21, The gender of care-givers). The presence of vegetation or other spawning substrates plays a role in some species. Synchrony is important not just to insure contact between the sperm and eggs and to prevent hybridization. In many species, gametes decline in fertility rapidly after ovulation and spermiation. Hence, a small temporal window of spawning receptivity and opportunity exists.
3. **Terminating cues** signal the end of the spawning period. Because breeding conditions remain optimal

for a short period, including the above-mentioned changes in gamete viability, breeding seasons are typically short. Gonad regression occurs after breeding in response to environmental cues (i.e., changes in predictive cues), exhaustion of gametes, or the departure or changes in behavior of conspecifics. Nest guarding species may respond to the presence of eggs in a nest, causing hormonal changes that inhibit spawning and encourage egg care and aggression.

4 The first three categories of cues can all be modified by secondary factors such as water quality, lunar cycle, adult nutrition, predator presence, and social interactions. These **modifying factors** are the causes of intraspecific variation in breeding at different latitudes or in different habitats.

Evolutionarily, why is seasonal breeding so prevalent in fishes? Gamete production, particularly in females, is energetically expensive. Gametes are usually released in batches; time and energy are required to replenish gametic products, even in males (Nakatsuru & Kramer 1982; Shapiro et al. 1994). Courtship and spawning, and parental care where it occurs, require time and energy and expose participants to predators. Few fishes can therefore afford to reproduce year round. Hence a decision in evolutionary terms must be made as to the optimal time to reproduce, optimality being defined in terms of the relative costs and benefits of current versus future reproduction (see Chapter 24, Life histories and reproductive ecology). The conditions for egg dispersal, larval survival and growth, and larval recruitment vary through the year and are dependent on seasonally driven climatic variation. In most species, spawning appears to be synchronized with periods most favorable for the survival of young. In temperate marine fishes with pelagic larvae, food availability is one critical determinant. Spawning coincides with seasonal blooms of zooplankton, thus maximizing the chances that larvae will encounter prey during the critical period shortly after they use up the energy stores of their yolk supply (the Match–Mismatch Hypothesis of Cushing (1973); see Chapter 9, Larval feeding and survival). Individuals that spawn at times when the probability of egg, larval, and their own survival are higher will be more successful than individuals that spawn at less suitable times (Munro 1990a).

Annual and supra-annual patterns: migrations

Many fishes engage in periodic long-distance movements. A vast literature exists on various aspects of migratory behavior (e.g., Harden-Jones 1968; Leggett 1977; Baker 1978; Northcote 1978; McCleave et al. 1984; McKeown 1984; Dodson 1997; Lucas & Baras 2001). Our focus will be on species that undergo fairly large-scale migratory cycles with an annual or greater period, either in the ocean or between the ocean and fresh water, with lesser treatment of the so-called potamodromous fishes that undergo reproductive migrations within fresh water (see Lucas & Baras 2001; Welcomme 2003).

Migrations take several general forms. Reproductive migrations take animals from a feeding locale to a spawning locale, moving the animal from a habitat that is optimal for adult survival to one that is better for larval or juvenile survival. Fish that spawn several times in their lives (the **iteroparous** condition) may undergo this migration more than once (e.g., Atlantic Sturgeon, American Shad, Atlantic Salmon, and the world's largest salmon, the Taimen Salmon of Siberia, *Hucho taimen*, which may weigh 70 kg). **Semelparous** fishes, those that spawn once and die, undergo the migration only once (e.g., sea lampreys, anguillid eels, Pacific salmons, some galaxiids).

Inherent in reproductively migrating species is the complementary migration that juveniles take to juvenile and adult feeding areas. In some species, nonspawning juveniles and adults also migrate between feeding and spawning areas along with reproductively active individuals (e.g., sturgeon). Reproductive migrations may involve movement between lakes and tributary streams or between different parts of a river system, as occurs in large tropical characins and catfishes. Adults of the prochilodontid Coporo, *Prochilodus mariae*, in the Orinoco region migrate from Andean piedmont tributary rivers to wet-season spawning and feeding habitats in lowland floodplains, returning to tributaries as river levels fall. All such species are decimated by dam construction that blocks these extensive migrations (Barbarino-Duque et al. 1998; Lucas & Baras 2001). Other reproductive migrations involve fishes that move between the sea and fresh water (diadromy, see below), or may entail movements within ocean basins in a roughly circular or back-and-forth pattern (Bluefish, tunas). Additional species engage in transoceanic, seasonal migrations that do not appear linked directly to reproduction, but instead probably place adult fish in optimal locales to intercept seasonally available food sources (pelagic sharks, billfishes) or may move individuals away from climatically unfavorable areas to regions that are less harsh (e.g., Summer and Winter flounder).

Diadromy

Many species of migratory fishes move predictably between fresh and salt water at relatively fixed times in their lives. These **diadromous** ("running between two places") fishes include about 160 species, or a little less than 1% of all fish species, but many of them are very important commercially and their complex life histories are fascinating (Table 23.2). Diadromy takes three different forms, anadromy, catadromy, and amphidromy (Fig. 23.9). **Anadromous** fishes such as lampreys, sturgeons, shads, Pacific salmons, smelts, and Striped Bass spend most of their lives in the ocean and

Table 23.2

Families of known diadromous fishes. Modified from McDowall (1987).

Anadromous	Catadromous	Amphidromous
Petromyzontidae, lampreys	Anguillidae, true eels	Clupeidae, herrings
Geotriidae, southern lampreys	Galaxiidae, galaxiids	Plecoglossidae, Ayu
Mordaciidae, southern lampreys	Scorpaenidae, scorpionfishes	Prototroctidae, southern graylings
Acipenseridae, sturgeons	Moronidae, temperate basses	Galaxiidae, galaxiids
Clupeidae, herrings	Centropomidae, snooks	Syngnathidae, pipefishes
Ariidae, sea catfishes	Kuhliidae, aholeholes	Cottidae, sculpins
Salmonidae, salmons	Mugilidae, mullets	Mugiloididae, sandperches
Osmeridae, smelts	Bovichthyidae, bovichthyids	Eleotridae, sleepers
Retropinnidae, New Zealand smelts	Pleuronectidae, righteye flounders	Gobiidae, gobies
Galaxiidae, galaxiids		
Gadidae, cods		
Gasterosteidae, sticklebacks		
Cottidae, sculpins		
Moronidae, temperate basses		
Gobiidae, gobies		
Soleidae, soles		

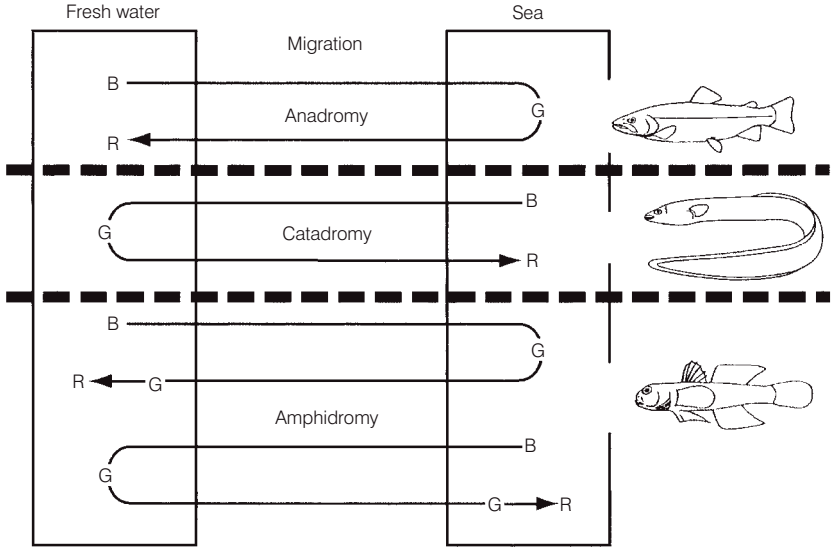


Figure 23.9

Diadromy takes three general forms: anadromy, catadromy, and amphidromy. In anadromy, adults spawn in fresh water, juveniles move to salt water for several years of feeding and growth, and then migrate back to fresh water to spawn. In catadromy, adults spawn at sea, juveniles migrate to fresh water for several years to feed, and return to the sea to spawn. In amphidromy, spawning can occur in either fresh or salt water (but usually fresh), larvae migrate to the other habitat for an initial feeding and growth period, then migrate to the original habitat as juveniles where they remain for additional feeding and growth prior to spawning. B, birth; G, growth; R, reproduction. Modified from Gross (1987).

then migrate to fresh water to spawn. Many anadromous species (Sea Lampreys, Alewives, Blueback Herring, Atlantic Salmon, Sockeye Salmon, Rainbow Trout) develop **landlocked** populations that never migrate to the sea but instead spawn in inlet streams to large lakes. **Catadromous** fishes such as anguillid eels, mullets, temperate basses, and some sculpins spend most of their lives in fresh water and then return to the ocean to spawn. **Amphidromous** fishes (Ayu, galaxiids, southern graylings, sandperches, sleepers, gobies) move between marine and fresh water at certain phases of their lives, but the final migration occurs long before maturation and spawning occur. The chief distinction between amphidromy and anadromy is that the migration into fresh water usually occurs in the juvenile stage in amphidromy and in the adult stage in anadromy (McDowall 2007). About half of all diadromous fishes are anadromous, the other half equally divided between catadromous and amphidromous forms (McDowall 1987, 1988, 1999).

The geographic distribution of the different forms of diadromy is interesting because it provides insight into the evolution of the behavior (Fig. 23.10). Anadromy is largely a northern hemisphere, high-latitude phenomenon, catadromy is more common at low latitudes and in the southern hemisphere, and amphidromy has a bimodal distribution at middle latitudes in both hemispheres, with greater representation in the southern hemisphere (McDowall 1987). Interpretations of why different forms of diadromy prevail at different latitudes are confounded by phylogenetic histories, but one appealing analysis views diadromous migrations as complex adaptations that function to place both larvae and adults in environments where food is most abundant (Gross 1987; Gross et al. 1988; see Dodson 1997 for a critique). For a long-distance migration to evolve, the gains in fitness from moving must exceed the fitness an individual would have achieved had it remained in its original habitat. Gains have to be sufficiently large to also overcome losses – including osmotic costs, energy and time lost, and predation risk – incurred while migrating. If an individual migrates during its life, it should ideally (i) spawn in a place of low predator density to minimize egg mortality but where (ii) larvae can drift passively to locations of higher productivity appropriate to their growth needs, and (iii) place juveniles and young adults in areas where they can maximize their feeding, thus allowing them to build up energy stores necessary for (iv) the long migration back to the optimal (low productivity) spawning locale.

Available evidence indicates very different growth and reproduction rates in the different habitats. Juvenile Pacific salmon may increase their daily growth rate by 50% during their first week in the ocean. Sockeye Salmon, *Oncorhynchus nerka*, are referred to as Kokanee when landlocked and seldom attain 25% of the body size of anadromous individuals. Comparisons between diadromous and non-diadromous stocks of the same salmonid species (Cutthroat Trout, Rainbow Trout, Atlantic Salmon, Brown Trout, and others) indicate that diadromous stocks produce on average three times as many eggs as non-diadromous conspecifics, probably because diadromous fish grow to larger size as a result of increased feeding in the ocean. Mortality rates are difficult to estimate; however, the three-fold reproductive advantage of diadromy would more than make up for greater mortality at sea before the benefits of diadromy were negated.

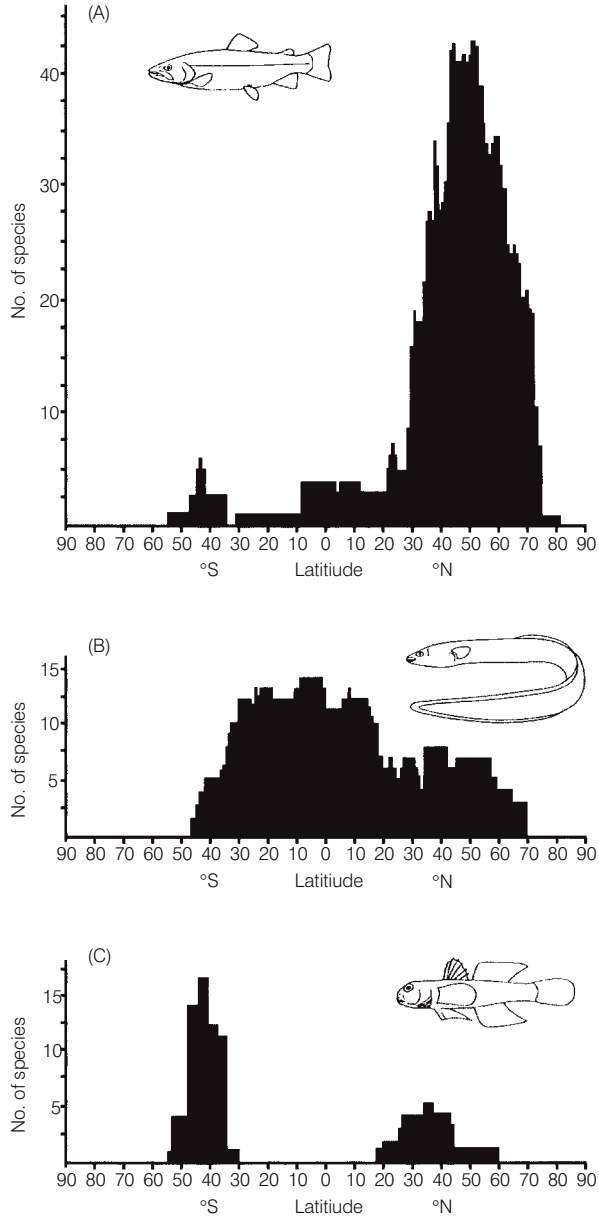


Figure 23.10

The latitudinal distribution and frequency of different forms of diadromy among major fish groups. The number of species employing each tactic is plotted as a function of latitude, showing: (A) anadromy to be largely a northern, temperate and polar phenomenon; (B) catadromy to be more tropical and subtropical in distribution; and (C) amphidromy to be more bipolar and temperate. Modified from McDowall (1987), used with permission.

Combining such growth and reproduction differences with information about relative productivity of fresh waters and oceans at different latitudes suggests that the temperate prevalence of anadromy and more tropical occurrence of catadromy are evolutionary logical. In temperate regions, oceans tend to be more productive than fresh waters, whereas fresh waters are more productive than the ocean in tropical regions. Hence the primary feeding habitat for a migratory species should be the ocean at high latitudes versus rivers and lakes at lower latitudes. The survival of young may be enhanced if spawning occurs where productivity, and also presumably predation, are least: streams and rivers at high latitudes, the ocean at lower latitudes. As long as the costs of movement between spawning and growth habitats are not excessive, the existence of anadromy in colder climates and catadromy in warmer climates appears adaptive. Amphidromy may serve as an intermediate or stepping stone condition in the evolution of anadromy or catadromy (the catadromous nature of American and European eels, discussed below, may reflect the evolutionary history of the family, which is primarily tropical and which still entails spawning at tropical latitudes) (Gross 1987; Gross et al. 1988).

Mechanisms of migration

Fishes may move thousands of kilometers through the open and seemingly landmark-free ocean. A great deal of research has focused on the means by which fish undertake long-distance migrations, specifically how they **orient** toward and **locate** their ultimate destinations. Research has identified numerous possible cues used in orientation, including sun and polarized light, geomagnetic and geoelectric fields, currents, olfaction, and temperature discontinuities and isolines (Leggett 1977; McCleave et al. 1984; McKeown 1984).

Birds use a **sun compass** and **internal clock** to orient. An animal must be able to sense the time of day, the altitude, azimuth (angle with the horizontal), and compass direction of the sun at a given time and date, correcting for the 15°/h movement of the sun across the sky. Experimental evidence suggests that some fishes use such a mechanism. Swordfish (*Xiphias gladius*) can maintain a constant compass heading in the open sea for several days. Displaced parrotfish return relatively directly to their home locations on sunny days. When the sun is obscured, when fitted with eyecaps, or when held in darkness such that their internal clocks have been shifted 6 h, displaced fish are disoriented or move in a direction appropriate for a 6 h clock shift. Juvenile Sockeye Salmon have a sun compass which they complement with a magnetic compass at night or during overcast conditions. **Polarized light** can also provide directional cues, and Sockeye Salmon are able to detect and discriminate between vertically and horizontally polarized light, which could aid them particularly during dawn and dusk migrations toward the sea, when light is maximally polarized. Minnows, other salmonids, halfbeaks (Hemiramphidae), damselfishes, and cichlids can also sense polarized light, which often involves detection of ultraviolet radiation undiscernible to the human eye (Quinn & Brannon 1982; McKeown 1984; Hawryshyn 1992; Mussi et al. 2005).

A magnetic compass implies a sensitivity to the earth's magnetic fields. Such a sensitivity has been demonstrated in elasmobranchs, anguillid eels, salmonids, and tunas (Collin & Whitehead 2004; see Chapter 6, Magnetic reception; Chapter 12, Sensory physiology). Sharks are theoretically capable of navigating using geomagnetic cues, since they can detect fields 10 to 100 times weaker than the earth's magnetic field, as well as fields created by ocean currents moving through the earth's magnetic field, or fields induced by their own movement. An induced field would change as the animal's compass heading changed, being strongest when moving east or west and weakest when heading north or south, thus giving it directional information. A magnetic compass could be useful in transoceanic migrations undertaken by large pelagic sharks (e.g., Blue, White, and Tiger sharks, see Chapter 12).

Orientation abilities are also needed for homing, as happens when Scalloped Hammerhead Sharks, *Sphyrna lewini*, return daily to small seamounts in the Sea of Cortez after foraging offshore at night. Scalloped Hammerheads may use a combination of directional cues, including visual landmarks, auditory cues produced by fishes and invertebrates, electrical cues induced by site-specific currents, and geomagnetic fields at seamounts. The use of multiple cues and redundant systems are a general feature of migratory animals. Redundant information increases the accuracy of the information, and backup systems provide information when conditions interfere with or negate the use of other cues (Kalmijn 1982; Klimley et al. 1988; Klimley 1995; Meyer et al. 2005).

Water currents serve to transport fish eggs, larvae, and adults, but may also provide orientational information. Where currents border on other water masses, differences in water density, turbulence, turbidity, temperature, salinity, chemical composition, oxygen content, and color could all act as landmarks to a migrating fish (once inside a current and out of sight of or contact with the bottom or other stationary objects, it is difficult to imagine that a fish could sense the water's movement, unless the fish could detect induced magnetic fields as discussed above). In shallow waters, many fishes show a positive or negative **rheotactic** response that causes them to move up- or downstream, respectively. The strength and direction of response may change with season and ontogeny. Selective tidal stream transport (see above) is such a response, whereby a fish moving upriver in an estuary swims actively against an ebbing tide and drifts passively with a flooding tide. Olfactory cues are often carried on currents. Homing of salmon to chemicals in the streams in which they were spawned

(see below) probably applies to many stream and intertidal fishes (e.g., minnows, sculpins, blennies), although the age at which a fish learns the chemical fingerprint of a water body will vary. Sensitivities to familiar chemicals are extreme, on the order of $1:1 \times 10^{-10}$ or 10^{-19}, depending on species, suggesting that just a few molecules of a substance are necessary for detection (Hara 1993).

Seasonal movement is induced or directed by *temperature* changes in several migratory species. American Shad, *Alosa sapidissima*, move north along the Atlantic seaboard in the spring, staying in their preferred water temperatures of 13–18°C. Individuals may winter as far south as Florida and spawn in Nova Scotia, 3000 km away. Some oceanic species follow specific isotherms during seasonal migrations. Albacore Tuna, *Thunnus alalunga*, move north during the summer along the Pacific coast of North America, staying within a fairly narrow 14.4–16.1°C temperature zone; east–west movements are contained within a temperature range of 14 and 20°C. Onshore arrival of water masses of the preferred temperature serve as predictors of the arrival of the fish. Many other tuna species also migrate to stay within fairly narrow temperature ranges.

Many pelagic fisheries, which rely on oceanic migrations to bring fish into regions on a seasonal basis, are highly dependent on water masses of the correct temperatures moving into specific areas. Cod and Capelin (*Mallotus villosus*) in the Barents Sea of northern Europe are available to Finnish fisheries in cold years when fish migrate farther west to warmer waters. In warm years, fish restrict their movements to the eastern side of the basin and are then exploited in the Murmansk area. The response to temperature may be a direct, behavioral one involving thermal preferenda, or an indirect response related to food abundance. Often, plankton blooms are associated with changing water temperatures and hence fish may be tracking food availability that responds to temperature. Herring in the Norwegian and Greenland seas migrate in response to the inflow of warm Atlantic water, which in turn stimulates plankton growth and food availability (Leggett 1977; McKeown 1984; Dadswell et al. 1987).

Representative life histories of migratory fishes

Among vertebrates, fishes stand out in terms of the complexity of their life histories, and migratory fishes have among the most complex life histories. Details of a few of the better known and more interesting species are highlighted below.

Anadromy

Some of the most spectacular examples of highly evolved, complex migrations involve fishes that spawn in fresh water but spend most of their lives at sea. Included among anadromous fishes are lampreys, sturgeons, shads and herrings, salmons and trouts, and striped bass (see Table 23.2). The classic case involves Pacific salmons. Chinook Salmon, *Oncorhynchus tshawytscha*, can serve as an example. Chinook Salmon spawn in streams of the Pacific northwest coast of North America during the summer and fall, depending on locale (e.g., Quinn et al. 2002). Eggs are buried in gravel nests and hatch into alevins (yolk-sac larvae), which emerge and make their way downstream, eventually transforming into silvery smolts after a few months to 2 years, depending on when they were spawned. Smolts move out into the ocean, grow into juveniles and adults, and move in a series of counterclockwise ellipses through the Northeast Pacific that may carry them as far north and west as the Aleutian Islands of Alaska or as far south as northern California, covering distances of several thousand kilometers (Sockeye Salmon, *O. nerka*, migrate even farther from land and in larger circles in the open sea, and may cover tens of thousands of kilometers).

After 1–8 years, these adults mature and return to the nearshore area. A coastal migration eventually carries them to the mouth of the river from which they migrated as smolts. They enter this river and work their way up, bypassing hundreds of potentially usable streams and innumerable, seemingly insurmountable barriers such as rapids and waterfalls. In this final stage, they cease feeding, change to a reddish color, and the males develop the characteristic hooknosed appearance known as kipe. They ultimately find the natal stream in which they were hatched – and even the exact place where they were incubated – where they spawn and die (Netboy 1980; Healey & Groot 1987; Brown 1990; Groot & Margolis 1991; Augerot 2005; Quinn et al. 2006).

At each juncture in this complicated journey, fish make directional decisions (e.g., Keefer et al. 2006). Numerous mechanisms, which vary depending on life history stage and habitat, have been proposed to provide directional information for a migrating fry, smolt, juvenile, and adult (Fig. 23.11). Movement by young fish from spawning sites in natal rivers to the ocean involves a combination of responses to light (including a sun compass and discrimination of polarized light), geomagnetic cues, and water currents. The fish must also **imprint** on (learn) the chemical fingerprint or **home stream olfactory bouquet** of its home stream and river, or even of multiple, sequential habitats (e.g., Dittman & Quinn 1996; Carruth et al. 2002).

Open ocean migration and eventual home stream selection offer very different problems that probably require different orientation systems. Quinn (1982) proposed a combined **map–compass–calendar** system to explain movements on the high seas. The map would involve learned or genetic knowledge of the distribution of the earth's magnetic field (which has also been mapped by oceanographers and is predictable). Compass directions, provided by celestial and magnetic cues, can be used to maintain directional

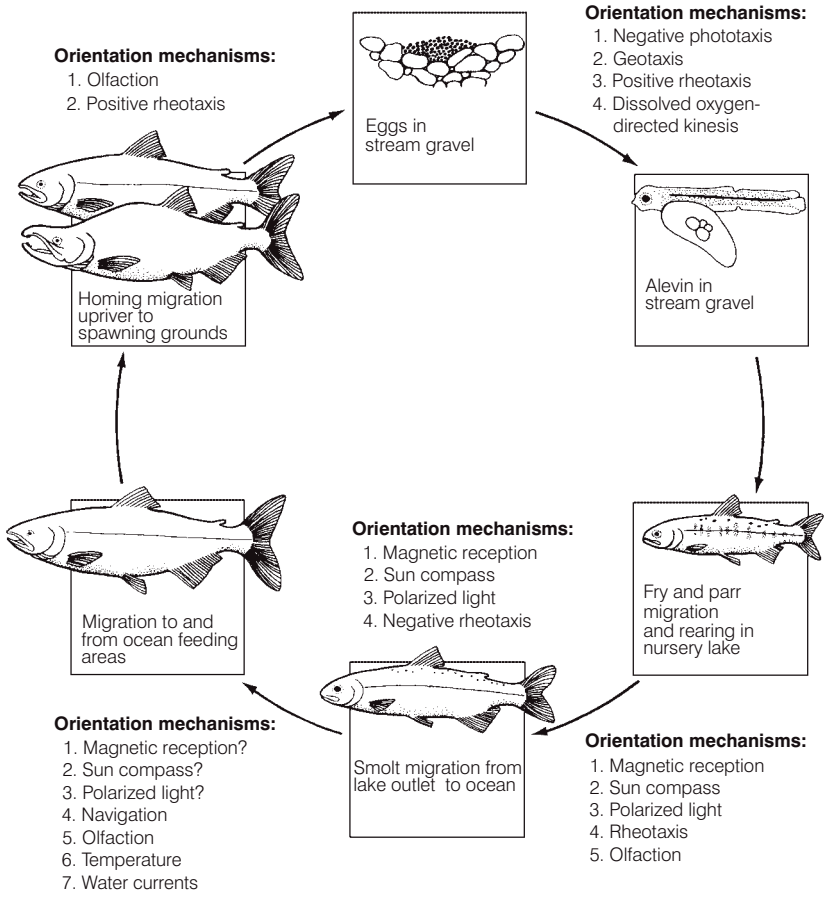


Figure 23.11

Characteristic life history of a Pacific salmon, as seen in the Sockeye Salmon, *Oncorhynchus nerka*. At different stages, different orientation mechanisms are likely to come into play to help the developing, growing, or maturing fish find its way to, through, and away from the sea and back to its natal river to spawn. Responses to light, gravity, and current are initially important for recent hatchlings. Later, sun compass and magnetic detection, backed up by other cues, aid a fish moving downstream and into the ocean. Finally, the memory of home stream chemicals on which the juvenile imprinted lead the maturing adult back to its spawning grounds. Redrawn after Quinn and Dittman (1990).

headings. The calendar would require an assessment of day length or change in day length, with input from an endogenous circa-annual clock. Integration of all this information would tell a fish where it was, where it was going, and how long it would take to get there, forming the basis of a navigational system.

Once a maturing adult arrived in the coastline region of its home river, it would shift to an olfactorally guided response to natural chemicals contained in different rivers. Having remembered the chemical fingerprint of its natal stream, it would move upriver and reject any stream mouth it passed that did not have the appropriate bouquet. Upon encountering the correct chemical cues, it would move upcurrent in that system until it arrived at the appropriate spawning site. The **olfactory hypothesis** has received experimental confirmation in studies with Coho Salmon, *O. kisutch*, transplanted into Lake Michigan. Fish were imprinted on synthetic chemicals in hatchery water and released. Eighteen months later, most chemically imprinted salmon that entered streams chose streams containing the synthetic chemicals (Hasler & Scholz 1983; Quinn & Dittman 1990).

Home stream return, perhaps involving olfactory guidance, also occurs in Striped Bass, *Morone saxatilis*, which forms stocks along the US Atlantic coast that are associated with major river systems. Fish migrate north in the spring and south in the fall along the Atlantic coast, but return each spring to spawn in their natal rivers. American Shad, Alewives, and Blueback Herring also home to their natal rivers to spawn (Boreman & Lewis 1987; Loesch 1987; Quinn & Leggett 1987).

Which is not to say that mistakes do not occur. Although as many as 98.6% of Chinook Salmon may home correctly to the Cowlitz River in Washington, the same species may show 10–13% **straying** rates in California rivers. In fact, tagging studies show that as many as 47% of fish may wind up in the wrong, or at least in a non-natal, stream. The pattern of straying is, however, adaptive. High fidelity (low straying) rates characterize species and populations that spawn in large, stable rivers, whereas straying is more common in fish that come primarily from small, unstable rivers with variable flow characteristics, where juvenile survival is also more variable. Straying can then be viewed as an alternative life history trait that functions as a bet-hedging tactic to insure survival of some offspring in situations where the natal river may become uninhabitable (Quinn 1984; see Chapter 21 for other examples of alternative reproductive tactics in salmonids).

Catadromy

Life history variation occurs among salmons and sturgeons, with some species and populations being landlocked or seldom entering the sea. In contrast, all 15 species of the eel family Anguillidae are thought to spawn in the sea but grow up in fresh water. The best known species are the European, Japanese, and American eels, all of which undergo larval and adult migrations of truly epic proportions. The American Eel, *Anguilla rostrata*, can serve as an example.

American Eels spawn in the Sargasso Sea, an unproductive region of the western Atlantic northeast of Hispaniola and the Bahamas. The exact locale of spawning remained a mystery until the 1920s, when Danish biologist Johannes Schmidt analyzed 25 years of oceanic plankton tows and determined that the smallest eel larvae of both American and European species (known as **leptocephali** and once thought to be a different species of fish altogether) were captured in this area. Schmidt's results have been subsequently confirmed by captures of even smaller larvae (<7 mm long) of both species at the same time from the same locale; American and European Eels spawn in overlapping areas during early spring and then drift northward with major ocean currents. European larvae apparently do not metamorphose until they are 2–3 years old, hence they float past the North American continent. American Eel leptocephali in contrast metamorphose after about 1 year and, using transport mechanisms that remain unresolved, move westward to inshore waters. Interestingly, hybrids between the European and American species stop halfway, in Iceland. Mysteriously, leptocephali are not thought to feed, or at least they have nonfunctional guts during most of their larval phase. Leptocephali are next attracted by the mixture of organic materials dissolved in outflowing fresh waters and migrate upriver, moving by selective tidal stream transport (see above) and transforming into transparent, miniature (50 mm) eels known as **glass eels**. As they move upriver, they become pigmented and are called **elvers**.

Elvers grow into juvenile **yellow eels** that take up residence in fresh water for periods that range from 3 to 40 years, the time depending on sex and latitude. Males are more abundant in southerly latitudes and in estuaries. They never grow larger than 44 cm and usually mature after 3–10 years. Females are likely to be found throughout a river system, from the estuary all the way up to the headwaters. In fact, female American Eels probably have the widest geographic and environmental range of any nonintroduced freshwater fish anywhere in the world. Their habitats include rapidly flowing, clear, headwater streams, large lakes and rivers, underground cave springs, lowland rivers and swamps, down to estuarine saltmarshes. They are found from Iceland to Venezuela, including most Caribbean islands and Bermuda, and range up the Mississippi River to its headwaters and as far west as the Yucatan Peninsula.

Maturation varies as a function of this range. In general, more northerly populations and those farther from the Sargasso Sea contain older, larger (and usually female) animals. Maturation may take from 4 to 13 years at southerly locales and as much as 43 years in Nova Scotia (Jessop 1987). As the animals mature, they turn a silvery-bronze color, the pectoral fins become pointed, the eyes enlarge (particularly in males), and fat stores are accumulated. These nonfeeding, **silver eels** then migrate back to the Sargasso Sea, migrations beginning earlier for animals traveling farther, which apparently synchronizes the time of arrival at the spawning grounds. Silver eels travel as much as 5000 km to spawn and then apparently die. Conjecture surrounds this stage because no one has seen a fully mature anguillid eel, nor located an adult eel at the presumed spawning grounds (Tesch 1977; McCleave et al. 1987; Helfman et al. 1987; Avise et al. 1990).

Oceanodromy

Oceanodromous fishes migrate within ocean basins, usually in a circuit and usually traveling with major ocean currents. The migration serves to place different life history stages in seasonally appropriate locales. The range may therefore include an area for spawning from which eggs and larvae float to a nursery area, winter and summer feeding areas for juveniles and adults, and also migratory zones through which a stock moves. Juveniles may move between seasonal feeding areas for several years before maturing and migrating to spawning grounds. The great tunas (*Thunnus*, Scombridae), particularly those living in temperate waters, are representative. Subspecies or stocks have been suggested for different ocean basins in the past, but movement across ocean basins and probable mixing of stocks tends to eliminate genetic differences (e.g., for the highly migratory Albacore Tuna, *Thunnus alalunga*; Graves & Dizon 1987).

Bluefin tuna are subdivided into Bluefin, *Thunnus thynnus*, in the Atlantic and Mediterranean; Pacific Bluefin, *T. orientalis*; and Southern Bluefin, *T. maccoyii*, off Australia, New Zealand, and South Africa. Bluefin tagged off Florida have been recaptured in Norway, involving a minimum migration distance of 10,000 km. In addition, fish of different sizes have different migratory patterns, and adults of different sizes may spawn at different times and places. In the western North Atlantic, the largest Bluefin (120–900 kg) have a migratory cycle that begins on summer feeding grounds (May to September) over the continental shelf from Cape Hatteras to Nova Scotia. This is followed by fall and winter movements offshore and south to wintering grounds that include the Bahamas, Greater Antilles, and into the Caribbean and Gulf of Mexico. In the spring, the giants move northward in oceanic waters and then onto the continental shelf in late spring and then back to the summer feeding grounds. Spawning occurs in southern waters (Gulf

of Mexico, Straits of Florida) in May and June, and in the Mediterranean and Black seas during the warm summer months. Mixing may involve as many as 30% of fish crossing the Atlantic from west to east (mixing from east to west is less well known) (McClane 1974; Richards 1976; Rivas 1978; Lutcavage et al. 1999; Block et al. 2001; Block & Stevens 2001).

Differentiation into **stocks**, some that mix and some that do not, appears common among oceanodromous fishes. Atlantic Herring (*Clupea harengus*) are subdivided into several spawning groups or stocks (six alone in the Northeast Atlantic) that may be further subdivided into isolated stocks in various estuaries and inlets. Migrations carry different stocks to overlapping feeding areas but spawning occurs at separate times and places. Atlantic Cod (*Gadus morhua*, Gadidae) and Plaice (*Pleuronectes platessa*, Pleuronectidae) are also differentiated into several migratory stocks with distinct spawning grounds. Bluefish (*Pomatomus saltatrix*, Pomatomidae) occur worldwide in warmer oceans except for the eastern Pacific. Schools apparently migrate onshore and offshore with the seasons, perhaps following baitfish. Along the US Atlantic coast, this migration involves an inshore migration in spring and summer and a return to offshore locales in fall and winter, which corresponds with movements of a primary prey species, Menhaden (*Brevoortia tyrannus*). Bluefish movements occur progressively later as one travels north, and the pattern is complicated by a degree of north–south migration (McKeown 1984; Hersey 1988). Other, larger predators, such as Blue Marlin (*Makaira nigricans*, Istiophoridae), also are oceanodromous, move seasonally, and form local but wide-ranging stocks (see also Chapter 12 on pelagic sharks).

Summary

SUMMARY

1. Biological systems are cyclical in nature. On a 24 h, diel cycle, most fishes are diurnal, being active by day and resting at night. Fewer species are nocturnal, and some predators are crepuscular, being active primarily during dusk and dawn twilight periods. The external cue for activity and inactivity appears to be the setting and rising of the sun. Distinctive activity cycles are most pronounced in tropical environments, less so at higher latitudes.
2. Circadian rhythms have a period of approximately 24 h, driven by an internal (endogenous) clock. Activity patterns in many fishes have an underlying circadian rhythm, as does hormone secretion. Other endogenous cycles include circatidal patterns in intertidal fishes that correspond to twice-daily high and low tides.
3. Intertidal fishes either move in and out with tides (juveniles using the shallows as a nursery area) or remain in the intertidal at low tide and seek shelter to avoid heat, desiccation, and oxygen stress (resident families such as gunnels, sculpins, blennies, and gobies). Nursery species gain access to tidal areas by moving up into the water column with flooding currents and by hugging the bottom on ebbing currents.
4. Many fishes spawn on a biweekly (semilunar) or monthly (lunar) cycle. For example, grunion spawn every 2 weeks during the summer, laying their eggs in the sand high on the beach just as the tide turns. Their eggs then hatch 2 weeks later when the next spring tides cover them. Many coral reef species spawn biweekly or monthly when tides and therefore currents are maximal, which may help move the eggs away from abundant, reef-dwelling zooplanktivores. Nonreproductive migrations in many fishes (eels, salmons) are also tied to lunar cycles.
5. Fishes at non-tropical latitudes spawn more seasonally, usually during spring, probably to allow larvae and juveniles to take advantage of spring and summer blooms of plankton. Cycles are set in motion by changing day length. Winter activities of many temperate species are poorly understood; burying and aggregating in deeper water have been documented. Problems of low oxygen under ice can be overcome by inhaling bubbles that form directly under ice. Freshwater tropical fishes spawn seasonally in response to changing rainfall regimes, often migrating into flooded forests and swamps to reproduce.
6. The life cycle of many fishes includes a migration over long distances, either as part of reproduction or to take advantage of seasonal changes in food availability. Movement between fresh and salt water is called diadromy; anadromous species spawn in fresh water but grow in the ocean (lampreys, sturgeons, salmons), catadromous species spawn at sea and grow in fresh water (eels, mullets, temperate basses), and amphidromous species move between habitats

more than once (galaxiids, southern graylings, sleepers). Anadromy is more common at temperate, northern locales, whereas catadromy occurs more at southern locales and at low latitudes. These patterns place early life history stages in habitats most favorable for growth.

7 Fishes navigate across distances by orienting to cues of light, geomagnetism, currents, odors, and temperature. Sun compasses are used by many species, as is polarized light. Elasmobranchs, eels, salmons, and tunas are sensitive to the earth's magnetic field. Chemical sensitivities in fishes are extreme, on the order of $1:1 \times 10^{-10}$ or 10^{-19}. Pacific salmons learn the odor "fingerprint" of the stream in which they are born and then return to their natal stream after years at sea using olfactory cues. Catadromous eels begin life in tropical seas, float to continental areas on currents as larvae, grow in fresh water, and then migrate thousands of kilometers back to their open ocean spawning region using orientation cues that remain a mystery.

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SUPPLEMENTARY READING

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Chapter **24**

Individuals, populations, and assemblages

Chapter contents

CHAPTER CONTENTS

Fishes interact with their own and other fish species, with other animals and plants, and with their physical surroundings. These interactions affect the birth, growth, reproduction, death, and movement of individuals, the distribution and abundance of populations, the transport and exchange of energy and nutrients among members of communities, and the flow of matter and energy into, out of, and between ecosystems. The science of **ecology** is concerned with the relationship between organisms and the biotic and abiotic environment, and more specifically how environmental variation influences the distribution, abundance, and function of organisms. Ecology is a vast subject, and the literature on fish ecology is voluminous. The bibliography of one relatively recent and comprehensive textbook covering freshwater fishes alone (Matthews 1998) contains over 1900 citations; such a large topic can obviously receive only cursory treatment in two chapters.

Our focus will be at different levels of ecological organization: individuals, populations, and assemblages in this chapter, communities and ecosystems in the next. These distinctions are recognizably artificial; one cannot understand ecological attributes of individuals of one species in an area (a **population**) without also considering the other species of fishes (the **assemblage**), other taxa with which the individuals interact (the **community**), and abiotic influences on individuals, including patterns of nutrient and energy transfer (the **ecosystem**). Our emphasis once again is on the diversity of adaptations shown by fishes in an ecological context. Certain topics that commonly fall under the heading of "ecology" have been treated elsewhere and will only be examined briefly here (e.g., feeding and predator–prey relations in Chapters 19, 20; growth and reproduction in Chapters 9, 10, 21; energetics in Chapter 5; symbioses in Chapter 22; and conservation in Chapter 26).

Individuals

Ecological adaptations are traits of an individual that insure its survival and reproduction in response to selection pressures from the biotic and abiotic environment. It is important to emphasize the individual as the basic unit of adaptation since natural selection operates primarily at the level of the individual, favoring individuals of one genotype while selecting against individuals with less favorable genotypes. We can then ask if survival and reproduction are enhanced by how an individual selects an appropriate habitat in which to live (discussed below, under Assemblages), how it budgets its time and energy among the activities and conflicting demands presented to it on a daily basis, and how it eventually partitions energy into growth versus reproduction.

Life histories and reproductive ecology

A **life history** can be viewed as how an individual divides up its time and resources among the often-conflicting demands associated with maintenance, growth, reproduction, mortality, and migration. Life history characteristics or **traits** are measurable aspects of an individual's life

history and include age- and size-specific birth rates (and associated characteristics such as clutch size, egg size, offspring provisioning, and clutch frequency), and the probabilities of death and migration (Congdon et al. 1982; Dunham et al. 1989). These traits vary among species, among populations within a species, and among individuals and sexes within a population in ways that make evolutionary sense, indicating their adaptiveness. The challenge to biologists is to identify trends in life history traits, identify the likely selection pressures causing variation, and interpret the adaptiveness of the variation (Potts & Wootton 1984; Stearns 1992; Winemiller & Rose 1992; Matthews 1998). Many life history traits are correlated, which means they are inherited together and change in direct relationship with one another, making it somewhat difficult to isolate the exact interaction between environment and adaptation. Nonetheless, their importance in determining reproductive success is obvious.

Analyses of life history traits focus on females, in part because female reproductive effort produces eggs, each of which has a much greater likelihood of becoming a new individual than is the case for the millions of sperm produced by a male. About one dozen life history characteristics (termed "traits" by some but not all authors) have direct links with reproduction and have been identified and quantified in many fishes. Background detail on reproductive biology and anatomy is presented in Chapters 9 and 10. A thorough treatment of life history characteristics can be found in Matthews (1998).

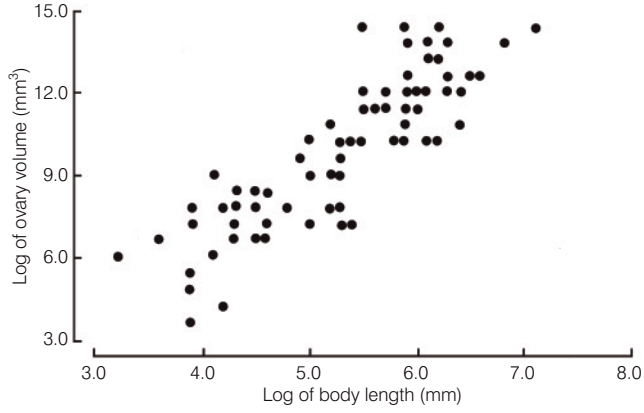

Figure 24.1

Bigger fish produce more eggs, both within and among species. Since fish grow throughout their lives (= indeterminate growth), older fish are usually larger. Within a species, larger individuals generally produce more eggs and often larger eggs. The generalization even holds for pregnant male seahorses, with larger individuals possessing larger pouches capable of holding more embryos (Woods 2005). Values are plotted for a variety of Canadian freshwater species. Redrawn after Wootton (1990).

1. *Age and size at maturation*. A complex but fascinating trade-off exists between **early versus late maturation**; the trade-off depends on the probability of successful reproduction versus the risk of death. A female that delays maturation until she is larger and older will produce more eggs at each spawning but runs the risk of dying before she ever reproduces (Fig. 24.1). A fish that spawns at an earlier age stands a greater chance of getting some genes into the next generation at least once. However, younger fish are smaller and hence produce fewer and often smaller eggs, which lessens the chance that any will make it past egg and larval predators and starvation. Also, by allocating energy to reproduction, the earlier spawning fish has slower somatic (body) growth and is then more subject to predation because of smaller body size (Werner et al. 1983). Additionally, reproduction uses up much energy, potentially placing a smaller fish with lesser energy stores in a weakened condition, which reduces the chances of future reproduction. Theoretically, females in populations where adult survival is poor should reproduce at an earlier age than in populations where survival is better. Female Guppies in downstream locales in Trinidad where predators are abundant do mature earlier than upstream populations with fewer predators (Reznick & Endler 1982). Similarly, individuals in commercially exploited fish populations, particularly those where adults are targeted by the fishery, often reproduce at earlier ages than do fish in unexploited populations (e.g., O'Brien et al. 1993) (Box 24.1).
2. *Body size*. Even very large predators eat relatively small prey, but only large predators can eat large prey. Therefore, larger fishes are susceptible to predation by fewer predators while at the same time larger fish can catch and swallow a broader range of prey types. Larger fishes are also able to store more energy, to swim faster and farther, and to better overcome harsh abiotic conditions such as strong currents (Karr et al. 1992). Size determines territorial interactions as well as male mating success in many fishes. Also, larger fish emerge from winter with greater energy stores and in better condition than do smaller individuals (Cargnelli & Gross 1997), and larger fish produce eggs with higher hatching success and higher larval survival (Trippel 1995). This premium on large size comes, however, at a cost because energy allocated to somatic growth is unavailable for immediate reproduction, as discussed above.
3. *Longevity*. The longer an individual lives, the more reproductive opportunities it should have, discounted by how long it waits until first reproduction (point 1 above) and how long an interval exists between reproductive periods (point 10 below).
4. *Clutch size*. How many eggs a female produces at each spawning varies as a function of body condition and size, age, egg size, and number of spawnings per

Box 24.1

Fishing effects on life history traits

Exploitation-caused changes in life history attributes have long been documented in the fisheries literature (Helfman 2007). In fact, growth adjustments underlie the **basic theory of fishing**: growth compensation by surviving individuals will accompany moderate exploitation, and maximal harvest rates (**maximum sustainable yields** of surplus production) are achieved by maintaining a population at some intermediate level through fishing (e.g., Ross 1997; Hart & Reynolds 2002b; or any basic fisheries text). Typically, reductions in abundance cause increased body growth in the remaining individuals, and the ensuing faster growth rates generally result in maturation at smaller sizes and younger ages. The proximate stimulus of this generalized **compensatory** change is assumed to be reduced competition for limiting resources. The ultimate cause, according to life history theory, is that heavy predation pressure favors fishes that are capable of initiating reproduction sooner, before they are eaten (see Trippel 1995).

The fisheries literature contains many examples of **exploited** stocks that show changes in weight at age, length at age, length at maturation, and age at maturation, with most species showing reduced weights, lengths, and ages, as well as accelerated growth. Law (2000, table 1) reviewed findings on 16 species of flatfishes, gadoids, and salmons, most of which showed decreases in life history traits. Data on Atlantic Cod are complete and telling: among eight exploited stocks monitored for 7–53 years, median age at maturity declined between 16% and 56%, representing a 0.9–3.6-year reduction in age at maturity; *longer periods of exploitation produced greater changes in age*. Natural variation in age at maturation was small or negligible when fishing pressure was light (Trippel 1995). Data on flatfishes, gadoids, and salmon and on commercially fished western Atlantic sharks, herrings, scorpionfishes, snappers, drums, groupers, eel-pouts, butterfishes, and mackerels similarly revealed reduced lengths and ages at maturation (Upton 1992; O'Brien et al. 1993; Lessa et al. 1999; Vannuccini 1999). The mean length of captured Patagonian Toothfish, *Dissostichus eleginoides*, declined 30% in just the first few years of fishing (ISOFISH 2002). Among other examples are freshwater species subjected to intensive commercial and recreational fishing (Bluegill, Walleye, whitefish, Yellow Perch, Northern Pike, Brown Trout, and Arctic Char; Trippel 1995; Drake et al. 1997). Again, *decreased length and age at maturity are the rule*.

The ironic upshot of this phenomenon is that overfishing produces fish populations characterized by smaller, less fecund individuals that reproduce at smaller and smaller sizes, just the opposite of what good management practices hope to attain.

season (egg number is referred to as **fecundity** and can be subdivided into batch, breeding season, or lifetime fecundity, although fecundity commonly refers to the number of eggs or young produced per year; see also Chapter 9, Eggs and sperm). Combining clutch size with egg size (point 5 below) gives a measure of **reproductive allotment**, which is the percentage of a female's weight devoted to eggs or embryos. Theoretically, females in populations where adult survival is poor should devote more energy to reproduction than in populations where survival is better. Reproductive allotment in female guppies in predator-dense populations is 30% greater than in females subject to less predation (Reznick & Endler 1982). Commercially exploited species (e.g., pike, halibut) show increased fecundities as compared to unexploited populations, a change in a life history trait which could compensate for high levels of predation or exploitation (Policansky 1993b).

5 *Egg size and size at birth*. Both the mean and range of egg size vary within species and within individuals (Matthews 1998; Wootton 1999). Eggs spawned early in a season for multiple spawners tend to be larger. In the Least Killifish, *Heterandria formosa* (Poeciliidae), the more broods a female produces, the smaller the young from each brood will be. In the Orangethroat Darter, *Etheostoma spectabile* (Percidae), offspring hatched from larger eggs are larger and are less likely to starve (Marsh 1986). Greater investment in each egg, largely in terms of amount of yolk, increases the chances of survival for that offspring. A larger larva is better able to avoid predators and feed independently (e.g., Richards & Lindeman 1987). The volume of the ovarian space in a female determines fecundity, producing an inverse relationship between egg size and number of eggs. Fish that produce larger eggs have lower batch fecundities.

6 *Time until hatching and exogenous feeding*. For egg-laying species, which is most fishes, eggs are deposited on substrates or in the water column and are essentially defenseless, either immobile or floating. After hatching, yolk-sac fry are inefficient swimmers. The longer a larva spends growing inside the egg or absorbing yolk resources, the larger it will become before having to obtain its own food. A larva trades off the increased vulnerability it experiences while being passive against the advantages it will have in finding food and avoiding predators once it achieves independence from the egg shell and yolk sac.

7 *Larval growth rate and interval length*. Rapid growth provides a larva with the same advantages as large egg size or yolk supply, namely achieving a larger size earlier. However, rapid growth requires more energy and higher metabolism, which in turn demands more efficient or faster feeding and an increased likelihood of starvation. A short larval period means larvae can transform quickly into juveniles, and settle from the plankton and into the generally safer juvenile habitat. But if a larva finds itself in an inappropriate habitat at the end of its larval period – such as far out at sea for a species adapted to shallow water existence as a juvenile and adult – then a short larval life provides little advantage (but see below, Synthesis: what determines assemblage structure among coral reef fishes?). Conversely, a long larval interval can permit long-distance dispersal. However, extended planktonic life exposes the larva for a longer time to the extreme hazards of planktonic existence, when >99% of larvae are eaten or starve. Growth rates of juveniles and adults are subject to advantages and constraints as discussed in point 2.

8 *Spawning bouts per year and duration of spawning season*. The number of times an individual, particularly a female, spawns each year tells much about the allocation of energy to reproduction. Duration of the spawning season is more a population than an individual characteristic and is useful in assessing potential recruitment into that population.

9 *Number of spawnings per lifetime*. Most fishes are **iteroparous** (itero = to repeat, as in reiterate; parous = to give birth), spawning repeatedly throughout their lives. One-time spawners, termed **semelparous**, devote all their energy to a single, massive spawning event, after which they die (anguillid eels, many Pacific salmons, lampreys, some gobies).

10 *Reproductive interval*. The time spent between reproductive bouts for iteroparous species varies greatly, from daily spawners that reproduce year-round in some low-latitude coral reef fishes (e.g., wrasses), to fishes that spawn every few weeks during a protracted season (e.g., Grunion, darters), to seasonal spawners that may spawn only once or a few times during a limited season (snappers, groupers, larger percids, centrarchid basses), to internal bearers with long gestation periods of a year or more (some sharks), to species that may wait several years between spawnings (sturgeon). For iteroparous species that spawn repeatedly each year, the reproductive interval can theoretically be adjusted in response to expected mortality levels. Where the probability of mortality is high, reproductive intervals should be short. As was the case for variable age at first reproduction and reproductive allotment (see above), female guppies exposed to high levels of predation have relatively short reproductive intervals (Reznick & Endler 1982).

11 *Parental care*. The degree of care given has an overwhelming influence on the mortality rate of the young and is generally inversely proportional to fecundity (see Chapter 21, Parental care). Parental care is often distinguished as **prezygotic** (e.g., nest preparation) and **postzygotic** (e.g., internal brooding, guarding young). Care may be nonexistent to rather elaborate. Broadcast spawners release large numbers of eggs into the water column and provide no further care (tarpon, cods, tunas). Moderate care occurs in fishes that spawn intermediate numbers of eggs on substrates and may involve some substrate preparation such as nest construction or egg covering (salmons, Grunion). More extensive care occurs in fishes that prepare a nest and then guard relatively few eggs until they hatch and perhaps a little later (sticklebacks, sunfishes, some cichlids). Intensive care is usually associated with relatively low numbers of large eggs, such as fishes that gestate young internally (livebearers, embiotocid surfperches) or incubate the eggs orally (cardinalfishes); some oral incubators continue to protect the young after hatching (some catfishes) and some cichlids even feed their young with external body secretions. Male Bowfin (*Amia calva*) are egg layers without mouth brooding that guard their young until they are several centimeters long, a rarity among pre-teleosteans and teleosts alike. Parental care increases survival of the young but occurs at a cost to the parents because extended care increases the interval between spawnings.

12 *Gender change and sex ratio variation*. Fishes in several families change sex, beginning as males and changing to females (**protandry**) or vice versa (**protogyny**) (see Chapters 10, 21). The timing of the change is largely determined by the relative reproductive success males or females experience at the same body size. Sex change occurs at a cost in immediate reproductive output, because converting the actual machinery of gamete production from one

sex to another may require weeks or months. In many vertebrates (crocodilians, turtles, lizards, possums, monkeys), the sex of offspring may be determined by conditions such as the temperature at which the eggs or embryos develop (= **environmental sex determination, ESD**). Extreme temperatures affect sex determination in a few fishes, mostly atheriniforms such as rivulins, ricefish, and livebearers; pH can also influence sex determination in some cichlids and a livebearer (Rubin 1985; Francis 1992). Naturally occurring variation in temperature determines the sex of developing Atlantic Silversides, *Menidia menidia* (Atherinidae). Offspring produced early in the year at relatively low temperatures tend to be female, whereas young produced later at higher temperatures tend to be male (see Chapter 10, Determination, differentiation, and maturation). Females could theoretically manipulate the sex ratio of their offspring to take advantage of disproportionate numbers of one sex or of environmental conditions that favor one sex over another. Whether and why a female silverside actively manipulates the sex ratio of her young is a matter of conjecture. It is difficult to imagine how a female would assess current sex ratios; in addition, larvae are dispersed widely and are unlikely to be recruited into the same population and environment as the mother (Conover & Kynard 1981; Conover & Van Voorhees 1990; D. Conover, pers. comm.).

13 *Geographic patterns and phylogenetic constraints.* In many families, related species living in different habitats often adopt life history patterns appropriate for that habitat, and unrelated fishes converge on suites of life history adaptations. Mouth-brooding fishes worldwide have converged on small clutches of large eggs, slow growth rates, and protracted breeding seasons (bonytongues, marine catfishes, cichlids). Such convergence is evidence of the importance of environmental selection factors promoting one life history over another and can be found at relatively large geographic scales. Among freshwater fishes in North America, species that mature relatively late in life tend to have larger body sizes, longer life spans, higher fecundities, smaller eggs, few multiple spawnings, and a short spawning season (sturgeons, Paddlefish, shads, muskellunge, charrs, Burbot). Fishes with extended spawning seasons tend to have larger eggs, multiple spawning bouts, and exhibit more parental care (cavefishes, madtom catfishes). Marine fishes that have extensive geographic ranges (tarpon, cods) also tend to have high fecundity. Anadromous species, such as salmons, Striped Bass, and sturgeons, mature late, grow fast as adults, live long, and have large eggs (Winemiller & Rose 1992).

As with any evolved characteristic, life history traits are influenced by the evolutionary history of the lineage to which an animal belongs. Consequently, an animal may not have the life history characteristics that we expect given current conditions. Unless selection pressures have been relatively stable for many generations, an animal's adaptations will not necessarily reflect present conditions but will instead reflect past adaptive scenarios and selection pressures. For relatively conservative traits that are shared among many members of a lineage (the symplesiomorphies of cladistic analysis; see Chapter 2), historical constraints may be difficult to overcome and species will retain seemingly nonadaptive or nonoptimal characteristics. Regardless of latitude and habitat, percopsiforms (Troutperch, Pirate Perch, cave fishes) tend to be small, produce small clutches of large eggs, exhibit extensive parental care, and have protracted spawning seasons and slow growth rates. Within the cypriniforms, suckers in the genus *Ictiobus* are large with large clutches and few spawning bouts whereas minnows in the genus *Notropis* are small, have small clutches, and frequent spawning bouts. Flatfishes as a group mature at large size, produce large clutches of small eggs during short spawning seasons, and grow rapidly when young (Winemiller & Rose 1992).

Populations

Simply defined, a **population** consists of all the individuals of a particular species in a given area. Because populations form the matrix in which individual survival and reproduction occur, expanded definitions recognize the importance of genetic structure: a population is therefore "a gene pool that has continuity through time because of the reproductive activities of the individuals in the population" (Wootton 1990, p. 280). Populations grow and shrink in numbers as a result of the actions and interactions of their individuals, which can change relative gene frequencies (the **genetic structure**; see Chapter 17) of the population. Much of ecology has been devoted to describing, understanding, and predicting the nature and causes of population numerical growth and decline and of genetic structure (the effects of competition and predation on population size are discussed in the context of "Assemblages" below).

Population dynamics and regulation

Population size changes as a function of four major processes: birth, death, immigration, and emigration. **Birth** and **death** rates (**age-specific reproduction** and **survivorship** rates of individuals) can be used to calculate the approx-

Table 24.1

A life table for a cohort of Brook Trout, *Salvelinus fontinalis*, in Hunt Creek, Michigan for the year 1952. Survivorship (l_x) is the probability that an individual female will live to age x, reproductive output (m_x) is the mean number of daughters produced by a female of that age (estimated as half the number of eggs produced). The reproductive rate of the population (net reproductive rate, R_0) is the sum of the survivorship and reproductive output columns ($= \Sigma l_x m_x$), which equals the average number of females being produced per female in the cohort. When R_0 is greater than 1 the population is growing, when it is less than 1 the population is shrinking. After Wootton (1990), based on data of McFadden et al. (1967).

Age class, in years (x)	Survivorship (l_x)	Reproductive output per female (m_x)	Reproductive rate of population ($l_x m_x$)
0	1.0000	0	0
1	0.0528	0	0
2	0.0206	33.7	0.6952
3	0.0039	125.6	0.4898
4	0.00051	326.9	0.1667
			$R_0 = 1.352$

imate rate at which a population will change in size (Table 24.1). Such **life table** statistics are usually calculated only for females in a population; relatively few have been constructed for fishes.

Migration, both in and out of a population, greatly complicates any attempt at predicting future population size. Fish populations increase in size due to migration as a result of either recruitment or colonization. **Recruitment** usually refers to the addition to the population through reproduction, as when larvae settle out of the plankton and into the population. In fisheries terminology, recruitment generally refers to the addition of potentially catchable individuals to the **stock** in question, stock being essentially synonymous with population. **Colonization** is the addition by movement of established individuals between habitats, such as when juveniles move from a nursery habitat to an adult habitat.

Because many fishes export their reproductive products in the form of pelagic larvae that are dispersed widely, reproductive events in a particular population may have little effect on later local population size. As a result, it was widely held that, for most marine populations, minimal correspondence existed between stock and recruitment (the **stock : recruitment relationship**). Minimal relationship meant that current population size was not a reliable predictor of future population size, suggesting that intense local fishing did not necessarily drive down future stocks (e.g., Rothschild 1986). However, more recent analyses suggest that a positive relationship does exist between stock and recruitment in many fisheries, in part perhaps because "export" of larvae from parental habitat is not as general as traditionally thought (e.g., Sponaugle et al. 2002; Gerlach et al. 2007). Myers and Barrowman (1996) found a generally positive stock : recruitment relationship in 83 mostly marine species indicating that (i) higher recruitment occurred when spawner abundance was high; (ii) lower recruitment occurred when abundance was low; and (iii) populations below the median abundance level had lower recruitment than populations above it. Specific examples included such well-known, depleted fisheries as Bluefin Tuna, Atlantic Cod, and large sharks. Life tables are therefore useful not only in relatively closed populations, such as in ponds and lakes, but also in many commercially important marine species.

Regardless of locale, fish populations vary widely and notoriously in size. The concept of the **year class** or **cohort** is important in understanding these dynamics. High population density may not necessarily indicate a sustainably reproducing population because many of the individuals in that population may come from a single year class, whereas most other years may have seen little successful reproduction (Fig. 24.2). If the successful year class is approaching the usual maximum age for that species and no younger year class is abundant, overexploitation of the dominant year class can lead to very rapid population collapse. Year class strength then becomes a critical statistic in determining management schemes for exploited populations. The spectacular success of the campaign to restore Striped Bass, *Morone saxatilis* (Moronidae), to the Chesapeake Bay focused on protecting the 1982 year class until 95% of those females had matured (Ross 1997; Secor 2000).

Variation in numbers among year classes points out another important feature of fish populations, which is that they are **size structured**. Indeterminate growth and over-

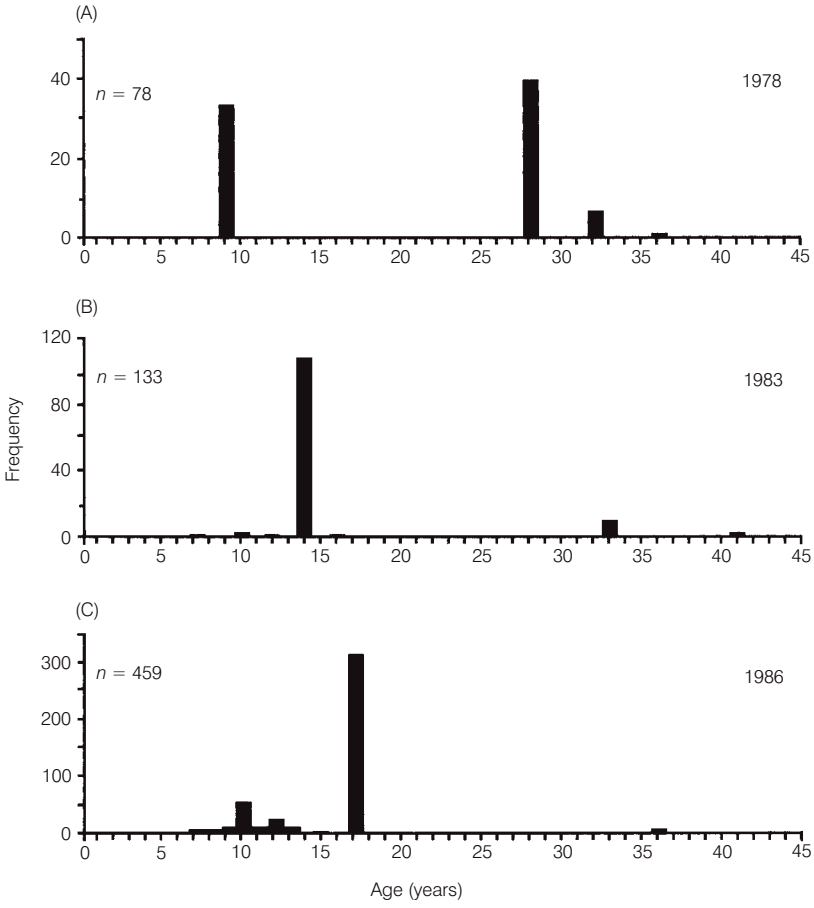

Figure 24.2

Year class strength in an endangered sucker. The Cui-ui, *Chasmistes cujus* (Catostomidae), presently occurs only in Pyramid Lake, Nevada. Its long life span, approaching 45 years, has probably saved it from extinction. Reproductive failure in most years has resulted from drought and human diversion of water from its spawning habitat in the lower Truckee River. (A) Samples of spawning fish in 1978 indicate that the entire species has been maintained by two year classes, one born in 1950 and the other in 1969. (B) Mortality had all but eliminated the 1950 year class by 1983. (C) A bypass channel built in 1976 gave fish access to the river even at low water levels, and some successful reproduction had occurred in subsequent years (no fish occur in the 0–6-year classes because reproduction does not start until age 6). The inset shows an adult Cui-ui held in a captive propagation facility, Pyramid Lake, Nevada. From Scoppetone and Vinyard (1991), used with permission; photo courtesy of the US Bureau of Reclamation, www.usbr.gov/mp/lbao/endangered_species.html.

lapping generations create a situation where a population may include individuals of very different sizes, differing in body mass by as much as four or more orders of magnitude (e.g., consider Bluefin Tuna that weigh a fraction of a gram at birth and grow to an adult size exceeding 500 kg in mass, a range of seven orders of magnitude). Size structuring can affect population regulation because multiple size classes provide the potential for intraspecific competition and cannibalism, which in turn may lead to differences in habitat and other resource use because of avoidance of one group by another.

Such intraspecific variation has led to the concept of the **ontogenetic niche**, which recognizes the very different ecological roles that different age and size conspecifics are likely to play in an assemblage (Werner & Gilliam 1984; Osenberg et al. 1992). For example, Pinfish (*Lagodon rhomboides*, Sparidae) start off as a carnivore and progressively shift to increasing herbivory in five distinct phases

(Stoner & Livingston 1984). Largemouth Bass (*Micropterus salmoides*, Centrarchidae) initially feed on zooplankton, then on littoral invertebrates, and then finally on fish, including conspecifics. As juveniles, they compete with adult Bluegill (*Lepomis macrochirus*) for zooplankton. Young Largemouth are, however, miniature adults and are morphologically constructed as piscivores. They are consequently less efficient planktivores than are adult Bluegill, and this morphological constraint makes them inferior competitors (they even the score later when Bluegill become their major prey) (Werner & Gilliam 1984). At each size, a fish is likely to have a different set of competitors and predators, some overlapping with the previous set, producing an incredibly complex set of interactions within a community containing even a small number of species (e.g., Fig. 25.14).

Death can come at any time, but certain life history stages are more dangerous than others. Eggs and larvae are by far the most vulnerable periods (see Chapter 9, Larval feeding and survival). Estimates of mortality for marine fish populations range from about 10% to 85% per day for eggs, from 5% to 70% per day for yolk-sac larvae, and from 5% to 55% per day for feeding larvae (Bailey & Houde 1989). These are daily rates. When compounded over the larval life of a species, the magnitude of the loss is more striking. For example, jack mackerel, *Trachurus symmetricus*, require 8 days from hatching until they resorb their yolk sac and begin independent feeding. During this time, when mortality falls from 80% to 50% per day, 99.5–99.9% of larvae are lost to predation. Exogenous feeding adds the hazard of starvation; during the first week after yolk-sac absorption, larvae die at a rate of 45% per day from starvation alone, to which can be added predation losses (Hewitt et al. 1985).

Most workers agree that predation is the major source of mortality for eggs and larvae and that mortality is strongest on eggs and small larvae. The list of predators on larvae is long and includes numerous invertebrates (ctenophores, siphonophores, jellyfishes, copepods, chaetognaths, euphausiids, shrimps, amphipods) as well as fishes. As fish grow, their strength, swimming speed, food getting ability, and general escape ability increase. Estimates of the mortality of juveniles and adults are diametrically different from the rates experienced by eggs and larvae, for example 99.9% daily survival for juvenile or adult nototheniid icefishes, English Sole, Winter Flounder, cutlassfishes (Trichiuridae), mackerel, and tuna (McGurk 1986; Richards & Lindeman 1987). Freshwater salmonids (Brown Trout, Brook Trout, Rainbow Trout, Coho Salmon) sustain relatively high annual mortality rates of 60–90% of the adult population, which is still less than the values experienced by eggs and larvae (Alexander 1979).

Cannibalism (intraspecific predation) is widespread in fishes and may play a dominant role in population regulation in some species (Dominey & Blumer 1984; Smith & Reay 1991; Elgar & Crespi 1992). Cannibalism occurs in many chondrichthyans and in at least 36 families of teleost fishes, including herbivores, scavengers, planktivores, and piscivores. Cannibalism can have a significant impact on population dynamics. Between 30% and 70% of egg consumption is caused by conspecifics among anchovies (Engraulidae) and whitefishes (Salmonidae). In addition, adults may eat larvae and juveniles, including their own offspring, and young fish may eat siblings as well as unrelated individuals. Sixty percent of annual mortality in Walleye Pollock, *Theragra chalcogramma* (Gadidae), and 25% of mortality in Yellow Perch, *Perca flavescens*, has been attributed to cannibalism of juveniles. Year class strength is thought to be strongly dependent on cannibalism rates in Pike (Esocidae), Cod, Haddock, and Whiting (Gadidae), Walleye and Perch (Percidae), and Nile Perch (Latidae). In Lake Victoria Nile Perch, cannibalism is considered the major cause of perch mortality, with important consequences for assemblage structure and human welfare alike (see Chapter 26, Introduced predators). In lakes where one or only a few species occur, cannibalism may be *the* major population regulatory mechanism. In such situations, giant cannibal morphs that are specialized to feed on conspecifics may develop (e.g., landlocked Arctic Char, *Salvelinus alpinus*; Sparholt 1985; Riget et al. 1986) (Fig. 24.3); such cannibalistic **polyphenism** is also known among larval salamanders and frogs.

At first glance, cannibalism might appear counterproductive evolutionarily. However, as long as the cannibal is not eating close relatives, no fitness costs are incurred, aside from possible transmission of host-specific pathogens and parasites, whereas potential competitors are eliminated. More importantly, conspecifics represent a highly nutritious protein meal made up of optimum proportions of vitamins, minerals, and amino acids for the species in question, producing high growth rates (e.g., walleye, Walleye Pollock) and enhanced reproductive output (e.g., Mosquitofish, Poeciliidae). Even when kin are consumed, the benefits to the cannibal of reduced competition, increased growth, and enhanced reproduction could outweigh the current costs of losing a few relatives (Dominey & Blumer 1984; Smith & Reay 1991; Sogard & Olla 1994).

Production

A topic of general interest to population ecologists and of particular interest to fisheries managers is the concept of **production**. How much biomass (or fish flesh) is a population producing, and how much of this is available to predators, including humans, without causing the population to crash? Can production be predicted from such measurable population traits as the birth and death schedules of different age classes (i.e., from calculations using life table characteristics discussed above)?

Production is calculated as the growth rate of individuals

Figure 24.3
Four morphs of Arctic Char that differ anatomically, behaviorally, and ecologically can be found in a single lake. Shown here are adults of the four morphs from an Icelandic lake. They are, from top to bottom, the large, benthic feeding morph (33 cm long), the small benthic feeding morph (8 cm), the piscivorous morph (35 cm), and the plantivorous morph (19 cm). Photo by S. Skulason, from Skulason and Smith (1995), used with permission.

over a time period multiplied by the biomass of the age class, corrected for mortality occurring during the time period (Ricker 1975; Gulland 1983; Wootton 1990; Ross 1997). Natural production values for different populations of temperate freshwater fishes vary widely, from <0.1 g/m^2/year for Sockeye Salmon in an Oregon lake to 155 g/m^2/year for desert pupfish (*Cyprinodon nevadensis*, Cyprinodontidae) in a desert stream in California. Most populations fall near the lower end of these values, in the 1–10 g/m^2/year range. Tropical and fertilized ponds often show higher values (Chapman 1978). Knowing production also allows one to calculate **annual turnover**, which is the ratio of production to biomass (P : B). Turnover is an index of how productive populations and subpopulations are; it can be quite useful in understanding ecosystem processes. Among different age classes, very young fishes, although constituting relatively little of the biomass of the overall population, contribute 60–80% of population production because of their high P : B ratios. Young fish have very high growth rates relative to their sizes and hence have high turnover rates.

Yields to predators are therefore relatively higher when predators feed on young fish rather than eating older, slower growing fish. Whether high rates of exploitation of young age classes by predators reflect some form of optimal exploitation due to relative P : B ratios, or whether they just reflect ease of capture, would make an interesting study. Regardless, overfishing might be reduced if fisheries targeted younger age classes instead of imposing minimum size limits and targeting reproductively mature individuals. Such a management approach would more closely mimic natural predator–prey and assemblage interactions, relationships to which prey species have adjusted their life history traits over evolutionary time (Helfman 2007).

Genetic structure of populations

Determining the physical boundaries of a population can be easy (as in isolated ponds and lakes) or difficult (large rivers and lakes, oceanic regions). **Gene flow**, the exchange of genes across boundaries and between populations, can blur the distinction between populations (see Chapter 17). Coregonine whitefishes in many lakes in Canada and sticklebacks in lakes, ponds, and rivers on the Pacific coast of North America are reproductively isolated from each other and consequently form distinct genetic groupings (**demes**) (Hagen & McPhail 1970; Bell & Richkind 1981; Smith

1981b). In contrast, American Eels, although distributed in ponds, lakes, streams, and rivers from Iceland to Venezuela, all return to a single spawning locale in the Sargasso Sea, remixing their genes at each reproductive episode. Such **panmictic spawning** means that the entire species consists of only one population (Avise et al. 1986). Similar lack of genetic structure, in terms of genetically discrete populations, has been shown in other anguillids such as European and Japanese Eels (Sang et al. 1994; Lintas et al. 1998), although different authors using different methods have found evidence of genetically unique populations in these species (Wirth & Bernatchez 2001; Tseng et al. 2006). Nearshore marine species generally show levels of gene flow that are strongly related to dispersal capability and distance between populations; good dispersers that are close together are very similar genetically (Waples 1987).

Genetic analysis of high seas species often indicates a lack of differentiation among widely spread populations that were once thought of as several species. Albacore Tuna (*Thunnus alalunga*) in the North Pacific and South Atlantic and Skipjack Tuna (*Katsuwonus pelamis*) and Yellowfin Tuna in the Atlantic and Pacific are three examples (Graves & Dizon 1987; Scoles & Graves 1993). Migration over long distances or close proximity in a nearshore marine area do not, however, guarantee gene flow. Salmon of Pacific northwestern rivers (*Oncorhynchus* spp.) migrate and intermix in the ocean during much of their lives, but genetically discrete stocks separate and return to their natal streams to reproduce, conserving the genetic identity of the more than 200 stocks (Nehlsen et al. 1991; see Fig. 23.6). At the extreme of genetic diversity, rainbow/steelhead trout/salmon, *O. mykiss*, from the west coast of the Kamchatka Peninsula of Russia differentiate into as many as six distinct life history types (riverine/estuarine, estuarine, anadromous A, anadromous B, anadromous B half-pounders, and resident), with evidence that all six may come from the same spawning redd (Savvaitova et al. 2000; Augerot 2005). Populations of live-bearing Black Surfperch, *Embiotoca jacksoni*, separated by only 40–80 km in California and Mexico, show genetic differences of a magnitude that is normally found between different species within a genus (Waples 1987; Utter & Ryman 1993).

Even an isolated lake may have more than one genetically distinct population of a species. Arctic Char differentiate into different forms in a number of Scandinavian lakes. In Thingvallavatn, Iceland (the suffix "vatn" means lake in Icelandic), Arctic Char far outnumber the other two species present, a stickleback and a trout. The Char exist as four distinct forms that occupy different habitats and feed on different food types (see Fig. 24.3). A large and a small morph remain near the bottom and feed on benthic invertebrates in the shallow littoral zone, whereas two other morphs frequent the water column where one feeds on zooplankton in the limnetic (pelagic) region and the other feeds on fishes both inshore and offshore. Morphologically (and appropriately), the benthic-feeding morphs have subterminal mouths and relatively dark coloration, whereas the more pelagic forms have terminal mouths and silvery, countershaded coloration. Spawning times vary among the morphs, and the morphological differences show up shortly after hatching and hence are not **ecophenotypic**, i.e., they do not result from environmental influences experienced by different individuals.

The morphological and behavioral differences among morphs have a strong genetic basis, as offspring of the different morphs retain their trophic specializations even when raised in a common laboratory environment (Skulason et al. 1993). Genetic differences can also be demonstrated biochemically. Interestingly, the different morphs do not differ genetically, with the exception of the small benthivorous morph, which differs from the other three morphs at one esterase enzyme locus out of 36 loci tested. The morphs may have evolved because of the availability of habitats (**adaptive zones** or open niches) brought on by the absence of other species in the lake to fill those ecological vacancies (Magnusson & Ferguson 1987; Sandlund et al. 1988). Remarkably, predation by Arctic Char in Thingvallavatn varies sufficiently across habitats that it has selected for two very different morphs of Threespine Stickleback, *Gasterosteus aculeatus* (Ólafsdóttir et al. 2007). Sticklebacks are well known for differentiating into distinct benthic and limnetic forms in response to predation pressure and food availability (e.g., McPhail 1994; Schluter 2000). Other fish species demonstrating marked intraspecific diversity, often with a genetic basis, include Crucian Carp, *Carassius carassius* (Bronmark & Miner 1992); Sockeye Salmon, *Oncorhynchus nerka* (Hendry & Quinn 1997; Hendry 2001); Pumpkinseed Sunfish, *Lepomis gibbosus* (Parsons & Robinson 2007); and, of course, Lake Malawi cichlids (Arnegard et al. 1999).

Populations have **genetic structure** (see Chapter 17). The distribution of genotypes can be characterized, either by assaying directly for relative frequencies of alleles of genes or by studying the distribution of phenotypes. Genetic analyses of populations can be a powerful technique for solving systematic questions. For example, five species and eight subspecies of kelpfishes (*Gibbonsia*, Clinidae) were recognized from western North America, based on traditional meristic and morphometric analyses. Reanalysis using allozyme data obtained by electrophoresis of enzymes extracted from various tissues indicated very little genetic differentiation among the subspecies and even between some species, suggesting a high degree of gene flow among populations (Stepien & Rosenblatt 1991). Three nominal species, the Scarlet Kelpfish (*G. erythra*), the Crevice Kelpfish (*G. montereyensis*), and an offshore Mexican endemic (*G. norae*), showed no significant differences in the frequencies of different alleles at 40 gene loci (the term **nominal** refers to a population that has been described as a separate species).

Reanalysis of morphometric data showed that many anatomical differences were instead sexual dimorphisms or anatomical trends that changed continually as a function of water temperature or with depth (the latter are ecophenotypic differences because they represent phenotypes that differ consistently and result from depth of occurrence). All scarlet kelpfish, distinguished by more caudal peduncle scales and a higher dorsal spine, were in fact males. All nominally Crevice Kelpfish were females. *G. norae* differed only in lower counts of scale rows and fin rays, but it is generally observed that fish that develop in warmer water lay down fewer meristic elements (Barlow 1961; see Chapter 9, Meristic variation). Hence *G. erythra*, *G. norae*, and *G. montereyensis* represent different populations of a single species, *G. montereyensis*. Subspecies of kelpfishes also showed little genetic differentiation. Anatomical differences occurred in populations that occupied different depth zones, but characters such as dorsal spine height generally increased with depth of occurrence and were probably ecophenotypic, not genetic, traits. The combined analysis – genetic, morphological, distributional, and ecological – indicated that three rather than five species and no subspecies of kelpfish existed. Hence, genetic analysis showed the true taxonomic relationships among the different species.

Understanding the genetic make-up of a population has become increasingly important as environmental degradation and overexploitation place many populations and species at risk. A key character is the degree of **genetic variation** in a population. Genetic variation results from selection, mutation, dispersal (emigration out of and gene flow into populations), non-random mating, and genetic drift (random changes in gene frequencies, particularly in small, isolated populations). Genetic variation is a chief driving force of evolution; natural selection acts on such variation, favoring genotypes that are adapted to current conditions. Measures of genotypic variation and frequencies can tell us whether a population has become dangerously inbred and lacks the genetic diversity necessary to allow for adaptation to changing environmental conditions, whether gene flow is occurring between populations, and whether hybridization with introduced species is occurring (and hence if the genetic identity of a species is threatened) (Schonewald-Cox et al. 1983; Meffe 1986).

Recognizing the importance of genetic structure among populations has led to the concept of **metapopulations**, which describes populations of a species linked by gene flow via migration, recruitment, or colonization. Metapopulations are thought to exist in a variety of species, including widely distributed, commercially exploited marine fishes (e.g., Atlantic Cod, Atlantic Herring; McQuinn 1997; Wright et al. 2006), among fishes in a stream network (Cutthroat Trout, Bayou Darters; Slack et al. 2004; Neville et al. 2006), among anadromous and estuarine species (Pacific Salmon, Tidewater Goby; Policansky & Magnuson 1998; Lafferty et al. 1999), and among populations of reef fishes (surgeonfish, parrotfish; Planes et al. 1996; Geertjes et al. 2004). Such a focus has important implications for the management of fishery species as well as for the design of protected species and areas because it points to linkages among distant locales (e.g., Fausch et al. 2002). For example, protecting crucial habitat and populations in a few specific locales along a 1000 km long region of the Gulf of California (Sea of Cortez) is likely to assure larval sources linked by ocean currents to many other Gulf areas of biological and socioeconomic importance (e.g., Sala et al. 2002).

Hybridization

An individual contains combinations of genes that have evolved together over millions of years. Different species contain different gene combinations, which means that a hybrid individual brings together genes that have not undergone such fine-tuned co-evolution. The result is that hybrid individuals are typically aberrant in some aspect of their biology, which can be expressed as faster growth or more vigorous mating behavior, a phenomenon referred to as **hybrid vigor** or **heterosis**. However, most natural hybrids are inefficient reproductively, ecologically, biochemically, physiologically, or behaviorally. They are therefore likely to be reproductive failures because of sterility, relatively infertility, or an inability to find or attract mates, or will be ecological failures because they will be outcompeted for resources or be more prone to capture by predators than are individuals from single species matings. Natural selection will obviously favor spawning individuals that avoid mating with members of other species. This separation of species during mating is accomplished via **species isolating mechanisms**, which are usually anatomical or behavioral traits that keep individuals of different species from breeding with one another. Species isolating mechanisms include genitalia that do not match up correctly, as in internally fertilized livebearers or elasmobranchs, or they may result from incompatibility between sperm and eggs, or differences in courtship patterns, timing, or location of spawning. Any inappropriate cues given by one or the other member of a spawning pair can lead to termination of the spawning act.

Hybridization in fishes often occurs when one species experiences a substantial reduction in abundance. When a rare species breeds in the same place and time as an abundant species, interspecific matings are more likely (Hubbs 1955). Hybridization is also common in disturbed habitats where the preferred spawning sites of one species are lacking, forcing them to spawn in another habitat and hence with another species. When exotic but related species are introduced into a region, isolating mechanisms between the introduced and the established species may not have evolved and hybridization may occur.

Among fishes, instances of hybridization are most common in freshwater fishes and less well documented among marine species (e.g., Schwartz 1981, 2001; Epifanio & Nielsen 2000; Scribner et al. 2000). Freshwater families among which natural hybrids are often found include the minnows (Cyprinidae), suckers (Catostomidae), salmons and trouts (Salmonidae), sunfishes and black basses (Centrarchidae), and darters (Percidae). Artificial hybrids produced in aquaculture are also common, as in the sunshine bass (a cross between a male Striped Bass, *Morone saxatilis*, and a female White Bass, *M. chrysops*), the splake (a cross between a Lake Trout, *Salvelinus namaycush*, and a Brook Trout, *S. fontinalis*), and the tiger muskellunge (a cross between a Northern Pike, *Esox lucius*, and a Muskellunge, *E. masquinongy*). Hybrid marine fishes are much less common. The most common marine examples occur in the reef fish families of butterflyfishes (Chaetodontidae) and angelfishes (Pomacanthidae), although distinctive, complex color patterns and popularity among aquarium keepers make hybrids in these families more likely to be detected (Pyle & Randall 1994). Other marine groups known to hybridize include anguillid eels, serranid seabasses, acanthurid surgeonfishes, pleuronectiform flatfishes, and balistid triggerfishes (Bostrom et al. 2002; Randall et al. 2002; Garrett 2005; Albert et al. 2006).

The disproportionate numbers of hybrids among freshwater species could reflect the greater degree of physical disturbance and of species introductions in freshwater habitats (see Chapter 26). Examples of disturbance-induced hybridization include cichlids in Lake Victoria, where females cannot distinguish among males of different species because turbidity impairs light transmission at long and short wavelengths of light (Fig. 21.4). In the Pecos River of New Mexico and Texas, the Critically Endangered Pecos River Pupfish, *Cyprinodon pecosensis*, is restricted to two sinkhole habitats. Its habitat has been invaded by a widespread, introduced species, the Sheepshead Minnow, *C. variegatus*. Hybrids between Sheepshead Minnow and Pecos River Pupfish have completely replaced the endemic pupfish along 500 km of the Pecos River (Echelle & Echelle 1997). In Europe, where habitat disruption is all too prevalent, several endemic cyprinids are impacted by introduced species. In southern Italy, Italian Bleak, *Alburnus albidus* (designated Vulnerable by the International Union for the Conservation of Nature, IUCN) hybridizes with an introduced cyprinid, *Leuciscus cephalus cabeda*; another endemic cyprinid, *Chondrostoma toxostoma arrigonis*, hybridizes with introduced *C. polylepis polylepis* in Spain (Crivelli 1995).

Hybridization is usually a dead end for the individuals produced by the hybrid cross, although successful new species may be produced via hybridization, as in the case of the parthenogenetic, unisexual live-bearers of the genus *Poecilia* in Mexico (see Chapter 21, Gender roles in fishes).

Assemblages

An assemblage consists of the various species populations of a larger taxon in a defined area. **Assemblage structure** refers mainly to the number of individuals, species, and families, and the predator–prey interactions and other trophic relationships between fishes (e.g., Matthews 1998). Ecological interactions thus occur within a fish assemblage, within a spider assemblage, etc. Focusing on assemblages is admittedly myopic, since fishes interact with invertebrate prey and parasites, with plants as food and shelter, with reptiles, birds, and mammals as predators, etc. However, fish–fish interactions are particularly obvious, it is often logistically difficult to deal with all components of an ecosystem, and researchers tend to specialize and develop expertise in certain taxonomic groups (hence the rationale for producing an ichthyology or any other taxon-oriented textbook). For the purposes of the present discussion, we will look at competitive and predator–prey interactions that tend to involve fishes of different species, and discuss prevalent ideas on how assemblages are structured and ordered, i.e., how interactions between fishes affect species composition and maintenance of assemblages.

Niches and guilds: the ecological role of a species

Most discussions of the composition of natural assemblages focus on the **functional roles** of the different species. The ecological function of a species is synonymous with its **niche**, a broadly defined term that essentially describes what an animal eats and what eats it, its environmental and microhabitat requirements (temperature, oxygen concentration, pH, salinity, substrate type), and symbiotic associations in which it participates. Characterizing and measuring niche components and dimensions allows us to compare niches among species and measure changes in niche use that occur when species are added to or subtracted from an assemblage.

An additional, useful concept for understanding the ecological roles of different species within an assemblage is the **guild**. The guild concept emphasizes ecological rather than taxonomic similarities (Gerking 1994). A guild consists of the different species in an area that exploit similar resources in a similar way. Hence the many fishes that hover in the water column along the face of a coral reef and feed on zooplankton make up the zooplanktivore guild, as do the large predatory invertebrates feeding in the same area on the same resource. The diurnal zooplanktivore guild on a reef face includes anthiine seabasses, snappers, fusiliers, butterflyfishes, damselfishes, wrasses, surgeonfishes, and triggerfishes, among others. At night, a different set of species exploits the larger (and hence different) zooplankton resource, constituting the nocturnal zooplanktivore

guild: anchovies, herrings, silversides, squirrelfishes, copper sweepers, cardinalfishes, grunts, and glasseye snappers (Hobson 1975).

A species may be a member of different guilds at different times in its life. Angelfishes, wrasses, and leatherjackets (*Scomberoides*, Carangidae) may belong to the cleanerfish guild as juveniles, but as adults change to feeding on sessile invertebrates, mobile invertebrates, or small fishes, respectively. In streams, fishes can be classified by their habitat preferences as members of a benthic guild (e.g., some minnows, suckers, sculpins, darters) that feed largely on benthic invertebrates living among rocks or buried in sediments, or as members of a water column guild feeding largely on drifting insects or on insects that fall onto the water's surface (trouts, several minnows) (Grossman & Freeman 1987). In tropical streams, guilds can include algivores, aquatic and general insectivores, piscivores, scale and fin eaters, terrestrial herbivores, and omnivores (Angermeier & Karr 1983). We can also recognize tidepool guilds, kelpbed water column guilds, pelagic predator guilds, wave-zone sand-dwelling guilds, rock-dwelling lake guilds, buried benthic predatory guilds, etc., depending largely on habitat and foraging activities. For example, the shallow water (10–200 m), soft bottom assemblage of fishes off the southern California coast can be divided into approximately 18 foraging guilds, based on how and what they eat and their position in the water column (Allen 2006) (Fig. 24.4). A drawback to the guild concept is that it overlooks the opportunism that characterizes the feeding habits of so many fishes, especially as adults (Matthews 1998; Hobson et al. 2001; Allan & Castillo 2007).

Habitat use and choice

An important component of a species' niche, and one that can easily differ among species, is its habitat. Habitat can often be described and quantified in detail. Among stream fishes, species often differ in height above bottom (Fig. 24.5), preferred current strength, bottom type (particle size and type), structure, distance from shore, amount of vegetation, and type and amount of food resources. A survey of major habitats in an eastern North American stream (rapids, riffles, runs, pools, overhangs) often shows that species segregate along vertical dimensions, with certain species typically found in contact with the bottom (catfishes, darters, sculpins, eels, grazing minnows), some just above the bottom (suckers), some species low and others higher in the water column (planktivorous minnows, trout), some close to the surface (silversides, livebearers, topminnows), some in swift water (darters, trout), and others in moderate flow or in slow flow near more rapidly flowing water (catfishes, minnows, pickerel, sunfishes). The existence of particular species in particular habitats implies an active choice by individuals (e.g., Gorman 1988). Experimental studies, usually of juveniles, generally show that individuals actively choose habitats, that the ones they prefer are the ones in which the species is most often found, and that preferred habitats are ones in which a species can successfully feed, avoid predators, and reproduce, i.e., habitat choice is an evolved aspect of a species' niche (e.g., Sale 1969). Habitat choice is, however, dynamic within a species, varying on the basis of age, size, sex, reproductive condition, geographic area, and environmental conditions (e.g., Karr et al. 1982; Allan & Castillo 2007).

Similar descriptions, based on habitat characteristics, apply to assemblages in most major habitat types. Different faunas in different geographic locales often occupy similar habitats and, in essence, converge on many niche characteristics. The Chinese Algae Eater, *Gyrinocheilus* (Gyrinocheilidae), belongs to a Southeast Asian family related to loaches. It lives in rivers where it feeds on algae attached to rocks. It has a sucking mouth with which it clings to

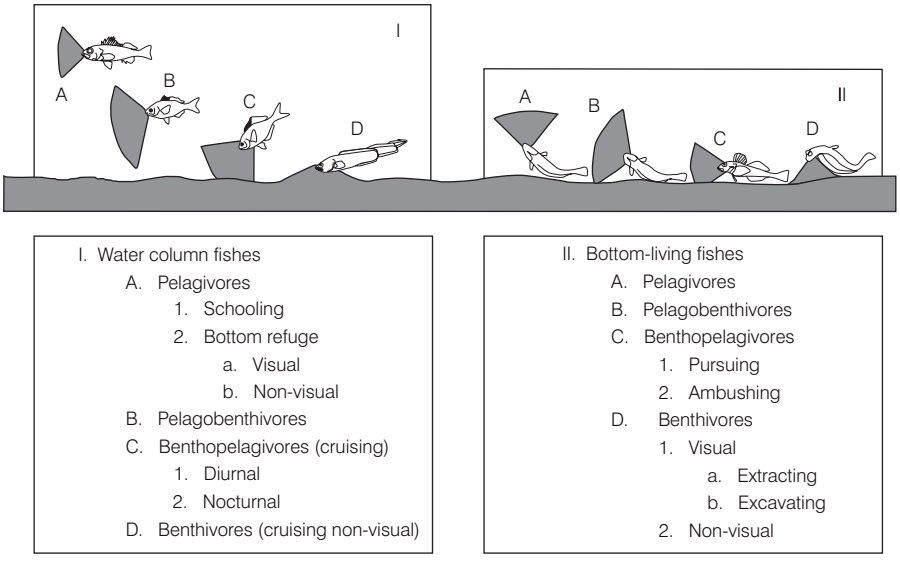

Figure 24.4

Foraging guilds of soft bottom fishes on the southern California shelf. Two general groups are recognized: those that swim above the bottom and those that are in contact with the bottom. The actual guilds take into account height above bottom, foraging type (search and capture activities), and time of feeding. From Allen (2006), used with permission.

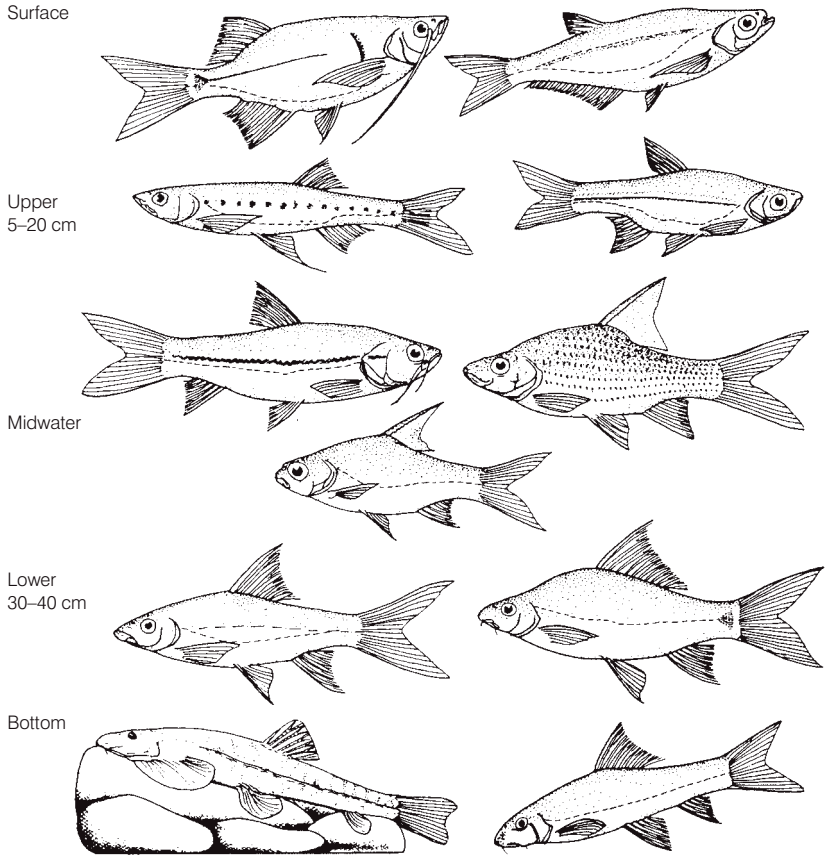

Figure 24.5
Habitat choice in stream fishes as demonstrated by vertical segregation among cyprinid fishes in a Borneo stream. Habitat choice is one aspect of the niche of a species; species choose habitats according to specific characteristics, and species often differ in one or more quantifiable characteristics of habitat. From Welcomme (1985), used with permission.

rocks even while feeding in high-flow situations. A South American catfish, *Otocinclus* (Loricariidae), similarly feeds on algae-covered rocks in flowing water. It is convergent with the Algae Eater in body form and size, suctorial mouth, and even coloration (see Chapter 18, Strong currents and turbulent water). Stream-dwelling galaxiids of the southern hemisphere, especially in New Zealand and Australia, occupy niches very similar to those of salmonid trouts in the northern hemisphere. They are convergent in body morphology, habitat, and foraging habits and have been rapidly exterminated by the introduction of trout in many locales due to competition and predation. A characin, the Dorado, *Salminus maxillosus*, is a desirable gamefish that lives in streams of the Amazon region (Fig. 24.6). Its morphology, coloration, and piscivorous foraging habits are, as its generic name implies, remarkably convergent with stream-dwelling salmonids such as Brown Trout (Esteves & Lobo 2001).

A very broad and striking convergence occurs among approximately 60 families of fishes that fill the **eel niche** in their respective assemblages. Only 22 of these families belong to the order Anguilliformes and are "true" eels. Many of these fishes are convergent in habitat choice, occurring on and often in the bottom in soft sediments or among the interstices of rocks and other structure. They share other characteristics: elongated dorsal and anal fins that often lack hard spines, increased vertebral counts,

Figure 24.6
The characid Dorado, a popular gamefish of the Amazon Basin, is ecologically convergent with large riverine salmonids. Photo from Rio Paraná, Ayollas, Paraguay, courtesy of www.planetapesca.com.

reduced opercula, missing pelvic or pectoral fins, missing or embedded scales, and a pointed tail. Behaviorally they are carnivores and scavengers (some are parasitic), can swim backwards and forwards with equal facility (**palindro-**

mic locomotion), and tear pieces off their prey by holding on and rotating rapidly along their long body axis (Helfman 1990; see Box 19.2).

Habitat choice changes with the seasons (see Chapter 23), with size and age of fish (see Chapters 9, 10), and also with the presence of other species, particularly predators and competitors. Many stream species, such as darters and benthic minnows and suckers, occupy increasingly swift water as they grow older. Often the distribution results from spawning habits: adults migrate upstream to spawn in headwaters and young move progressively downstream with growth (e.g., Hall 1972). Such an **ontogenetic habitat shift** could reflect a body size constraint related to the current speed at which an individual can hold position without expending excess energy or using too much oxygen (see below and Fig. 5.7). A general and somewhat unexplained pattern of increasing depth with age occurs in a number of freshwater and marine species. In many species, this trend reflects the use of inshore, shallow, productive nursery areas that are reputed to be relatively predator-free (e.g., saltmarshes, mangroves); these fishes move offshore as they grow. In other species (minnows, copper sweepers, damselfishes, surgeonfishes, sunfishes, croakers, percids, clinids, wrasses, Great Barracuda), an actual size–depth correlation has been found (Helfman 1978; Power 1987). That the relationship exists in a diversity of habitats and involves a number of unrelated species (e.g., Polloni et al. 1979) implies a convergent, adaptive trait, but the details of this adaptation remain to be worked out in most cases.

"Bigger–deeper" distributions within species and other types of habitat shifts may result from avoidance of predators, influenced by differences in vulnerability between different size classes of prey. When predatory sunfishes (*Lepomis* spp.) are present and Largemouth Bass are absent, young-of-the-year Stoneroller Minnows (*Campostoma anomalum*) occupy shallows of pools, whereas larger Stonerollers prefer deeper portions. Sunfishes occupy deeper portions of pools and can eat young minnows but are too small to eat larger minnows. When bass, which can eat all minnows and also prefer deep sections, are added, all size classes of Stoneroller are confined to shallow margins or emigrate from pools.

A combination of fish, avian, and mammalian predators affect the depth distributions of loricariid catfishes (including the "plecostomus" species of the aquarium trade) in Panamanian streams. These herbivores feed on algae that grow most abundantly in the shallows of pools. Small catfishes live in the more productive shallows, whereas large catfishes occur in deeper water where algal production is minimal and where the fish lose fat reserves and cease growing. The habitat differences of the two size groups are enforced by the balanced impact of terrestrial predators and piscivorous fishes. Birds and mammals can capture any size prey whereas piscivorous characins are gape-limited and cannot swallow the large catfishes. Large catfishes are therefore forced into deeper, less productive regions by terrestrial predation. The small catfishes avoid predatory fishes that live in deep water but can hide from the birds and mammals in shallow water by seeking refuge among rocks; however these refuges are too small for larger catfishes (Power 1987; Power et al. 1989; see also Chapter 25, Predation, and Fig. 25.1). Cannibalism can also influence habitat shifts, forcing smaller fish into suboptimal habitats where their growth rates suffer. Smaller sculpins (*Cottus*) use a diversity of habitats in some streams and prefer deeper water in others when large conspecifics are missing. If larger fish are present or are added experimentally, the smaller fish shift to shallower habitats. Similar habitat shifts, resulting in the occupation of suboptimal feeding habitats by small prey, have been demonstrated in other minnow species and Bluegill Sunfish (Werner et al. 1983; Gilliam & Fraser 1987; Schlosser 1987; Freeman & Stouder 1989).

Habitat choice and spatial structure: zonation

Researchers have compared the fish species that occur in different habitats along environmental gradients, such as from headwaters to mouths of streams and rivers, vertically within kelp forests, across rocky intertidal zones, or from shore to reef face or continental shelf, or across the sublittoral regions of oceans and lakes out to the limnetic or pelagic zone (Horn & Martin 2006; Stephens et al. 2006) (Fig. 24.7). These investigations have led to generalizations about zonation in various habitats.

Almost every fish habitat that has been studied can be divided into more or less distinctive zones. Early work of this type focused on stream and river (riverine, lotic, or fluviatile) fishes in the British Isles and Europe, where analogous **longitudinal zones** (habitat types along the length of a river) were identified in different systems. The zones were often named based on the common fish species present, which in turn reflected species' preferences with respect to gradient (slope), water velocity, stream width, stream depth, temperature variation, oxygenation, and sediment type. These habitat characteristics also influenced the presence and type of vegetation both in and along a river, bottom characteristics, and invertebrate fauna. A popular classification recognized four basic zones, beginning with the headwaters and moving to the lowlands (Huet 1959; Hawkes 1975):

1. The **trout zone**: the narrow, shallow, cold, steep (often torrential), highly oxygenated headwater region with large rocks or gravel; common fish species show morphological or behavioral adaptions to high flow and include Brown Trout, Atlantic Salmon fry, Bullhead Sculpin (*Cottus gobio*), and Minnow (*Phoxinus phoxinus*).
2. The **grayling zone**: deeper, less steep, with alternating riffles and pools, relatively strong currents, less rocky,

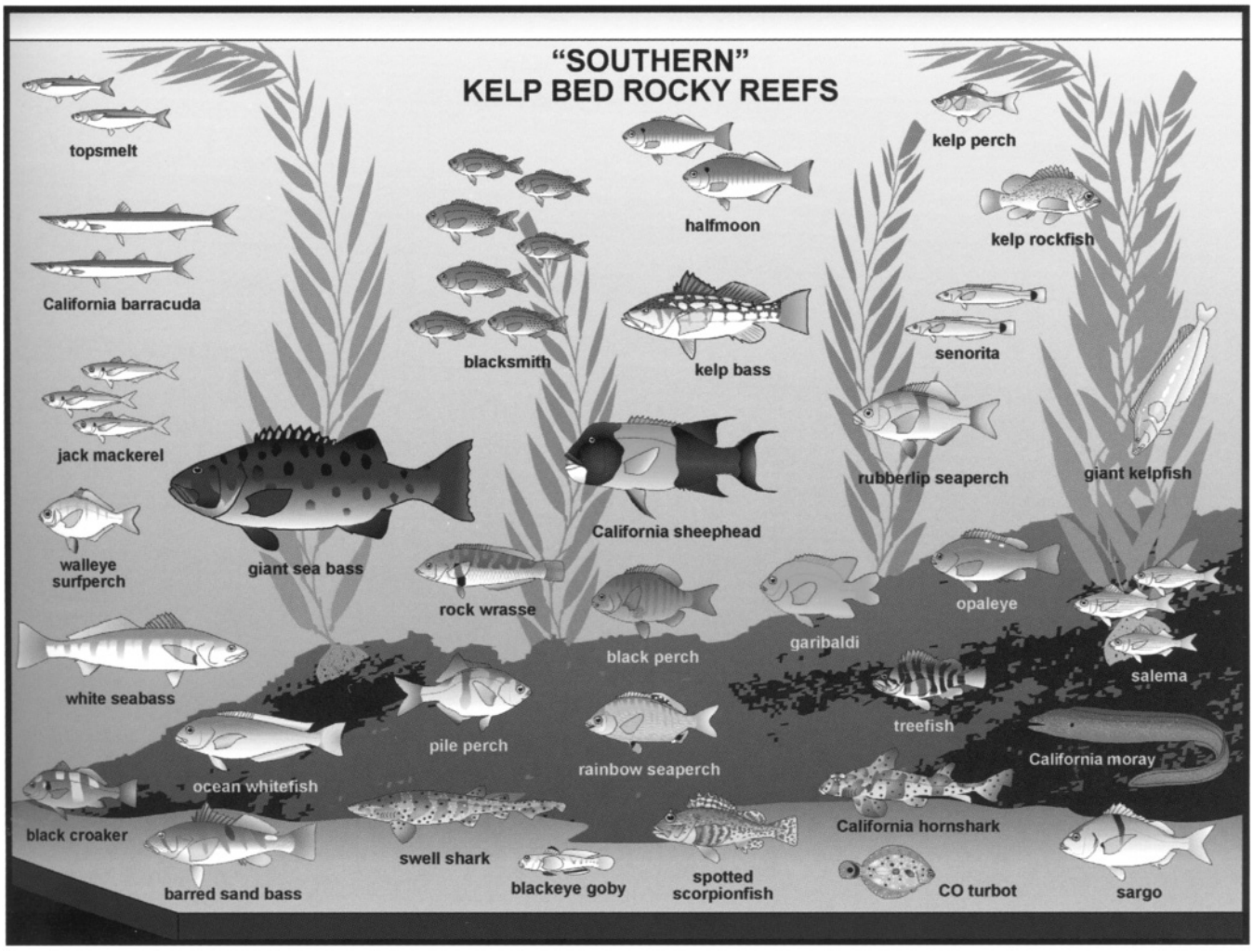

Figure 24.7

Vertical zonation of fishes in a kelp bed. Species portrayed are the more common fishes found in southern California rocky kelpbed reefs. The assemblage is a mixture of three biogeographic faunal elements, involving tropical- and subtropical-derivative families (chubs, grunts, croakers, damselfishes, wrasses), cool temperate Oregonian families (rockfishes, surfperches, greenlings, sculpins), and cool temperate San Diegan species such as kelp rockfish and black perch. From Stephens et al. (2006), used with permission.

more gravelly bottom, cool, slightly less oxygenated, with salmonids in the rapids and rheophilic (current-loving) minnows in the pools; common fishes are grayling (*Thymallus thymallus*), species of the trout zone, and rheophilic minnows (Barbel, Chub, Hotu, Gudgeon).

3 The **barbel zone**: riverine conditions of moderate gradient and current, greater depth, alternating rapids and runs (quieter flowing water), fluctuating temperatures; common fishes are rheophilic cyprinids, other cyprinids (roach, rudd, dace), and predators (Pike, Perch, European Eel).

4 The **bream zone**: lowland reaches that include rivers, canals, and ditches, little current, high summer temperatures with oxygen depletion, and turbid water; common fishes are Roach, Rudd, Dace, and predators of the barbel zone plus slow-water cyprinids (Carp, Tench, Bream).

Alternative classifications emphasize different species in different areas, but the recognition of **longitudinal succession** in habitats and species, often involving three to eight basic zones that differ in a few essential physical features, is common to most classificatory schemes (e.g., head stream, trout beck, minnow reach, lowland course; spring zone, upper, middle, and lower salmonid region, barbel region). Underlying causes of zonation have focused on the physical factors listed above, which often correlate with **stream order**. Order is determined by tributary number: small, headwater streams are first order, two first order streams join to form a second order stream, two second order

streams join to form a third order stream, etc. (Kuehne 1962). The world's largest rivers are seldom much more than 10th order. For example, the Mississippi from its confluence with the Ohio to its mouth, a distance of almost 1000 km, is about an 11th order river. To be larger, another 11th order river would have to flow into it (Fremling et al. 1989). Faunal breaks, where species type and number change in direct correspondence with stream order, have been identified in several systems (Lotrich 1973; Horwitz 1978; Evans & Noble 1979), but other studies have shown that elevation, gradient, historical factors, and especially upstream drainage area and discharge are also likely correlates of species richness and faunal change (Matthews 1986a, 1998; Beecher et al. 1988; Hughes & Omernik 1990).

One popular alternative to a stream order classification is measurement of **downstream**- or **D-links** (Osborne & Wiley 1992). The D-link approach emphasizes the importance of proximity of tributary streams to larger rivers. Small streams flowing into larger rivers have a greater source of colonists and migrants than is the case for tributary streams flowing into small rivers, and seasonal flooding of rivers often causes water and fishes to enter tributaries, drastically altering their species composition. It is therefore necessary to know "the position of a given stream within the overall basin drainage network in order to adequately predict its potential for species richness" (Matthews 1998, p. 312).

Longitudinal zonation among fishes has been described in numerous tropical and temperate riverine systems (Moyle & Nichols 1974; Horwitz 1978; Balon & Stewart 1983; Welcomme 1985). In eastern North America, headwater streams may contain only a single species, such as Brook Trout, sculpin, or Creek Chub. Downstream, where streams increase in both size and velocity, habitat diversity increases and species adapted to high-flow conditions (e.g., darters, hogsuckers, Longnose Dace, rheophilic minnows, sculpin, Smallmouth Bass) are added. Further downstream, as the system widens and deepens, sediments are deposited and primary and secondary production increase. Swift water species characteristic of upstream areas may drop out, but many more species are added. Food webs become less dependent on inputs of food from the surrounding watershed (**allochthonous inputs** such as falling leaves and falling insects) and more dependent on production from the stream itself (**autochthonous inputs** from periphyton, macrophytes, and associated animals). Deep pools and slow flowing conditions alternate with shoals and rapids. Fish diversity increases to include suckers, herbivorous minnows, catfishes, and Largemouth Bass. In large, slow-flowing rivers with little gradient, planktonic organisms and planktivores are added (shad, herring, silversides, Paddlefish, and predators such as Striped Bass and pickerel, all species that also inhabit lakes) as are larger carnivores such as sturgeon. Production of food is largely from the river itself, much of it in the form of detritus-eating insects that live on snags formed by fallen trees from the gallery forest. The floodplain and its forest contribute substantially both as sources of nutrients and as nursery areas during seasonal flooding. A fish fauna of backwaters, oxbows, and sloughs is added, including some that are adapted to swampy, periodically deoxygenated conditions (many sunfishes, small pickerels, livebearers, killifishes, Swampfish, Pirate Perch, Mudminnows, gars, Bowfin). Finally, as the river enters the coastal zone and is subject to both the tidal and salinity influence of the ocean, a very diverse assemblage that includes freshwater species from the lower river reaches and marine species from nearshore zones inhabit the saltmarsh or other estuarine region. In all zones, fairly characteristic species are associated with relatively definable habitats.

Since the original formulations of the idea of longitudinal zonation, many corrections, modifications, and exceptions have occurred. Zones were originally thought to be distinct; border lines were even drawn between them on maps. Sharp delineation between zones is probably more the exception than the rule. For example it occurs most often where montane streams flow into foothills or lowlands, such as in western North America where a cold water fauna exists in a high elevation region but the fauna changes as the stream leaves the mountains (Matthews 1998). In reality, zones usually grade into one another, with "border zones" that are intermediate in physical nature and species composition connecting the zones. Sometimes these border zones may be longer than the fish zones they presumably separate.

In fact, the faunas of different zones are not necessarily distinct from one another. A commonality in flowing water is that species diversity increases as one goes downstream, and this increase is generally due to **additions**, not **replacements**, of species (see the listing above of European river zones for an example). Rather than species dropping out from faunal lists as one progresses downstream, additional species are found: headwater fishes are often found in downstream habitat patches (e.g., a swift shoal), although downstream species seldom occur in headwaters. Other complications include missing zones, as where rivers appear suddenly due to the emergence of major springs (e.g., northern Florida), or disappear suddenly (western deserts). Reversals in zones may occur in rivers that have a stairstep course, with repeated slow-flowing flat sections that become steeper, or in rivers that flow through lakes that are cooler than the incoming river water. Seasonal migrations among zones and out of rivers and into lakes and the ocean change assemblage composition dramatically. Benthic invertebrates also occur in zones, but these zones may or may not correspond with fish zones.

Most of these exceptions do not contradict the idea of zonation because they can be anticipated from the specific environments involved. The basic idea of a relatively few, generalizable zones, with characteristic fish species living under characteristic flow and temperature regimes, has

remained a viable descriptor and predictor of fish assemblages in a surprisingly large number of lotic situations (Hawkes 1975), and can serve to indicate disruptions due to human causes (e.g., Fausch et al. 1984). The major shortcoming of viewing a river, or any aquatic habitat, as isolated sections or zones containing relatively independent and distinct assemblages is that it ignores the critical, functional linkages among sections and subsets of the biota. In this regard, the **river continuum concept** (**RCC**; Vannote et al. 1980; Minshall et al. 1985) can be usefully applied to fish assemblages in rivers. The RCC views a river as an orderly progression of predictably intergrading, dependent regions containing organisms whose ecological roles reflect changes in river basin geomorphology, current speed, gradient, sediment and organic matter composition, and allochthonous versus autochthonous production (among aquatic insects, shredders and gathering collectors predominate in headwaters, shredders are replaced by scrapers in middle reaches, and filter feeders predominate in higher order sections). The integration of fishes into the RCC remains an ongoing challenge in fish (and riverine) ecology (see Matthews 1998; Allan & Castillo 2007), but the realization that a river is a heterogeneous system of multiple habitat types linked by both water and fish movement – a **riverscape** – is gaining increasing acceptance and application (Fausch et al. 2002).

Competition

Competition occurs when two consumers require a resource that is in insufficient abundance to meet the needs of both. Members of the same species can compete (**intraspecific competition**) as can members of different species (**interspecific competition**). Although intraspecific competition can affect an individual's ability to acquire resources, interspecific competition has received more attention because of the insight it provides into the coexistence of different species in an assemblage, which addresses the more general question of how biodiversity is created and maintained. In general, individuals can compete for food, feeding and resting sites, and refuges from predators and the elements (competition for mates and breeding sites is viewed as part of the reproductive biology of a species rather than as traditional competition).

To avoid or reduce competition, organisms may change the way they exploit a resource. Competition may lead to differences in resource use (**resource partitioning**), such as when two **sympatric** ("living together") species feed on different sizes of a prey type or eat similar prey but in different microhabitats. Competition is more strongly implicated if these same predators feed on identical prey when they are **allopatric** ("living separately"). Also, competitive interactions can be suspected if potential competitors shift their resource use when resources become seasonally limiting, or if population reductions of one species occur when a suspected competitor is introduced into an area. However, ecological differences among species can also be caused by differences in nutritional requirements, foraging or locomotory capabilities, predator vulnerability, and phylogeny. Also, introduced species can alter predator–prey relationships or serve as vectors for parasites and diseases, which would also affect population densities of previous residents. Consequently it is generally necessary to perform experimental manipulations of resource abundance or distribution, or of population densities of suspected competitors, to prove that competition is in fact the cause of the dissimilarities. In such experiments, competition can be invoked if an inferior competitor or less aggressive species that occupies suboptimal regions in sympatry expands its habitat or feeding habits when the superior competitor is eliminated. Reciprocal removal of the inferior competitor should have little effect on the habits of the superior species. Such experiments may be conducted fortuitously or deliberately.

A fortuitous manipulation of resource partitioning, mediated by both competition and predation, is conducted annually in Lake Tjeukemeer, the Netherlands (Lammens et al. 1985). Bream (*Abramis brama*, Cyprinidae) and European Eels (*Anguilla anguilla*, Anguillidae) occur year round in fairly stable numbers in the lake, where their chief foods are waterfleas and juvenile midges, respectively. Smelt (*Osmerus eperlanus*, Osmeridae), a zooplanktivore, enter the lake each spring as juveniles when water is pumped from a nearby lake as part of a water stabilization program. Smelt do not persist in the lake because the adults are almost all consumed by predatory Pikeperch (*Sander lucioperca*, Percidae). When large numbers of juvenile smelt are recruited into the lake, they depress zooplankton populations, having their strongest effects on the size classes of zooplankton most used by Bream. Bream respond to reductions in zooplankton resources by switching to benthic invertebrates such as midge larvae, thereby depressing that resource. Eels then respond to depletion of their primary food by switching to piscivory. When Smelt are abundant, both Bream and Eels suffer reductions in condition (weight/length) and Bream show poor gonad development. In years when Smelt recruitment is low, Bream and Eels switch back to their waterflea/midge diets and their growth and reproduction improve.

A well-studied example that includes the experiments necessary to establish the causes of shifts in resource use involves sunfishes in North America. As many as eight species of centrarchid sunfishes and basses may co-occur in a single lake. Many of these species are very similar morphologically. How do they coexist without competing? When stocked separately in ponds as year-old fish, three species, Bluegill Sunfish (*Lepomis macrochirus*), Green Sunfish (*L. cyanellus*), and Pumpkinseed Sunfish (*L. gibbosus*), use similar habitats and feed on similar food types. All three concentrate their time and effort on vegetation-

associated invertebrates. When stocked together, Bluegill and Pumpkinseed shift their habitats and diet in apparent avoidance of the competitively superior Green Sunfish. Bluegill shift to feeding on zooplankton in open water, and Pumpkinseed include more benthic prey in their diet. Green Sunfish maintain a diet of vegetation-associated insects. All three species show reduced growth rates, indicating competitive reduction of resources for each species, but Bluegill show the greatest declines. When Bluegill and Green Sunfish are stocked together in ponds with little open water habitat (i.e., no alternative habitat for the Bluegill), Green Sunfish show better growth, fuller stomachs, and a higher survival rate than Bluegill. Competition among these species has an ontogenetic component that is felt most strongly by young fish. As the fish grow older, they begin to specialize more on different habitats. Bluegill become more adept at maneuvering in open water and suction feeding on zooplankton, and Pumpkinseed develop pharyngeal dentition with which they can crush mollusks that live in sediments. Hence the potential for competition is reduced in older fish under natural conditions (Werner & Hall 1979; Werner 1984; Mittelbach 1988; Osenberg et al. 1988; Wootton 1999).

Many other investigations have demonstrated strong competitive interactions among fishes in various habitat types (e.g., tropical streams, Zaret & Rand 1971; temperate streams, Schlosser 1982; temperate marine nearshore, Hixon 1980b, Holbrook & Schmitt 1989; coral reefs, Hixon & Beets 1989, Munday et al. 2001, Holbrook & Schmitt 2002; see reviews in Ross 1986; Ebeling & Hixon 1991; Grant 1997; Hixon 2006). In general, of the kinds of resources for which fishes can compete, competition for food resources, or at least differences in trophic resource use, is more common among fishes than are interspecific differences in habitat use; the reverse is true in terrestrial communities (Ross 1986).

Some traits that reflect apparent adjustments to present-day competition may result from historical interactions between species, the so-called "ghosts of competition past". The influence of historical competition is frustratingly difficult to determine: are two species different today because of their current impacts on one another or because of past interactions? Experimental manipulations of the resource in question are almost always needed to prove competition, but obviously one cannot manipulate the history of two species and hence we can only speculate on but not demonstrate historical competition (Connell 1980).

Historical factors must also be considered when comparing ecological characteristics of species from unrelated taxonomic groups. The more distantly related two fish species are, the less similar they tend to be ecologically (Ross 1986). For example, generalist predators on coral reefs tend to be active at twilight or at night, have large mouths, and feed on fishes, whereas specialists are diurnal, have small mouths, and feed on sessile or small invertebrates (Hobson 1974, 1975, 2006). Resource partitioning along both trophic and temporal resource dimensions could be invoked here. However, generalist reef species tend to belong to more primitive acanthopterygian (spiny-rayed) groups (squirrelfishes, scorpionfishes, groupers), whereas specialists belong to more advanced groups (butterflyfishes, wrasses, triggerfishes). Feeding habits, morphology, and activity times in one lineage are likely to have evolved independently of what happened in a later evolving lineage. Differing ecologies may therefore simply reflect differing phylogenetic histories. Interpreting differences in resource use as a result of competition may also be erroneous because of physiological differences among species (Box 24.2).

Some of the strongest impacts of introduced species on natives involve **competitive displacement**, suggesting that competition has been historically reduced via evolutionary adjustments (see Chapter 26, Competition). In Lake Michigan, a coregonine salmonid, the planktivorous Bloater, *Coregonus hoyi* (designated Vulnerable by IUCN), was replaced by introduced planktivorous Alewives, *Alosa pseudoharengus* (Clupeidae) in the 1960s, apparently as a result of competition for plankton. As Alewife numbers grew, Bloaters declined in abundance, shifted to a diet of benthic invertebrates at an earlier age, and apparently evolved fewer and shorter gill rakers (Crowder 1984). Five other coregonine species were extirpated from Lake Michigan during the same period.

Other indirect evidence of competitive displacement of natives by invaders includes habitat displacement of (federally Threatened) Spikedace, *Meda fulgida* (Cyprinidae), by Red Shiners, *Cyprinella lutrensis*, a well-known invasive. Red Shiners were introduced into the lower Colorado River. Spikedace disappeared simultaneously and progressively as Red Shiners proliferated, while dams and water withdrawals led to degraded habitat. Both species occupied slow current regions when alone, but where they co-occurred the more aggressive Red Shiners remained in slow current areas while Spikedace were displaced into regions of swifter current (Douglas et al. 1994). Introduced trout are often implicated in competitive displacement of native trout (e.g., Gatz et al. 1987; Fausch 1988). In a Michigan stream, introduced Brown Trout displaced native Brook Trout from the best foraging habitats, forcing brookies into faster water where the energetic costs of maintaining position were higher and where they were more likely to be caught by anglers (Fausch & White 1986; see also Waters 1983). Rainbow Trout displaced two native Japanese salmonids (Dolly Varden, *Salvelinus malma*, and White-spotted Char, *S. leucomaenis*) because of timing differences in spawning. Natives spawned in fall but rainbows spawned the next spring, at a time when embryos of the fall-spawning natives were developing in the gravel. The digging and spawning activities of the introduced species disturbed the redds of the natives (Taniguchi et al. 2000).

Box 24.2

Habitat choice and environmental physiology: a cautionary note

Species differences in habitat choice can be attributed to interactions among competitors or between predators and prey. One should not, however, immediately assume that habitat choice in general results from such **biotic interactions**. An alternative, and often simpler, explanation is that a species occurs where it does because the fish functions best there, which is to say that choice of habitat reflects use of *physiologically* optimal environments rather than being the result of interactions with other species over limiting resources such as food or shelter.

Headwater streams often contain small assemblages of ecologically distinct species. In the southern Appalachian Mountains of the USA, the assemblage typically consists of <10 species that are often found at different heights above the bottom and at different water velocities. Four common species are the Rosyside Dace (*Clinostomus funduloides*) and introduced Rainbow Trout (*Oncorhynchus mykiss*) in the water column, and Longnose Dace (*Rhinichthys cataractae*) and Mottled Sculpin (*Cottus bairdi*) on the bottom. Facey and Grossman (1990, 1992) tested whether distribution differences among these four fishes could be explained not by **interactive segregation** (competition), but instead by energetic efficiencies, that is whether fishes were using physiologically optimal habitats. They found that Longnose Dace showed no real preference but were distributed in proportion to the available velocities in the stream (interactions with other species are unlikely to produce such a statistically random distribution). Rainbow Trout, Rosyside Dace, and Mottled Sculpin chose velocities that were lower than would be expected if they were distributed at random. Tests of energy use in flowing water respirometers indicated that trout and dace used more oxygen as water velocity increased, i.e., they occupied low-velocity regions because it was energetically expensive to live in high-flow areas. Also, trout and dace preferred velocities in which they were most efficient at capturing drifting invertebrate prey (Hill & Grossman 1993). Hence physiological costs associated with holding position at high velocities and optimal velocities for capturing prey, not interactions with other species, are the most likely determinants of where in a stream these two species are found.

Sculpin, however, occupied low-flow regions even though the respirometry data indicated they incurred little added cost at higher velocities. Their microhabitat preferences might therefore be explained by food availability, predator avoidance, or competitive interactions. Experimental manipulations involving sculpin and its most likely competitor, Longnose Dace, indicated minimal effects on sculpin (Barrett 1989; Stouder 1990). In headwater streams, highly variable environmental features, characterized by large fluctuations in water level and velocity (droughts and floods), combined with physiological constraints, prey capture abilities, and intraspecific competition (Freeman & Stouder 1989), appear to have a greater influence on occurrence, distribution, abundance, foraging, and habitat choice than do interspecific interactions.

Predation

Predator–prey interactions among species in an assemblage can have direct and indirect effects on prey population size and distribution. **Direct effects** include immediate mortality or delayed mortality due to injury. **Indirect effects** involve habitat shifts caused by a predator's presence that force potential prey to use suboptimal habitats, which can affect individual growth and reproduction (see above). Population-level responses associated with predation are usually density dependent and vary with the age of the prey. **Density-dependent** changes occur when the size of the prey population determines the impact of the predator. Direct density dependence is referred to as **compensatory**, meaning that predation increases to compensate for increases in prey population size. Predation by seabirds on schooling pelagic fishes is often compensatory in both the short and long term. The feeding activities of one bird draws the attention of other birds and the number of predators arriving at the site increases in direct relation to the size of the fish school on which they are feeding. Successful feeding by the birds in turn increases survivorship of their young, which means an increase in predators in the next generation, all dependent on the size of the fish resource.

Intercohort cannibalism, in which older fish eat younger age classes, can have a strong density-dependent impact on year class strength. Consider a population with three year classes. A large cannibalistic cohort can depress the numbers of the next, younger cohort. When the younger cohort reaches a size where it is a threat to the third, youngest age

class, reduced numbers in the second age group have relatively little impact, which translates into high survivorship in the third group. In this way, population cycles can be established through the density-dependent effects of cannibalism. Just this type of scenario has been invoked to explain 2-year cycles of abundance in Pink Salmon, *Oncorhynchus gorbuscha*, in the Pacific Northwest (Ricker 1962).

Inverse density dependence is considered **depensatory** because relative predation risk and impact decrease as prey numbers increase. Depensatory predation occurs when a fixed number of predators become swamped or saturated by large numbers of prey. Under such conditions, the proportion of the prey captured decreases as prey numbers increase. For example, an individual salmon smolt that is migrating to the sea reduces its risk of death if it can time its downstream migration to coincide with that of other smolts, since predators take only a small number of migrants. By extension, the proportion of the prey population killed decreases as the population increases (Wootton 1990).

Regardless of the nature of the relationship between predator and prey densities, predation can have dramatic effects on prey population size. It is generally held that most of the mortality in eggs and larvae of species with planktonic young is due to predation, with predators taking >99% of the individuals (Bailey & Houde 1989; see above). When older, fish are still subject to predation, but the threat falls off progressively with increasing age and size, forming what is described as **exponentially declining mortality** (Fig. 24.8). Refuge availability may influence the impact that predators have on later life history stages. Observations and experimental manipulations on coral reefs indicate that prey population density is directly related to the number and availability of holes where prey can hide, which also implies that competition for refuge sites could interact with predation to determine population density and diversity. Several experimental studies on reef fishes have in fact shown that removing predators leads to increased density of prey, reinforcing descriptions of dramatic trophic cascades (see Chapter 25, Indirect effects and trophic cascades). The effects of predator density on prey diversity may follow a similar pattern (Hixon 1991; Hixon & Beets 1993). Regardless, regulation of population size ultimately involves an interplay of competition and predation, often mediated by habitat availability (e.g., Holbrook & Schmitt 2002; Hixon & Jones 2005).

Predation can also affect gene frequencies in populations through the evolution of antipredator adaptations. Guppies in small streams in Venezuela and on the island of Trinidad occur in pools that differ in levels of predation. Upstream areas tend to have few if any predators, often limited to a single topminnow species, *Rivulus marmoratus* (Cyprinodontidae). Further downstream, more predators occur, including a cichlid (*Crenicichla*), a characin (*Hoplias*), and freshwater prawns. In areas of low predation, males tend to have many bright, colorful spots that are attractive to females but are also conspicuous to predators. Spot number, size, and brightness are inherited; the offspring of brightly colored males are brightly colored. In a series of experiments, fish from several populations were exposed to different levels of predation over several generations or transferred between areas with high and low predation intensity. There was a regular decline in spot number, spot size, and spot brightness in populations subjected to more predation both in the field and lab (Endler 1980, 1983). Even the pattern of size-specific predation affected heritable

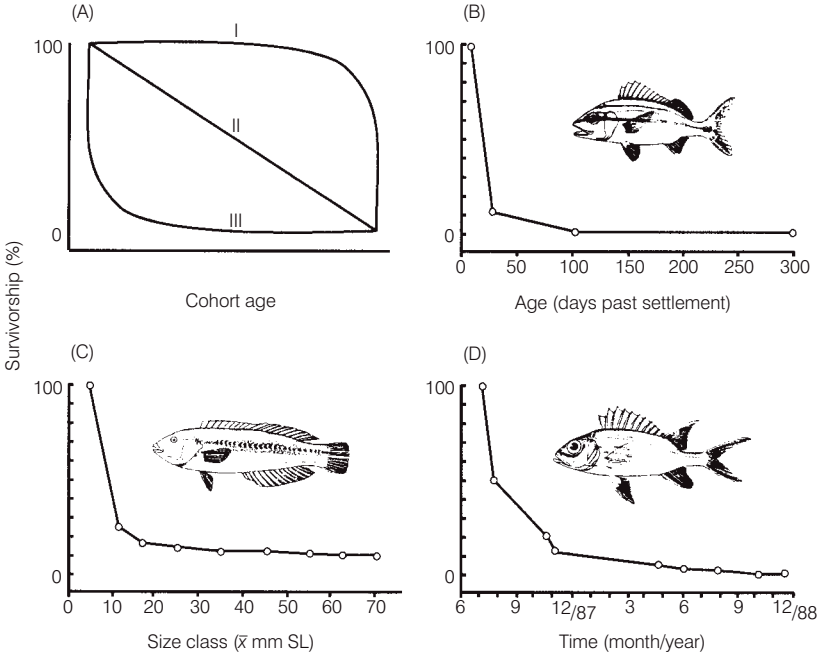

Figure 24.8

Survivorship curves in theory and practice. (A) Three general forms of survivorship (percent surviving at the end of each year or within each age class) are found in natural populations. Because predation tends to be most heavily focused on young and small fishes, populations that display type III survivorship curves are most likely to be regulated by predation, as seen in curves B through D. (B) A grunt (Haemulidae) population in the Virgin Islands. (C) A wrasse (Labridae) population in Panama. (D) A squirrelfish (Holocentridae) population in the Virgin Islands. SL, standard length. After Hixon (1991), used with permission; fish drawings from Gilligan (1989).

traits in a predictable fashion. Where Guppies were exposed to cichlids, which tend to prey chiefly on larger Guppies, Guppies matured later at larger sizes, whereas where the predator was the topminnow, which targets predominantly smaller Guppies, maturation occurred earlier at smaller sizes (Reznick et al. 1990, 1997).

As was pointed out with respect to competition, non-native predators have unequivocal impacts on native fishes wherever they are introduced, having eliminated populations and even species in many locales. Examples abound (see Chapter 26, Introduced predators), but strongest impacts have come from species introduced to improve sport fishing (e.g., Flathead Catfish, Brown and Rainbow trout, Smallmouth and Largemouth black bass, Peacock Cichlid, Nile Perch, Northern Pike and Pikeperch, and even Mosquitofish) (Fuller et al. 1999; Rahel 2002; Helfman 2007).

Synthesis: what determines assemblage structure among coral reef fishes?

Coral reefs contain more species of fishes than any other habitat. Almost 700 shallow water species occur in the Caribbean, and Indo-Pacific reefs are home to more than 3000 species (see Chapter 16, Marine zoogeographic regions). This incredible diversity (plus colorful fishes and clear, warm water) has understandably drawn the attention of fish ecologists and led to some surprisingly emotional controversies. Probably the most divisive debate concerns the maintenance of this high diversity. How does a coral reef support so many different fishes? What determines the number of species and individuals that will occur on a reef? Can one predict what kinds of fishes (both taxonomically and ecologically) will occur on different reefs or on the same reef at different times? Do the processes that determine species abundance and diversity in one tropical ocean apply to reefs in another ocean? These questions have more than theoretical value. Understanding spatial and temporal patterns of recruitment and the factors that determine the success of recruits can influence fisheries management and conservation practices such as seasonal closures, protected area and species protection, and artificial reef design and placement (Beets 1989; Bohnsack et al. 1994; NRC 2001).

These and related topics have nurtured what has become known as the "**stochastic–deterministic debate**". The terms refer to the two general processes affecting the maintenance of diversity. **Stochastic** processes are largely random in operation. An extreme adherent of the stochastic school would argue that chance events affecting planktonic larvae and newly recruited juveniles play too large a role for us to be able to predict species composition. The ocean is a huge place with very little shallow water habitat. A larval fish that was not eaten or that did not starve to death must also be lucky enough to encounter a reef during the brief period when it is **competent** to settle. The larva is also likely to get eaten by zooplanktivorous predators that abound on reefs, and it must finally find a suitable, unoccupied site in which to settle. These chance events, which are further influenced by unpredictable storms (see Chapter 25, Extreme weather), reduce the accuracy with which we can predict the actual species and abundances of fishes that will occur on a specific reef, beyond knowing what occurs in a general geographic region.

An extreme **determinist**, in contrast, would argue that biological interactions such as competition, predation, and symbiosis have led to an evolutionarily fine-tuned assemblage of species. Each species has a well-defined ecological niche that includes competitive, cooperative, and predator–prey interactions with other species. Hence new recruits will become established depending on which residents already occur at a site and which niches are unfilled at a given time (a similar debate has developed around the question of assemblage stability in temperate stream fishes; see for example Grossman et al. (1982, 1985) "versus" Herbold (1984), Rahel et al. (1984), and Yant et al. (1984); reviewed by Strange et al. (1993)).

Few fish ecologists would adhere to either extreme view. The debate, after accounting for differences in methodology and study site, really boils down to an argument as to which phenomenon – chance events or biological interactions – plays the larger role in determining species composition at different locales. Observational and experimental studies in the Caribbean and Pacific, beginning largely with the work of Sale (1978) and Smith (1978), have led to different conclusions. *Observational studies* emphasize comparisons of underwater counts of individuals at several sites in one reef area, or at the same locale at several different times or after a hurricane strikes an area (in the latter situation, one must be "fortunate" enough to have been conducting work at the site before the hurricane struck). *Experimental studies* usually involve removal of individuals from small coral heads or patch reefs, or the addition of small patches of reef habitat followed by monitoring of recruitment and recolonization.

Reef fish assemblages are usually defined in terms of the adults present, but replacement of adults is seldom by other adults. When an adult is removed, either experimentally by a researcher or naturally by a predator, it is usually replaced by a newly settled (**recruited**) juvenile or a slightly older **colonist**. The question of interest then becomes one of whether adult population dynamics are determined by events before settlement (i.e., during the planktonic phase), during recruitment (i.e., by settling larvae), or after recruitment (i.e., due to interactions among juveniles, adults, and their competitors and predators) (Fig. 24.9).

Some workers emphasize the importance of events and interactions in the plankton in determining which species populate a reef (Doherty & Williams 1988; Wellington &

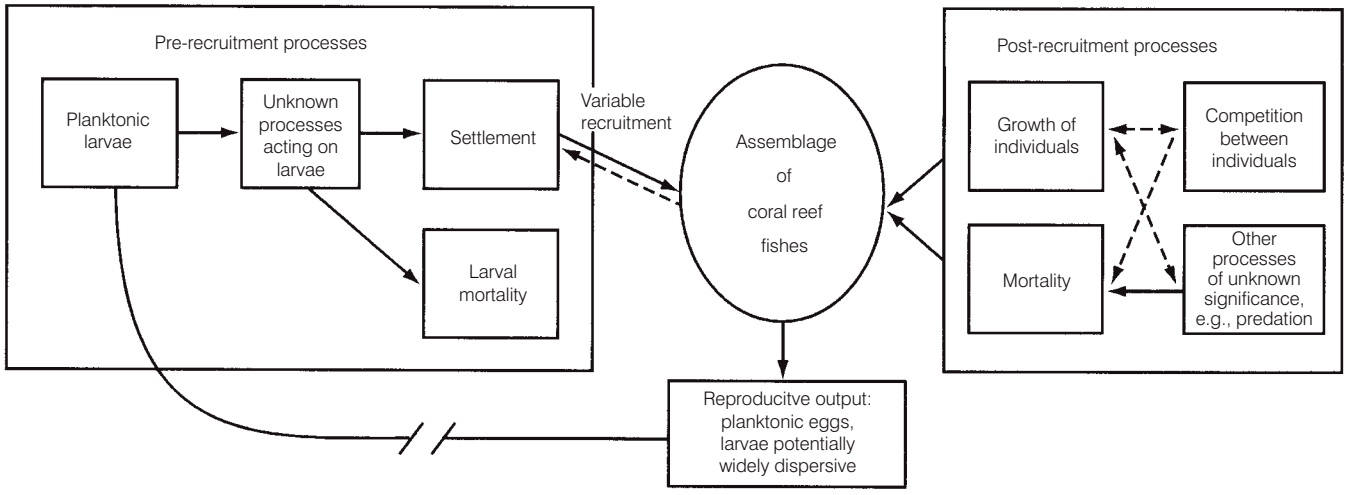

Figure 24.9

The various processes that operate to determine the diversity and abundance of fishes on a coral reef. Solid arrows indicate known interactions, dashed arrows possible interactions; the broken arrow between reproductive output and planktonic larvae refers to the uncertainty that reproduction on a reef may influence the number of recruits returning to a reef. From Mapstone and Fowler (1988), used with permission.

Victor 1988). This view developed from observations of similar, unexploited reefs in close proximity to one another that contained dissimilar species assemblages. Also, experimentally increased food and refuge availability on a reef does not necessarily lead to an increase in fish numbers at a site. Hence reefs may contain fewer individuals than they can theoretically support, i.e., they often exist below their **carrying capacity**. These findings suggest that adult populations may be limited by the number of larvae available to settle in the area, the so-called **recruitment** (or **settlement**) **limitation hypothesis**. Additional evidence of recruitment limitation includes differences in year class strength on a reef and the rarity of larvae of some species.

The alternative view – the **habitat limitation** or **interactive hypothesis** – proposes that appropriate habitat is limiting or that postsettlement biological interactions (predation, competition) determine the kinds and abundances of fishes on a reef, regardless of larval abundance. The habitat-limited or interactive scenario depicts a reef at carrying capacity, one that is less able to replace fish removed through fishing. Evidence includes superabundant larvae around reefs, reefs packed with recruits, and rates of predation that exceed 99% during the first year postsettlement (e.g., Shulman & Ogden 1987; reviewed in Roberts 1996; Hixon 1998; Hobson et al. 2001; Levin & Grimes 2002).

Many factors can affect larval abundance, regardless of numbers or habitat availability. These include predation on larvae by vertebrate and invertebrate planktivores, food availability for larvae, and dispersal away from appropriate settling areas. It is well known that mortality is the most likely fate awaiting a planktonic larva; most studies estimate that more than 99% of larvae die or are eaten before they settle (see above, Life histories and reproductive ecology). Thus antipredator, food-getting, and active dispersal adaptations of larvae themselves may be critical. Adults can also improve their offspring's chances of making it through the planktonic filter by spawning at times and places that minimize dispersal away from home reefs, which reduces the area over which larvae must search for an appropriate settling habitat. Carefully chosen spawning locales can also place larvae where planktonic food tends to be concentrated (but also where predators on planktonic fish larvae also abound) (Johannes 1978).

Periodically, vast numbers of larvae that are ready to settle can be found around reefs, indicating that habitat limitation can in fact be important at times (Victor 1991; Kaufman et al. 1992). Under such circumstances, conditions that prevail in the settlement area may determine the success of recruits and the ultimate species composition in an area. Several studies have shown that small artificial reefs placed in shallow water attract large numbers of recently settled larvae to areas that were previously devoid of larvae, suggesting that appropriate, unoccupied habitat can limit recruitment. But regardless of habitat availability, previous occupation of the habitat, known as **priority effects**, may be crucial in determining whether larvae settle successfully. If the first occupants of a coral patch are herbivores or small planktivores, a variety of larvae will follow and take up residence. However, if the first settlers are predators such as moray eels, squirrelfishes, grunts, snappers, or groupers, later recruitment will be greatly reduced as these small predators eat incoming fish larvae (Beets 1997; Tupper & Juanes 1999) (Fig. 24.10). Which larvae settle first is governed largely by chance because of the unpredictable nature of planktonic existence. Once larvae settle, their impact on later settlers is fairly predictable and depends

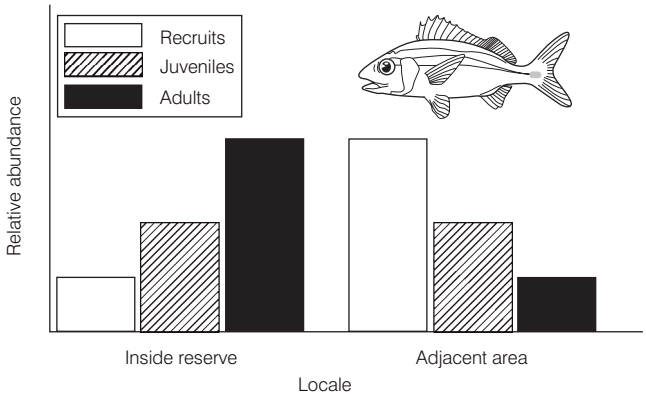

Figure 24.10

Priority effects. The foraging behavior of species that settle into an area determine the success of later arrivals. In the Barbados Marine Reserve, adult grunts (dark bars) were much more abundant inside the reserve than in adjacent, non-reserve areas, but recently settled grunts (open bars) were more abundant in adjacent than in reserve habitat. Juveniles (crosshatched bars) were equally abundant inside and outside the reserve. Lack of recruits in the reserve was thought to be the result of predation on settling larvae by resident adult grunts. Data from Tupper and Juanes (1999); grunt drawing from Gilligan (1989).

on the ecological role of the species in question. Hence both stochastic and deterministic forces are in operation (Shulman et al. 1983; Hixon & Beets 1989; Beets 1991).

A growing body of knowledge has changed our perception of larval life and behavior. The classical view was of passive larvae carried by ocean currents, settling when they reached some critical stage of competency. If a larva happened to be over appropriate habitat at that stage, its chances were good. If it was somewhere less favorable, such as over great ocean depths, then it was game over. We now know that larvae are much more active than this in their settling activities (see Chapter 9, Getting from here to there: larval transport mechanisms). Larvae are attracted to reef areas by both sounds and smells emitted by reefs, and move actively toward appropriate stimuli (Atema et al. 2002; Kingsford et al. 2002; Tolimieri et al. 2004; Gerlach et al. 2007). Once over a reef, larvae (or more accurately **transitional juveniles**) show strong habitat preferences that differ among species; some larvae will settle and then ascend back into the water column if conditions are inappropriate. Larval settlement is therefore not a parachute drop but more of a bungee jump (Kaufman et al. 1992; Lecchini 2005). Maintenance of high diversity on a reef demands protection of not just adult habitats but also of settlement habitats, which are often different from and far removed from adult habitats.

A larva that settles successfully onto a patch of reef and transforms into a juvenile is by no means guaranteed a long and productive life. Biological interactions involving predation, competition, and cooperation, and their interactions, can have a strong impact on individual success. Mortality rates remain high once larvae have settled; 25% of recruits may die in the first 5 days after settlement, but this rate falls to <10% after 6 days and continues to decrease thereafter (Doherty & Sale 1986). Although the rate may slow, the numbers killed remains high, varying between 65% and 99.9% during the first year after settlement (Sweatman 1984; Shulman & Ogden 1987). Mortality may also be density dependent, increasing as population size increases, as happens when large numbers of juvenile humbug damselfishes, *Dascyllus* spp., actively compete for preferred nighttime resting locales among branching corals. Less aggressive individuals are displaced to riskier locations, where they are subject to predation by crepuscular/nocturnal predators such as squirrelfishes. Again, diversity maintenance on a reef requires protection of both daytime feeding and nighttime resting habitats, which again may differ (Holbrook & Schmitt 2002; see also Hixon & Carr 1997).

Larvae may settle more successfully in isolated habitats away from major concentrations of larger fishes and then move later to the more extensive reef habitats. This may be one reason that back-reef areas, mangroves, and seagrass beds are often the preferred habitat for the juveniles of many "reef" species (Manson et al. 2005; Adams et al. 2006; Pollux et al. 2007). The move to the reef itself is also full of perils, as predators tend to patrol the edges of reefs and catch prey moving across refugeless zones (Shulman 1985a, 1985b). For species that have symbiotic relationships with invertebrates, such as anemonefishes, carapid pearlfishes, cardinalfishes, and many gobies, successful location of an unoccupied, species-specific host is probably a good guarantor of survival, but such hosts may be in limited supply. An added complication is the cannibalism that occurs if the species-specific host is already occupied by an adult of the larva's species (e.g., Tyler et al. 1992; see Chapter 22, Mutualism and commensalism).

One possibly influential difference between major oceans is the size of the eggs produced by residents (Thresher 1982). On average, egg sizes are smaller in the western Atlantic than the western Pacific. Smaller eggs imply greater fecundity among Atlantic species, which could lead to greater reproductive output in the western Atlantic. Assuming comparable larval mortality rates, more larvae mean more potential competition for space among recruits, tipping the scales in favor of a stronger role for deterministic interactions among Atlantic coral reef fishes than their Pacific relatives.

The bottom line to this discussion is that arguments about the relative importance of stochastic and deterministic factors and their influences on reef fish assemblage structure and dynamics oversimplify the situation. Both types of factor come into play and have different levels of influence at different times and in different places. Random events in the plankton undoubtedly influence which larvae will survive, and whether the larva settles successfully

depends on whether space is available for it on the reef. Space becomes available in part as a chance result of predation and storm disturbance. But larvae, juveniles, and adults often have specific habitat preferences, as shown by the fairly distinctive zones that occur on most coral reefs (lagoonal, patch reef, back reef, reef crest, shallow and deep reef front) and the fairly predictable assemblages of species found in each zone (e.g., Nanami et al. 2005; Ashworth et al. 2006). Non-random competitive, predatory, and mutualistic interactions affect the suitability of a site, the survivorship of its inhabitants, and ultimately its availability for new recruits and colonists. Space availability may depend on the guild of a fish that has been removed from the reef. We can predict that certain guilds are likely to be present on a reef, but we cannot predict which members of that guild will be present. The importance then of the different factors is going to vary from time to time and place to place.

Summary

SUMMARY

1. Ecology focuses on organism–environment interactions at the level of individuals, populations, assemblages, communities, ecosystems, and landscapes. An individual's life history results from differences in the allocation of energy and resources to the often-conflicting demands of maintenance, growth, reproduction, survival, and migration.
2. Large size is advantageous in fishes; larger fishes produce more eggs and escape more predators. Reproduction at an early age and small size incurs a substantial cost in future reproduction; delayed reproduction means more eggs spawned but occurs at the risk of dying before ever spawning. Theory accurately predicts the effects of mortality on reproductive age, size, interval, and allotment; individuals in populations with high adult mortality reproduce earlier and have higher fecundity and shorter reproductive intervals.
3. Populations grow and decline as a result of age-specific reproduction and survivorship rates. Because of dispersing larvae, migration into populations (recruitment and colonization) has a strong influence on year class strength. Different age fishes differ substantially in size and feeding habits, making cannibalism a frequent cause of mortality. Production is a measure of how much biomass a population produces yearly and is important in determining sustainable exploitation rates for commercial fishes. Most fish populations produce <10 g/m^2/year, most of which occurs in younger age classes.
4. Many populations are relatively isolated from other populations of the same species, which allows for genetic differentiation. Genetically distinct populations can exist in neighboring lakes (e.g., whitefishes, sticklebacks), and Pacific salmons occur as genetically isolated stocks in adjacent rivers. Genetic differences without apparent geographic separation occurs within populations of Arctic Char. In contrast, hybridization between species results when species-specific spawning habitat is unavailable or degraded, or when disproportionate numbers of one species exist. Hybridization is more common among freshwater fishes.
5. Species generally have relatively predictable habitat use patterns and predator–prey and competitive interactions (= niche). Species that utilize similar resources in similar ways are members of a guild, as in the zooplanktivore and cleanerfish guilds on coral reefs. Niches and guild memberships change as fish grow and their food and habitat preferences change. Two general aspects of habitat use in fishes is that bigger individuals within a species occur in deeper habitats and that habitats in rivers and the species occupying them differ as one moves downstream.
6. Competition within and between species results when two consumers use a limiting resource. Shifts in resource use due to competition result in resource partitioning. Competition for food resources is most common in fishes, which can lead to dramatic habitat shifts and can also influence predator–prey interactions. Differences in resource use do not automatically imply that competition is occurring; physiological requirements, phylogenetic constraints, and differential susceptibility to predation can also produce species differences in resource use. Introduced species frequently have strong, deleterious, competitive impacts on native species.
7. Predation can directly affect prey density through predator-caused mortality, or can have indirect effects through predator avoidance that places prey in suboptimal environments, thereby slowing individual growth and reproductive output. Predation can also cause genetic differences in coloration, habitat use,

and schooling and breeding behavior. Introduced predators have decimated natives in many locales.

8 The incredible diversity of coral reef fishes has fueled a debate over the relative importance of the physical environment versus biological interactions as determinants of how many and what kinds of fishes occur on any one reef. Much of the debate focuses on whether adult populations are determined by larval mortality (recruitment limitation) or by events occurring after recruitment, such as predator–prey and competitive interactions among juveniles and adults. It is likely that all factors contribute and that their relative importance differs temporally and spatially.

Supplementary reading

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Chapter 25

Communities, ecosystems, and the functional role of fishes

Chapter contents

CHAPTER CONTENTS

Ecology textbooks differ in their approach to communities *versus* ecosystems, treating them either as separate entities or dealing with one as a subset of the other. A **community** is by definition the plant and animal assemblages that live together in an area. This area may include arbitrarily determined boundaries based on geopolitics but not recognized by organisms (e.g., the marine communities of Florida or Kaneohe Bay, Hawaii) or may involve biologically relevant boundaries across which few fishes pass (Lake Tahoe, the Chattahoochee River). An **ecosystem** consists of the biotic community and the abiotic environment with which the community interacts. Hence one can talk about a stream ecosystem, a lake ecosystem, or an intertidal or offshore reef ecosystem. At a larger spatial scale, one can think in terms of **watersheds**, which take into account the land from which water flows into a series of streams and eventually into a lake or river, and the hydrological, geological, and biological forces at work there. The next level of organization is the **landscape** or **riverscape**, which recognizes interactions and linkages among ecosystems and the influence of human activities on these interactions (e.g., Schlosser 1991; Fausch et al. 2002). Traditionally, community ecology has focused on biotic interactions among different taxonomic groups and the effects that such interactions have on distribution and abundance. Ecosystem ecology has focused more on the flow of energy, nutrients, and materials among components of the ecosystem and the functional roles that plants and animals play in this exchange.

Community-level interactions between fishes and other taxonomic groups

Fishes do not restrict their ecological interactions – chiefly competition, predation, parasitism, and symbiosis – to other fishes. Evolved, fitness enhancing or reducing interactions are also common between fishes and other taxonomic groups, ranging from plants and invertebrates to other vertebrates. Often these interactions and their influences are relatively direct, e.g., through eating and being eaten. But some dramatic effects – such as changes in habitat use, food types, life history traits – take place through fairly indirect means, either incidental to or several steps removed from the activities of the fishes involved.

Competition

Fishes compete with a variety of organisms for food and space. Bluefish (*Pomatomus saltatrix*) and common terns (*Sterna hirundo*) have a complex feeding relationship that involves both commensalism and competition and that may be applicable to many other fish–bird interactions (Safina & Burger 1985). Both species feed on anchovies and Sand Lances. The seabirds are particularly dependent on prey fish during the early summer breeding season when they must meet their own energetic demands as well as those of their growing chicks. Off Long Island, New York, Bluefish

arrive in large numbers around mid-July each year as part of their annual migration (see Chapter 23, Oceanodromy). A commensal relationship exists between the Bluefish and terns in that the feeding activities of Bluefish drive prey up in the water column, concentrate them in space, and indicate the whereabouts of prey to the seabirds, all of which facilitate prey capture by the terns. However, newly arrived Bluefish consume large numbers of prey fish, which rapidly depresses the prey resource. Any birds that initiate breeding after the arrival of the Bluefish tend to be unsuccessful. Hence Bluefish may be significant competitors with terns and may have been a strong selective force in determining the timing of reproduction by the terns.

Predation

A wide variety of non-piscine predators are dependent on fishes as a major component of their diets. Numerous invertebrate predators capture fishes. Predaceous waterbugs (Belostomatidae) and dragonfly (Odonata) larvae prey on small freshwater fishes. Marine invertebrate predators are common, including jellyfish, anemones, siphonophores, squid, dwarf triton and cone snails, and crabs (e.g., Laughlin 1982; Bouchet & Perrine 1996). Among vertebrates, reptilian predators include turtles, crocodilians, varanid monitor lizards, a few iguanid lizards, and sea and water snakes; mammals include mink, raccoons, otters, seals, sea lions, bears, dolphins, whales, bats, and, of course, humans. Amphibian predation on fishes is poorly documented, although sirens, bullfrogs, and a few other large frogs (*Pipa*, *Xenopus*) are known to be fish predators, including the impacts of introduced species on endangered fishes (e.g., Lafferty & Page 1997). A host of seabirds concentrate on fishes, including terns, petrels, albatrosses, gannets, auks, murres, cormorants, skimmers, spoonbills, pelicans, penguins, and gulls. In fresh waters, osprey, eagles, loons, mergansers, goldeneye ducks, kingfishers, herons, egrets, and storks are a few of the birds that eat fish, often to the birds' detriment when the fish are in aquaculture facilities and "predator control" is put into practice. All of these non-fish groups have served as selective agents on the behavior and ecology of fishes, causing evolutionary adjustments in growth and reproductive traits that have allowed fish to thrive despite sometimes astronomical mortality rates. Many fishery-related problems arise from "unnatural" predation by humans and the evolutionary responses of fishes to such predation (see Chapter 26, Fishing as an evolutionary force).

The impact of non-fish predators on fish populations and behavior can be substantial. In the Au Sable River, Michigan, mortality of adult Brook and Brown trout averaged 70–90% annually, most of which was from predation. Non-fish and non-human predators (mergansers, heron, kingfisher, mink, otter) accounted for 28–35% of this mortality (Alexander 1979). When the potential threat of predatory birds is combined with that from piscivorous fishes, it is not surprising that the distribution of many prey species reflects the foraging locales of their predators (Fig. 25.1). This combined threat can include a third dimension during the breeding season. Male Dollar Sunfishes (*Lepomis marginatus*) construct nests in shallow water to avoid predatory fishes that are typically in deeper water. The males, however, must repeatedly abandon their nests to avoid being captured by herons and kingfishers. Each time the male flees, eggs and young in the nest are subject to predation by small fishes, forcing the male into a trade-off between the conflicting demands of protecting himself and protecting his offspring (Winkelman 1996).

Fishes also fall prey to less obvious but more insidious predators. Massive fish kills have long been attributed to **harmful algal blooms (HABs)** and especially dinoflagellate blooms ("red tides") in many nearshore marine areas, but fish death has usually been considered an incidental byproduct of a bloom, via such effects as insufficient oxygen concentrations or the toxicity of secondary plant chemicals. More recent events implicate an evolved, predatory response involving a dinoflagellate, *Pfiesteria piscicida*, and closely related forms, that has a life cycle of 20 or more flagellated, amoeboid, and cyst-like stages depending on environmental conditions, including the presence or absence of fish and fish byproducts in the water (Barker 1997; Burkholder & Glasgow 2001; Burkholder 2002). Resting cysts of the dinoflagellate are stimulated to break open in the presence of chemicals exuded by fish. The vegetative cells released from the cysts produce a neurotoxin and other substances that can kill fish in a matter of hours. The toxin induces immobility and death in fish; later-produced amoeboid cells and zoospores feed on the moribund and dead fish. Many dead and dying fish associated with *Pfiesteria* have ulcerated lesions (Fig. 25.2, inset). Skin sloughs off the dying fish and is attacked by the dinoflagellates, which then reproduce rapidly, leading to a massive fish kill; 1 billion Menhaden died during an episode in North Carolina's Neuse River estuary in 1991.

When a fish population declines to some level where the cyst-breaking chemical trigger is no longer sufficiently concentrated, the dinoflagellates return to the encysted form. Hence **density-dependent population regulation** of fishes could occur through the population responses of a microscopic predator. Increasing frequencies of *Pfiesteria*-caused fish kills correspond to increasing concentrations of human and agricultural waste-water (Fig. 25.2). One fish kill in the Neuse River estuary, North Carolina, in 1995 followed shortly on the heels of a major swine effluent spill, during which approximately 1×10^8 L of raw hog sewage was discharged from a ruptured, upstream, sewage lagoon (Burkholder & Glasgow 2001). Not only fish can be affected by *P. piscicida*; lesions and other pathological symptoms – including blurred vision, erratic heartbeat, and memory loss – can also occur in humans.

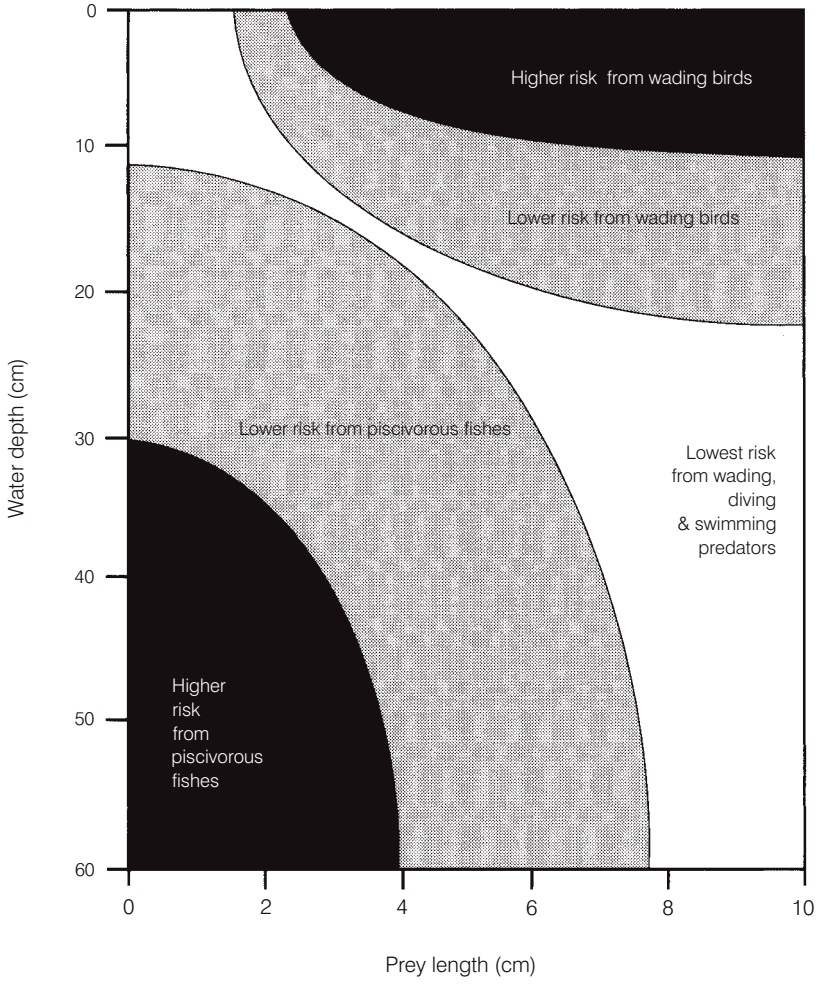


Figure 25.1

The distribution of prey fishes in shallow streams reflects the risk of predation from various sources. Piscivorous fishes, which are gape-limited, present the greatest threat in deeper water. Wading birds, which can dismember prey and are therefore not gape-limited, present the greatest threat in shallow water. Small prey fishes are safest in shallow water because they can hide from birds among structure, whereas larger prey fishes cannot fit into small spaces. However, larger prey are safer in deeper water because many predators cannot swallow them whole. Adapted from Power (1987).

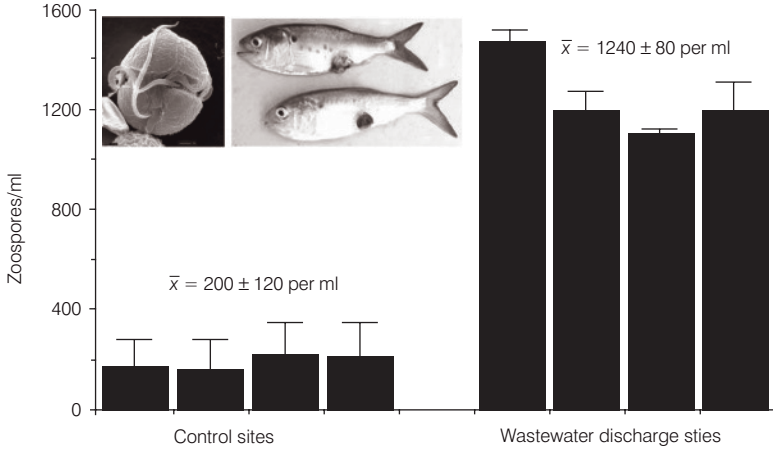


Figure 25.2

Growth of the predatory dinoflagellate, *Pfiesteria piscicida*, relative to nutrient conditions. Water samples from North Carolina show the dramatic increase in *Pfiesteria* zoospores within 100 m of wastewater discharge sites, where phosphorus and nitrogen compound concentrations exceeded 100 ppb. Left inset, a *Pfiesteria* zoospore. Right inset, deep focal lesions on Menhaden taken from a *Pfiesteria*-induced fish kill, Pamlico estuary, North Carolina. From Helfman (2007), after Burkholder and Glasgow (1997), used with permission; insets courtesy of North Carolina State University Center for Applied Aquatic Ecology, www.waterquality.ncsu.edu.

Parasitism

The previous example points out the difficulty of distinguishing predators, which consume most of their prey, from parasites, which consume only a small portion of their prey. All fishes have parasites, external and internal, with a great degree of host specificity (e.g., Bush et al. 2001; Combes 2001). Life cycles are complex and attachment sites are diverse, as in the 6 cm long copepod *Ommatokoita elongata* that anchors itself in the corneas of 6 m long

Greenland Sleeper Sharks, *Somniosus microcephalus*, commonly resulting in blindness (Borucinska et al. 1998). Parasite–host relationships often involve co-evolved responses (see Chapter 22, Interspecific relations: symbioses). One particularly bizarre relationship exists between fishes and parasitic isopods in the family Cymothoidae. These isopods are frequently observed on the heads and in the gills of numerous reef fishes. However, under some circumstances, the isopod attaches to the tongue of its host, causing the tongue to degenerate to a small stub (either through direct consumption or constriction of blood supply). Fish tongues lack skeletal musculature and are not protrusible, unlike in other vertebrates. Instead they fill the lower part of the mouth, covering the basibranchial and basihyal bones and serve the mechanical function of holding food against the vomerine and palatine teeth during processing. When the isopod *Cymothoa exigua* attaches to and destroys the tongue of the Spotted Rose Snapper (*Lutjanus guttatus*), it resembles the shape and size of the fish's tongue and occludes with the vomerine teeth when the fish feeds. Snappers with the isopod in place for extended periods are typically in good condition, with full stomachs and accumulated fat, which is often not the case for fish that have cymothoid isopods attached to their gills. In essence, the parasite functions as a prosthetic replacement tongue, allowing its host to survive normally and hence continue to provide the parasite the nourishment it needs for its own successful reproduction (Brusca & Gilligan 1983).

In the context of community relationships, parasitism can have profound effects on relationships among species, affecting the outcome of predator–prey and competitive interactions. In the lab, Prussian Carp, *Carassius auratus*, infected with metacercariae of the digenean *Posthodiplostomum cuticola*, were eaten more often by Perch, *Perca fluviatilis*, compared to nonparasitized carp, probably because parasitized individuals were in poorer condition and were visually conspicuous due to the presence of black spots associated with digenean infections (Ondrackova et al. 2006). Parasitism can also interact with availability of and competition for refuges to cause higher mortality in infected fish. When Bridled Goby, *Coryphopterus glaucofraenum*, were experimentally infected in the field with a copepod gill parasite, goby survival declined as a combined function of goby density, parasite occurrence, and refuge availability (Forrester & Finley 2006). The decline was steeper for parasitized gobies in reef habitats with fewer refuges than for unparasitized gobies in similar circumstances. Parasitism and a shortage of refuges jointly influenced the strength of density-dependent mortality in this reef fish, an interesting finding given that nocturnal refuges may be important in minimizing infection by other, nocturnally attacking fish parasites (e.g., Sikkel et al. 2006).

Parasites that infect fishes alter behavior (Barber et al. 2000). Some behavioral changes can facilitate transmission of the parasite to its final host. Killifish, *Fundulus parvipinnis*, are an intermediate host for trematodes. Killifish infected by larval trematodes alter their swimming behavior in ways that make them more conspicuous to bird predators, their definitive host. Parasitized fish in the field were 10–30 times more likely to be eaten than unparasitized fish (Lafferty & Morris 1996). Humans may be the ultimate host. The human diseases of schistosomiasis and opisthorchiasis are transmitted via fishes as intermediate hosts. Snails are an initial intermediate host for schistosomes. The snails are eaten by fishes, such as molluskivorous cichlids in Africa's great lakes, which are then eaten by humans (Evers 2006). Numerous cyprinids in Thai waters feed on snails that harbor the trematode metacercariae larvae of the liver fluke that causes opisthorchiasis, the most prevalent food-borne parasitic disease in Thailand (Kumchoo et al. 2005).

Parasites have gone to great lengths to find intermediate hosts, including capitalizing on symbiotic relationships among fish species. Cleaning behavior is a highly evolved mutualism on coral reefs, performed by juveniles of some species and best known among adult wrasses, particularly in the cleaning-specialist genus *Labroides* (see Chapter 22, Mutualism and commensalism). Digenean bucephalid trematodes have a complex life cycle usually involving at least a snail and a snail-eating fish as intermediate hosts, with a piscivorous fish as the definitive host. Adult bucephalids generally only occur in piscivores, the larvae having been ingested incidentally as a consequence of feeding on fish prey. However, recent surveys of labrids have shown that cleaner wrasses, especially *Labroides* spp., have incidences of bucephalid infection of 50–100%. The likely route of transmission is direct, the cleaners having ingested bucephalid larvae in the process of cleaning parasites from host fishes (Jones et al. 2004). The parasite has evolved a new route for transmission, exploiting the host–cleaner relationship in cleaning symbiosis.

The effects of fishes on plants

The activities of herbivores are usually divided into browsing versus grazing, which are different feeding modes that affect plants differently (Horn & Ferry-Graham 2006). **Browsing** involves removing parts of the plant on which the fish is feeding, such as the tips of leaves or the leaves themselves (e.g., Silver Dollar characins, many cichlids, damselfishes). **Grazing** involves biting the plant off at the substrate and even taking in some of the substrate itself, as in the case of parrotfishes that scrape coral surfaces in the process of eating algae. The ecological impacts of fishes on plants also vary among habitats, affecting plants by altering biomass, productivity, growth form, and species composition, by dispersing seeds, and by causing changes in the

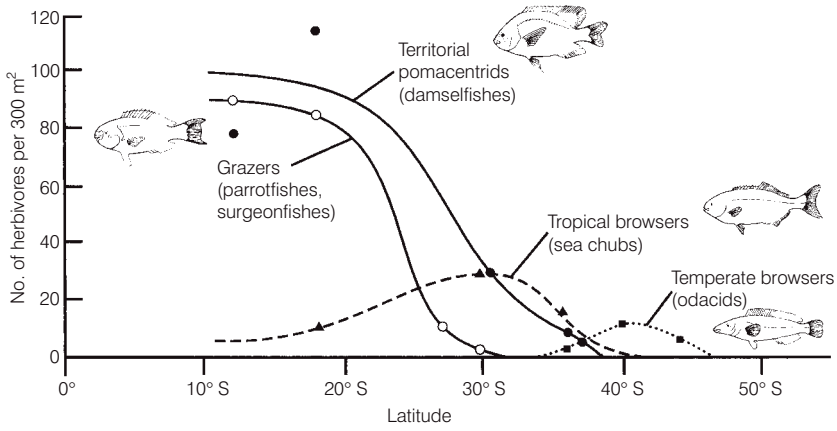


Figure 25.3

Relative numbers and types of herbivores as a function of latitude. More species and types of herbivores inhabit coral reefs than occur at higher latitudes, although browsing prevails at higher latitudes. Values shown are based on southern hemisphere comparisons, particularly Australia and New Zealand. However, the same or ecologically similar groups and numerical trends hold for northern hemisphere assemblages, e.g., sea chubs have temperate representatives in California (Halfmoon, Opaleye) and pricklebacks are functionally similar to aplodactylids. Exceptions may include the temperate east coasts of North America and southern Africa, which have relatively more browsers among the porgies (e.g., Hay 1986). Redrawn from Choat (1991), used with permission.

allocation of energy to vegetative versus reproductive structures.

Herbivory is variably developed in different communities. Latitude appears to be the greatest determinant of herbivore diversity. Above 40° north or south, herbivores are rare or lacking in marine and freshwater fish assemblages (**herbivory** is variously defined by different authors, but generally it means that a fish's diet consists of at least 25–50% plants). Herbivorous fishes are most diverse, are usually most dense, and make up a larger percentage of the assemblage in tropical than in temperate habitats. The number of species, relative abundance, and absolute density of herbivorous fishes often increases with decreasing latitude in a region (e.g., Floeter et al. 2004, 2005). Fewer than 25% of the species in a temperate stream are herbivorous, whereas 25–100% of the species in a tropical stream may be herbivorous. Temperate marine habitats contain 5–15% herbivorous species, whereas 30–50% of the species in coral reef assemblages are herbivorous (Horn 1989; Wootton & Oemke 1992) (Fig. 25.3). High-latitude herbivores exist, but their feeding behavior reflects the seasonal availability of plant material. At least one Antarctic icefish (*Notothenia neglecta*) eats macroalgae and diatoms during spring and summer, and switches to carnivory in fall and winter (Daniels 1982). Why herbivorous fishes, and fishes that rely on low-energy food sources such as detritus (e.g., mullets) are more common at lower latitudes remains a matter of conjecture. Explanations include the seasonal nature of the food source, the energetics of extracting carbon from low-energy food sources at low temperatures, and the biogeography of herbivorous taxa (e.g., Harmelin-Vivien 2002; Floeter et al. 2005). Comparative studies across latitudinal gradients, such as those of Ferreira et al. (2004) and Floeter et al. (2004), need to be conducted in other regions and habitats.

Tropical communities

In *tropical streams*, the most common families containing herbivores are minnows, characins (particularly several piranha relatives), and cichlids, and to a lesser extent catfishes, livebearers, and gouramis (Goulding 1980; Lowe-McConnell 1987). In Panama, experimental manipulations have shown that algal biomass is reduced by the feeding activity of loricariid catfishes in both shallow (<20 cm) and deep habitats. When algal-covered rocks are transplanted from shallow regions where biomass is usually higher to deeper regions, the algae are quickly cropped by catfishes. When the catfishes are removed, algal growth is similar at both depths. Higher standing stocks of algae are maintained in shallows because predatory birds limit the feeding activity of the catfishes there (Power et al. 1989; see above). Work in Costa Rican streams with a fish assemblage of at least 13 species that eat plants suggests that fishes consume a significant fraction of the **macrophytes** (a general term for rooted aquatic plants), algae, and grasses, as well as the leaves that fall into the stream (Wootton & Oemke 1992; see below for a discussion of seed consumption and dispersal in tropical streams).

Continuous consumption of **periphyton** (the algal covering on rocks) and leaves may have a strong effect on the development of an aquatic insect fauna. *Temperate streams* typically have a much more diverse assemblage of aquatic insects than do tropical streams; many of these insects live

in and feed on periphyton and leaves. The diversity and activities of herbivorous fishes in tropical streams may keep these resources at levels too low to permit the development of a diverse fauna of herbivorous aquatic insects, despite the incredible diversity of terrestrial insects in the tropics (e.g., Flecker & Allan 1984).

It is in *tropical river systems* that the role of fishes in dispersing seeds is best known. Fruiting of many trees coincides with the annual or semiannual flooding of the rivers (see Chapter 23, Seasonal patterns). Hence fishes gain access to the base of the trees, or trees gain access to the water. In South and Central America, fruits and seeds that fall into the water are consumed by several characoid fishes, such as Pacu (*Colossoma* spp.) and *Brycon guatemalensis*, and constitute the major part of the diets of these fishes during those periods. Fruits and seeds of at least 40 different tree species are eaten by fishes in the Rio Machado region of the Amazon. Although some fruits and seeds may be killed by digestive processes, many seeds pass through the gut unharmed; germination may even be aided by the time spent in a fish's gut. In the case of *Brycon* feeding on the seeds of a common riparian fig tree, no loss in germination occurred. Importantly, seeds remained in the fish's gut for 18–36 h, during which time some fish moved several kilometers. Hence consumption by fishes may aid dispersal of the tree's seeds, including dispersal in the otherwise unobtainable upstream direction (Goulding 1980; Agami & Waisel 1988; Horn 1993).

Tropical lakes have a large number of herbivorous fishes, particularly among the minnows, characins, catfishes, and cichlids. Phytoplanktivorous fishes can affect the relative abundances of phytoplankton species, even though a large fraction of the ingested phytoplankton cells may pass through a fish's gut unharmed (Miura & Wang 1985). Some cichlid species engage in **suspension feeding**, whereby they pump water into their mouth and out their gill openings, filtering out different size prey. In Blue Tilapia, *Tilapia aurea*, particles larger than 25 μm are retained by the gill rakers and by mucus-covered microbranchiospines on the gill arches; smaller particles pass through. In experimental ponds, large phytoplankton species are filtered out of the water and smaller species come to dominate and even increase in numbers. Small phytoplankters may thrive because of nutrient enrichment due to fish excretion and also because fish filter out zooplankton (rotifers, water fleas) that prey on the phytoplankton (see below).

Interactions between plants and fishes are probably best known on *coral reefs*, where herbivory has led to antiherbivore adaptations in plants and in turn to adaptations by fishes to overcome plant defenses (Choat & Clements 1998; see Fig. 25.3). Herbivore densities on reefs average 0.5 fish/m^2, as compared to 0.1 fish/m^2 in most temperate marine habitats. These values do not include the abundant sea urchins, snails, and microcrustaceans that also feed on reef plants (Horn 1989). Reef fishes affect plant biomass, productivity, species composition, distribution, and growth form; whether coral reef fishes distribute reproductive products is apparently unknown. Resident herbivorous fishes can consume most of the daily productivity of the algae on a reef and in the process stimulate higher production rates in cropped algae than in uncropped algal turfs (Carpenter 1986; Klumpp & Polunin 1989). Algae respond via adaptive changes in growth form. Algae subjected to cropping assume lower, spreading shapes, whereas an absence of herbivores leads to upright, foliose growth forms of the same species (e.g., *Lithophyllum* and *Padina*).

Defensive responses also commonly involve mechanical or chemical adjustments. Plants may be leathery or rubbery (e.g., *Sargassum*), or even hard, as in the case of coralline algae. Seaweeds also produce a variety of so-called "secondary compounds", usually halogenated terpenoids, which are distasteful to fishes; more than 20 such compounds have been isolated from marine algae (e.g., caulerpenyne from *Caulerpa*, halimedatrial from *Halimeda*, and several dictyols from *Dictyota*). Freshwater fishes also avoid plants with abundant phenolic compounds (Lodge 1991). Some tropical plants respond both mechanically and chemically, such as the green alga *Halimeda*, that deposits calcium carbonate in its tissues and also produces distasteful chemicals. Some plant species always possess such defenses, whereas others produce secondary compounds in direct response to recent herbivore activity. Most algae with such noxious properties are generally avoided by herbivorous fishes, although some fish species appear to specialize on particularly tough or chemically defended plant species. Sea chubs prefer brown seaweeds such as *Dictyota* that contain dictyols and are generally avoided by most other reef fishes (Horn 1989; Hay 1991).

A possible antiherbivore adaptation may be the production of **ciguatera** toxins, a class of substances that was first noticed because of its effects on humans. When a person eats a **ciguatoxic** fish, adverse reactions include a variety of gastrointestinal, neurological, and cardiovascular symptoms, including reversal of sensations (e.g., ice cream feeling hot) and possibly death from respiratory failure. Over 400 species of reef fishes have been implicated in ciguatera poisoning, but the most lethal sources have been large predators such as moray eels, groupers, snappers, and barracuda. These circumstances suggested that the ciguatera toxin was **magnified** as it passed through the reef food chain. Extensive research has verified that the toxin or toxins originate in unicellular dinoflagellates, primarily in the genera *Gambierdiscus*, *Ostreopsis*, and *Prorocentrum* (Landsberg 2002). These dinoflagellates grow as epiphytes on common reef macroalgae or on newly exposed coral surfaces, as occurs when reefs are disturbed during dredging, blasting, and ship anchoring. Herbivores ingest the dinoflagellates directly or indirectly when consuming plants. Herbivores such as parrotfishes and surgeonfishes can also be ciguatoxic. The toxin is apparently not broken down by

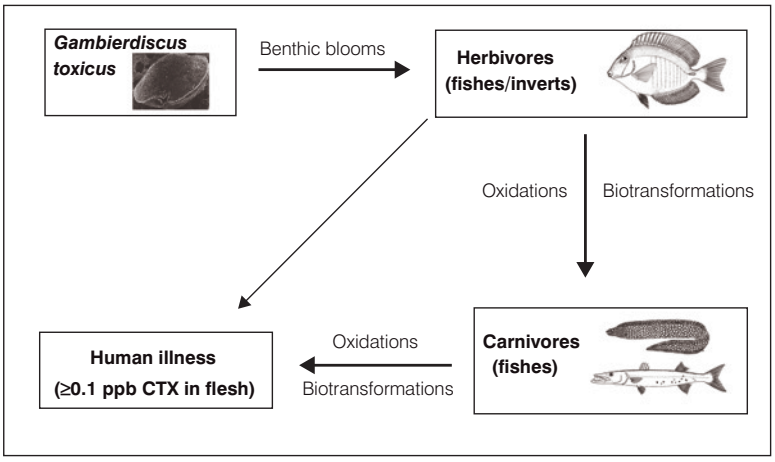


Figure 25.4
Food webs involving ciguatera fish poisoning in a reef community. Top predators, including humans, are affected because a single meal can contain significant amounts of a highly potent neurotoxin. *Gambierdiscus toxicus* is the dinoflagellate implicated in most ciguatera poisonings. CTX, ciguatera toxin; ppb, parts per billion. From Helfman (2007), after Lewis 2001; inset photo courtesy of the Florida Marine Research Institute, www.floridamarine.org.

the herbivore and hence predators high in the food chain obtain a prey fish's lifetime dosage of toxin each time a prey fish is eaten (Fig. 25.4).

Transmission of the toxin up the food chain may be facilitated because many fish species as well as crustaceans exhibit loss of equilibrium and erratic swimming after feeding on ciguatoxic plants and prey, which makes contaminated prey more susceptible to predation (Randall 1958; Davin et al. 1988; Kohler & Kohler 1994; Lewis 2001). Drying, freezing, and cooking fail to denature the toxins, which allows exported fish to cause problems far from the tropics. Twenty people at a dinner in Calgary, Alberta, suffered ciguatera poisoning from eating thawed-and-cooked reef fishes imported from Fiji (Haney 2002). No readily available, inexpensive means exist for testing for the toxin, although ToxiTecs, Inc. advertises the Cigua-Check® fish poison test kit (available at www.cigua.com, which also contains information on ciguatera). Clearly, the welfare of reef fish assemblages and reef communities can be directly linked to the integrity of the reef ecosystem itself. Where ciguatera is involved, human health is an added consideration.

One byproduct of differences in plant palatability, and a factor that can affect algal species composition on reefs, is the gardening behavior of damselfishes. The algal assemblage within a damselfish territory has been justly termed a "lawn" because it frequently consists of a few highly palatable algal species (e.g., the red alga, *Polysiphonia*) cropped down to a fairly even level; less desirable species are actively weeded out (Lassuy 1980; Irvine 1981). The lawn contrasts with the surrounding area, where abundant roving herbivores such as parrotfishes and surgeonfishes may graze most surfaces down to relatively bare rock or leave only crustose coralline algae. If heavy fishing pressure has removed large herbivores, surfaces outside damselfish territories may have a higher biomass of algae than inside such territories. Regardless, damselfishes, whose territories may cover 40–50% of a reef's surface, and other territorial herbivores (parrotfishes, blennies, surgeonfishes) can have a substantial effect on overall algal species diversity and distribution (Hixon & Brostoff 1983; Klumpp et al. 1987; Horn 1989; Hay 1991).

Hixon and Brostoff (1983) found that damselfish territoriality led to higher levels of algal species diversity (Fig. 25.5). The feeding rates of damselfish inside their territories were less intense than the levels of herbivory in unguarded areas outside the territories where parrotfishes and surgeonfishes were abundant. Roving herbivores kept algal diversity low outside territories because they grazed many surfaces bare. In caged enclosures that excluded both damselfishes and other herbivores, algal diversity was again lower than in damselfish territories because certain algal species were able to overgrow and eliminate other species. Hence the damselfish serves as a "**keystone**" species whose activities increase algal diversity by decreasing the disturbance created by roving herbivores and also by decreasing a competitive dominant alga's ability to monopolize the space resources of an area.

Temperate communities

In temperate streams and rivers, herbivory occurs primarily among minnows, catfishes, suckers, and killifishes. Perhaps 55 of the 950+ freshwater fish species in North America can be classified as primarily herbivorous (Allan & Castillo 2007). Although only a few species are exclusively or even strongly herbivorous, some dominate locally in numbers or biomass and have a strong effect on algal growth (e.g., several pupfishes, *Cyprinodon* spp.; some suckers, *Catostomus* spp.; Brown Bullhead Catfish, *Ameiurus nebulosus*). The Stoneroller Minnow, *Campostoma anomalum*, can attain densities of 10 fish/m^2 in midwestern US streams, each fish taking 10–15 bites/min at the algal substrate and consuming 27% of its mass in algae daily. This activity can reduce biomass, alter species composition, and increase growth rates of algal communities. The thick overstory of

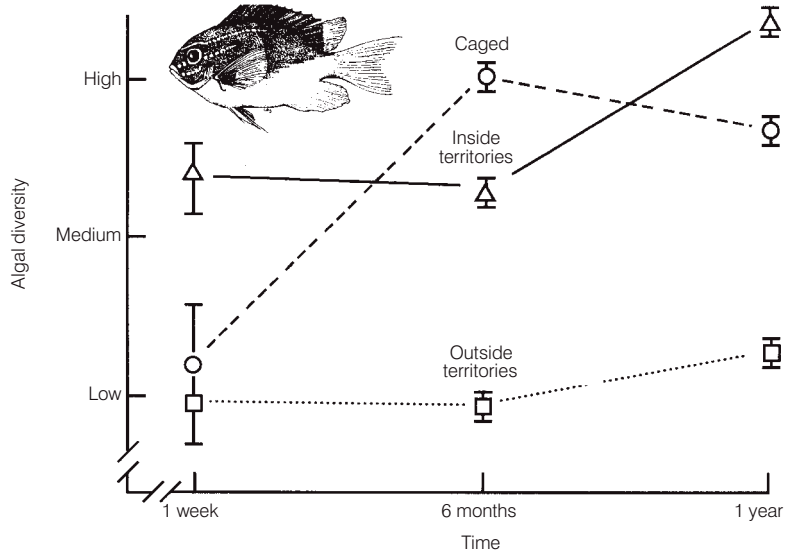


Figure 25.5
Damselfish territoriality leads to high algal species diversity. The diversity of algal species was measured over 1 year outside territories where roving herbivores were abundant, inside cages that excluded damselfish and other herbivores, and inside damselfish territories. Diversity remained low outside of cages and territories. Inside cages, diversity first increased then decreased as a red algal species became dominant. Inside territories, diversity was highest after 1 year because damselfish excluded roving herbivores that often stripped surfaces bare, while feeding by damselfish controlled the competitively dominant algal species. After Hixon and Brostoff (1983); damselfish drawing from Gilligan (1989).

filamentous green algae and diatoms is removed, leaving behind a thin layer of blue-green algae (cyanobacteria) that receives more light and more nutrients. Biomass-specific primary production is increased in areas grazed by minnows, which means that the plants left behind are more productive than those removed, probably because the algal types that are removed tend to be slow-growing forms and those left behind are faster-growing species (Matthews et al. 1987; Gelwick & Matthews 1992).

Few herbivores, especially at higher latitudes, are facultative plant consumers, even using the generous 25% plant-matter criterion to define the dietary guild (e.g., Allan & Castillo 2007). It is becoming increasingly evident that many if not most herbivorous fishes readily digest and probably actively seek out animal matter, either when taken in with plants or when opportunistically available. Even the weed-controlling Grass Carp (see below) requires some animal protein in its diet to achieve proper growth (Wiley & Wike 1986). Some omnivorous fishes consume large quantities of algae, particularly when preferred animal food is unavailable. Also, many carnivorous fishes can utilize algae as a supplemental food source when animal matter is unavailable (e.g., Kitchell & Windell 1970; Gunn et al. 1977). A Sonoran Desert minnow, the Longfin Dace (*Agosia chrysogaster*), prefers mayflies in the spring but takes in large quantities of algae in the fall when mayflies are no longer available. By increasing its feeding rate during the fall to allow for the lower nitrogen content of plant material, Longfin Dace maintain a relatively constant uptake rate of nitrogen. Nitrogen is then egested via feces and excreted across the gills into the stream in forms that are rapidly taken up by plants and may account for 10% of the nitrogen used by an otherwise nitrogen-limited stream ecosystem (Grimm 1988).

Herbivorous fishes in temperate lakes often belong to the same families as those that occur in rivers. Their impact on plant biomass can be considerable. Roach (*Rutilus rutilus*) and Rudd (*Scardinius erythrophthalmus*) in Lake Mikolajskie in Poland consume 1700 kg of macrophytes and 3800 kg of filamentous algae per hectare per year; the macrophyte values amount to about 15% of the annual total biomass (Prejs 1984). Strong selectivity is shown; Roach and Rudd prefer *Elodea* over *Potamogeton*, consuming 34% of the former and only 0.1% of the biomass of the latter, despite the low relative abundance of *Elodea*. An optimality analysis of benefits (amount of plant obtainable, nutritive value) and costs (plant toughness, availability of leaves and plants) indicates that the preference for *Elodea* exists because it provides a very high benefit : cost ratio as compared to other plant species.

The relative effectiveness of herbivorous lake fishes in consuming plant biomass is attested to by the widespread popularity and success of introductions of the Grass Carp, *Ctenopharyngodon idella*. Grass Carp, a native of China, have been widely introduced in the USA, Europe, and elsewhere to control unwanted aquatic plants, many of which are also introductions (e.g., Eurasian watermilfoil, *Hydrilla*, water hyacinth). Whereas most herbivorous fishes browse only the leaves of a plant and may in fact stimulate later growth, Grass Carp uproot and eat the entire plant. Grass Carp grow to a large size (to 30 kg) and consume 70–80% of their body weight daily; they can consequently eliminate all macrophytes in a lake, as happened in a Texas lake where 3650 ha of vegetation were eradicated within 2 years (Martyn et al. 1986). Total elimination of macrophytes is usually undesirable because, among other effects, it results in the destruction of critical habitat for invertebrates, amphibians, and juvenile fishes (Allen & Wattendorf 1987;

Murphy et al. 2002). Feeding preferences by Grass Carp can also lead to shifts in the relative abundances of different species, altering species compositions within the plant assemblage. In experimental ponds, Grass Carp reduced total plant biomass by feeding preferentially on *Chara*, *Elodea*, and *Potamogeton pectinatus*. Later, total plant biomass increased over original conditions because those species avoided by the Grass Carp (*Myriophyllum* and *P. natans*) occupied the space vacated by the preferred plants. When Grass Carp consume submerged vegetation, floating leafed plants can come to dominate (Fowler & Robson 1978; Shireman et al. 1986).

Phytoplanktivory also occurs in temperate lakes and can lead to reduction in phytoplankton abundance. Gizzard Shad, *Dorosoma cepedianum*, selectively remove larger phytoplankton species (Drenner et al. 1984a, 1984b). One form of phytoplanktivory, suspension feeding (see above), has been documented in numerous temperate as well as tropical families, including many commercially important species (e.g., herrings, anchovies, whitefishes, minnows, silversides, mullets, cichlids, mackerels; Lazzaro 1987). Particles can be captured on structures other than the gill rakers. A cyprinid, the Blackfish (*Orthodon microlepidotus*), captures particles on its palatal organ, a mucus-covered region in the roof of the mouth (Sanderson et al. 1991).

Herbivores in temperate marine habitats are often abundant, although species diversity is lower than on tropical reefs (Horn & Ojeda 1999; Horn & Ferry-Graham 2006; see Fig. 25.3). Many porgies are seasonal herbivores that take advantage of plant growth during warmer months. Temperate porgies can become particularly abundant, achieving densities of more than 7 fish/m^2 (Hay 1986). Temperate herbivores are usually browsers, eating the ends of algal fronds and other parts of seaweeds. Despite high seasonal abundance, available evidence indicates that temperate herbivores do not exercise the strong influence on algal ecology that is so evident in tropical marine environments. The strongest effects may be on the establishment and growth of young plants, as in the case of three California sea chub species that feed on young giant kelp, *Macrocystis*.

Territorial herbivores are generally lacking in temperate habitats, perhaps because a seasonally limited and variable plant resource makes territoriality impractical for most of the year (Horn 1989). Herbivory in temperate marine and fresh waters may be important, but invertebrates again probably exercise a greater influence than fishes. The association of "kelpbed" fishes with kelp beds is probably more of an attraction to the physical structure, refuge, and invertebrate production of the kelp than a dependence on the algae itself, with certain species and life history stages showing a stronger dependence on kelp than others (e.g., Kelp Perch, *Brachyistius frenatus*; Giant Kelpfish, *Heterostichus rostratus*; Kelp Clingfish, *Rimicola muscarum*; Kelp Rockfish, *Sebastes atrovirens*; Stephens et al. 2006); among the few consumers of macroalgae are the Halfmoon, *Medialuna californiensis*, and Opaleye, *Girella nigricans*, both derivative members of the tropical family Kyphosidae that abounds with herbivores (Horn & Ferry-Graham 2006).

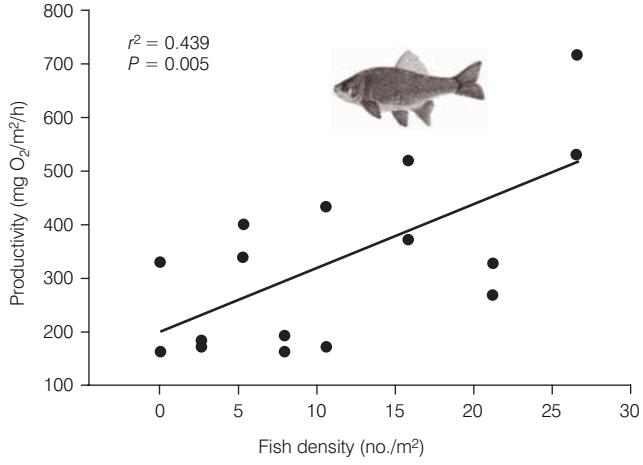


Figure 25.6

Algal productivity increases in relation to density of invertebrate feeding fishes. The relationship between primary productivity and fish density is shown for experimental streams in which Red Shiner density was manipulated. Productivity increased in direct proportion to the number of minnows present. After Gido and Matthews (2001); Shiner drawing from Texas Parks and Wildlife Department, ww.tpwd.state.tx.us.

The impact of fishes on plants may be an indirect one mediated by nutrient mobilization. For example, Red Shiners, *Cyprinella lutrensis*, in midwestern US streams feed heavily on insects that fall into the water. When shiner density was manipulated in experimental streams, benthic primary production increased in response to fish density, increasing 2.5-fold at high but natural densities of 27 fish/m^2 (Gido & Matthews 2001) (Fig. 25.6). Hence, water column minnows that feed on drifting insects can affect primary productivity by transferring nutrients from terrestrial sources to benthic producers in stream ecosystems (see also below, Nutrient cycling and transport by fishes).

The effects of fishes on invertebrate activity, distribution, and abundance

Effects on zooplankton

The influence that fishes have on invertebrate prey populations in fresh water differs according to habitat (Sih et al. 1985; Northcote 1988; Walls et al. 1990). Although exceptions occur, fishes in general have a strong and direct influence on water column prey such as zooplankton, and a lesser and sometimes undetectable influence on benthic

invertebrate populations. Fishes generally crop no more than 5–10% of zooplankton production annually, although the impact can be much greater, as when Alewives and Yellow Perch consumed 97% of the zooplankton in Lake Michigan in 1984 (Evans 1986). Fish predation on planktonic organisms normally causes a shift in size and species composition in freshwater zooplankton communities. **Size-selective predation** is a general phenomenon because fish prefer larger zooplankton. Larger zooplankton are caught preferentially by particulate feeding fishes that select individual prey visually. Large zooplankton are themselves predators on smaller zooplankters. In freshwater ponds and lakes that contain zooplanktivorous fishes, the zooplankton community will be dominated numerically by small-bodied cladocerans and rotifers (*Bosmina*, *Scapholebris*, *Ceriodaphnia*) because they are not eaten by the fishes and their chief predators have been eliminated. When zooplanktivorous fishes are absent, larger zooplankton (e.g., large copepods and cladocerans, *Daphnia* spp., *Simocephalus*) abound and feed on the smaller zooplankton and phytoplankton (Brooks & Dodson 1965; Janssen 1980; Zaret 1980; Newman & Waters 1984; Northcote 1988) (Fig. 25.7).

For size-selective predation to occur, a fish must be able to assess prey size and correct for distance in the three-dimensional, forward projecting hemisphere over which it normally searches. How this is accomplished is an area of active research. Fish size comes into play, with young fishes being apparently unable to detect small prey, whereas larger individuals have better acuity. In Bluegill Sunfish, 6 cm long fish can see objects half the size that 3.5 cm fish can detect. Some evidence indicates that apparent rather than absolute prey size may be important. When offered prey of different sizes at different distances, Bluegill, White Crappie, and sticklebacks chose the apparently larger prey, i.e., they preferred a smaller but nearer prey over a larger prey that was farther away and therefore appeared to be smaller (Hairston et al. 1982; O'Brien 1987).

Zooplanktivorous fishes cause other shifts in the ecology of their prey. Diel vertical migrations are probably a means of avoiding visually hunting fishes; plankters occur in deep, dark, cold, and relatively deoxygenated regions of lakes by day and rise into surface waters at night to feed. The extent of such migrations decreases when predation pressure from fishes is reduced. Adjustments in life history traits of prey include reductions in age at sexual maturity and average size of offspring. Predation also affects prey morphology and coloration. Some cladocerans (e.g., *Daphnia*) develop neck spines when exposed to water that has contained Bluegill. Some cladocerans are relatively dark when occurring in fish-free ponds, but are essentially transparent when co-occurring with fish in lakes; copepods are red in the absence of fish but take on a less vulnerable pale green color in ponds containing fishes. The costs of coloration are obvious from studies that show that some fishes will take

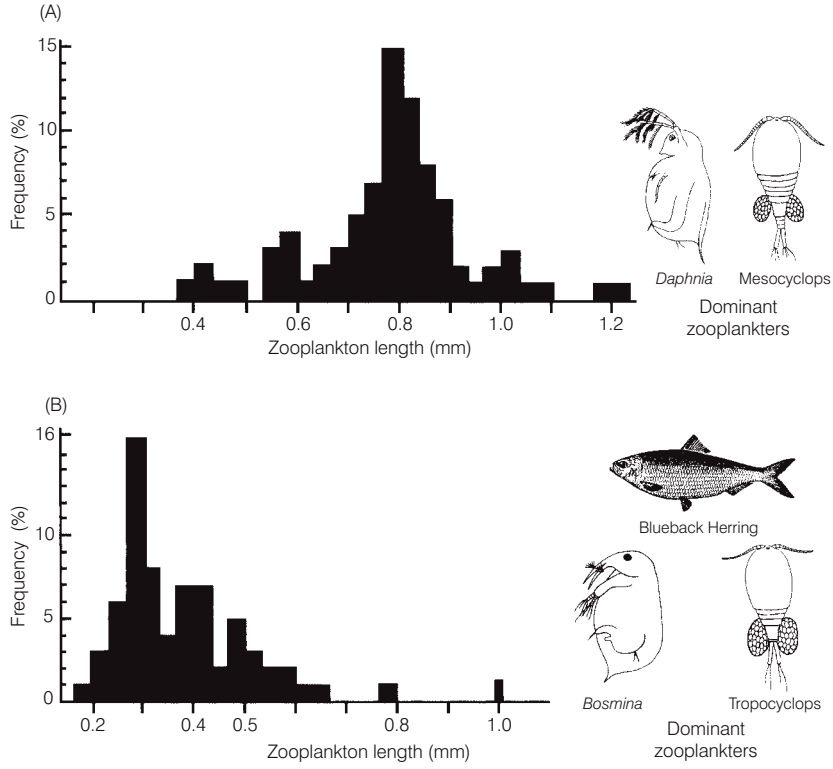


Figure 25.7
Effects of fish predation on zooplankton assemblage structure. (A) Before predators were introduced. (B) When Blueback Herring were introduced into a small Connecticut lake, size-selective predation by the fish caused the average size of zooplankters to decline. Predation favored smaller individuals within species as well as smaller species. After Brooks and Dodson (1965) and Bigelow and Schroeder (1953b).

the smaller of two forms if it is more pigmented, or will take prey with the large dark eyes over similar size prey with smaller eyes (Zaret 1980; Lazzaro 1987; O'Brien 1987; Walls et al. 1990; Hobson 1991).

Studies in temperate and tropical nearshore marine environments also suggest a strong influence of zooplanktivorous fishes on species composition and size structure of prey populations. Small (<1 mm), transparent zooplankters that are part of the pelagic community that is being carried by currents (e.g., dispersing fish eggs and larvae, small copepods, larvaceans) characterize the water column and fish diets during the day. The fishes tend to aggregate at the upcurrent edges of reefs and other structures, where they intercept the incoming pelagic forms. Densities of plankton are lower in downcurrent areas, indicating that fishes remove a significant number of plankters from the water column. At night, different species and sizes of zooplankters occur than are seen during the day. Larger, opaque animals (1–10 mm), such as mysids, large copepods, polychaete worms, amphipods, ostracods, and crustacean larvae, emerge from the substrate or migrate vertically upward and join the small, transient zooplankters.

Both groups encounter a different set of predators at night, generally large-mouthed fishes with large eyes (e.g., squirrelfishes, cardinalfishes, sweepers). Vision is the most widely used detection mode both by day and night, but nocturnal zooplanktivores are constrained by the lack of light, making it safer for larger zooplankton that would be easily detected during the day (small plankters are seldom found in the stomachs of nocturnal fishes). Verification of the influence of predators on oceanic plankton communities would require the kinds of predator removal or enclosure experiments that have been performed in fresh water, but the open nature of oceanic coastlines and the long-distance dispersal of the prey make these kinds of experiments virtually impossible (Bray 1981; Hobson et al. 1981; Hobson 1991).

Effects on benthic invertebrates

Populations of benthic invertebrates in streams appear to be minimally influenced by predatory fishes, although results vary in different habitats (for a review, see Allan & Castillo 2007). In Colorado, Brook Trout (*Salvelinus fontinalis*) were removed from a 1 km section of a stream. Invertebrate numbers and species composition were compared over 4 years in the removal section and in control sections both up- and downstream. No significant differences arose in experimental versus control sections, indicating that trout predation had little effect on invertebrate community dynamics. Similar results, involving fish removal or cages that excluded fish, have been found in streams in North Carolina, Kentucky, Czechoslovakia, England, and in ponds in New York and South Carolina (Allan 1982, 1983; Holomuzki & Stevenson 1992). In contrast, benthic invertebrate numbers were significantly depressed by the activities of Bluegill in lakes and by Creek Chub (*Semotilus atromaculatus*) in streams. Midges and stoneflies declined in direct proportion to sculpin and dace abundance in one study, but midges were unaffected in another. Bluegill Sunfish can also reduce invertebrate biomass and density of pond invertebrates, and Yellow Perch as an introduced species can eliminate 50% of the benthic invertebrate biomass of small lakes. Bottom type, topographic complexity, and current strength all influence the outcome. Predation in many of these experiments was size selective, with fish preferentially eating larger individuals and species and hence affecting community composition as well as numbers (Crowder & Cooper 1982; Mittelbach 1988; Northcote 1988; Gilliam et al. 1989; Allan & Castillo 2007).

Predators can affect more than absolute and relative prey numbers. **Distributional changes** arise as a result of behavioral adjustments to the threat of predation, which can have population consequences for prey. In the presence of predatory fishes such as sculpins, insect larvae such as mayflies avoid the surfaces of rocks where food availability is highest and instead are found under rocks (Kohler & McPeek 1989; Culp et al. 1991). When Smallmouth Bass (*Micropterus dolomieu*) are present, crayfish reduce both locomotory and foraging activities and select bottom types that provide more protection (Stein 1977). **Drift**, the movement of invertebrate larvae and adults downstream in the water column of lotic systems (streams and rivers), is also affected by fish activity. In the presence of Longnose Dace, *Rhinichthys cataractae*, mayfly drift first increases and then decreases compared with situations when predators are absent. Hence invertebrates may first move out of an area where predators occur and then later settle and take refuge. Amphipods respond to sculpin by reducing general activity, including drift (Andersson et al. 1986; Culp et al. 1991). Cooper (1984) showed that predation by trout can have both negative and positive effects on water striders. By preying on water striders, trout increase intraspecific competition by increasing the relative density of striders in refuges away from predation risk. However, trout predation benefits water striders in that trout prey on both competitors and predators of the water striders.

Disagreements about the responses of benthic invertebrates to fish predation may reflect differences in prey mobility in different areas (Cooper et al. 1990). In streams containing highly mobile or drifting prey, or in cage studies where mesh size is large enough to allow invertebrates to recolonize, prey that are eliminated by predators will be replaced by immigration. Where minimal exchange of prey occurs between habitats, or where cage mesh sizes are too small to allow recolonization, predators have a stronger depressing effect on prey populations. Not surprisingly then, drift-feeding fishes (e.g., salmonids) have lesser effects on prey, whereas benthic-feeding fishes (e.g., some minnows, sculpins, sunfishes) tend to reduce prey populations. Lakes,

ponds, and pool communities with their reduced flow regimes will be more affected by predation than will be riffles and runs. Current speed in lotic systems will operate analogously, fast currents serving to transport immigrants and slow currents tending to delay replacement. Predatory fishes therefore play different roles depending on whether the habitat is relatively open or closed.

The apparent minimal effect that fishes have on stream invertebrate populations may be interpreted as a lack of influence of fishes on their prey. However, the flip side of this situation is that stream fishes are therefore unlikely to limit their own food supply and are thus unlikely to find themselves competing for food. Insect abundance does, however, vary significantly and can be limiting. Seasonal cycles of insect abundance, driven by insect life histories more than by fish predation, include a midsummer low after many adults have emerged from the stream and before the next cohort of prey has reached edible size. Growth rates of fishes decrease during this midsummer period. Experimental additions of food to streams during midsummer can increase growth, survival, and energy stores of juvenile stream fishes, indicating that food was in fact limiting (Mason 1976; Schlosser 1982; Karr et al. 1992).

Fishes can also affect the numbers, species composition, and distribution of sessile and mobile marine invertebrates. Some corals appear to be restricted to shallow water habitats by the grazing activity of fishes. Triggerfish (*Balistapus undulatus*) occur on reef slopes and deep reef areas and eat corals such as *Pocillopora damicornis*. *Pocillopora* can be successfully transplanted to deeper water on reefs if placed in cages that exclude the triggerfish. Corals transplanted outside of cages are consumed (Neudecker 1979). Damselfish actively kill corals within their territories, which creates a growth surface for the algae on which the fish feed (Kaufman 1977). Since damselfish territories can cover a significant proportion of some shallow reefs, habitat modification by damselfish can influence the amount of coral cover. At the same time, damselfish algal turfs are important habitats for small crustaceans, polychaetes, and mollusks, and the territoriality of the damselfish protects these invertebrates from predatory fishes (Lobel 1980). Fish predation can also affect the diversity of encrusting species. Tunicates in caves on the Great Barrier Reef are heavily grazed by fishes. Inside enclosures, tunicates dominate other forms, whereas outside enclosures, removal of tunicates by fishes allows for growth of bryozoans. Tunicates grow successfully only where they have natural protection, such as at the base of stinging hydroids (Day 1985).

Fish predation can limit the distribution of such mobile invertebrates as polychaetes, burrowing sea urchins, snails, stomatopods, and hermit crabs on and near reefs. Predation by stingrays may reduce snail abundance on sandy substrates near reefs. The reef itself often provides a refuge from and for fishes. Herbivorous sea urchins shelter in the reef by day and venture into surrounding grass beds at night. Patch reefs in the Caribbean typically have a denuded ring of sand 2–10 m wide at their base which results from the nocturnal forays of the urchins. The width of this "halo" apparently reflects the distance that urchins can move from the reef and still return safely at dawn before diurnal predaceous fishes become active. The region around the reef, including the halo, is also relatively devoid of infaunal invertebrates. Invertebrate-feeding fishes venture off the reef and forage in the reef's vicinity, returning to the reef when threatened by predators and when resting. Invertebrate densities increase as one travels farther from the reef, unless another reef is close enough that the foraging regions of fishes from both reefs overlap (Ogden 1974; Randall 1974; Ambrose & Anderson 1990; Jones et al. 1991; Posey & Ambrose 1994).

Fishes, sea urchins, and plants interact as integrated parts of complex **trophic cascades** (see below, Fishes in the ecosystem); disrupting one part affects ecosystem components both above and below in a cascade. Overfishing of species such as large triggerfishes and wrasses that feed on coral-eating invertebrates apparently tips the competitive balance between fishes and invertebrates to favor invertebrates (Fig. 25.8). Sea urchins in particular become abundant because sea urchins outcompete herbivorous fishes under conditions of intense fishing on sea urchin predators (e.g., McClanahan & Muthiga 1988; Levitan 1992). Unlike most herbivorous fishes, grazing urchins actually scrape the substrate. This accelerates **bioerosion** of the reef, reduces coral cover, reduces topographic complexity, and produces a reef surface dominated by algal turf. Ultimately, fish diversity and fishery productivity decline (Glynn 1997). Additionally, rapid algal growth and reduced settling success of coral larvae apparently reduce the ability of reefs to recover from hurricane damage (e.g., Liddell & Ohlhorst 1993). Protecting urchin-eating fishes, as recommended by McClanahan (1995), would prevent the negative diversity and abundance consequences of urchin proliferation. Protecting urchin predators would also lower urchin numbers and thus direct benthic production into abundant herbivores such as parrotfishes, surgeonfishes, rudderfishes, and rabbitfishes.

Similar, dramatic fish–urchin–algae interactions have also been observed at high latitudes. In the Bering Sea, expansion of the Walleye Pollock fishery occurred concurrently with large declines among Steller sea lions, northern fur seals, and harbor seals (Goñi 1998). Reductions in pinnipeds have apparently caused orcas to feed on sea otters as alternative prey, thus releasing sea urchins from predation by the otters, and culminating in a loss of kelp forests because of overgrazing by the urchins (Estes et al. 1998). Many nearshore, high-latitude marine fishes are dependent on kelp forests as habitat (Stephens et al. 2006).

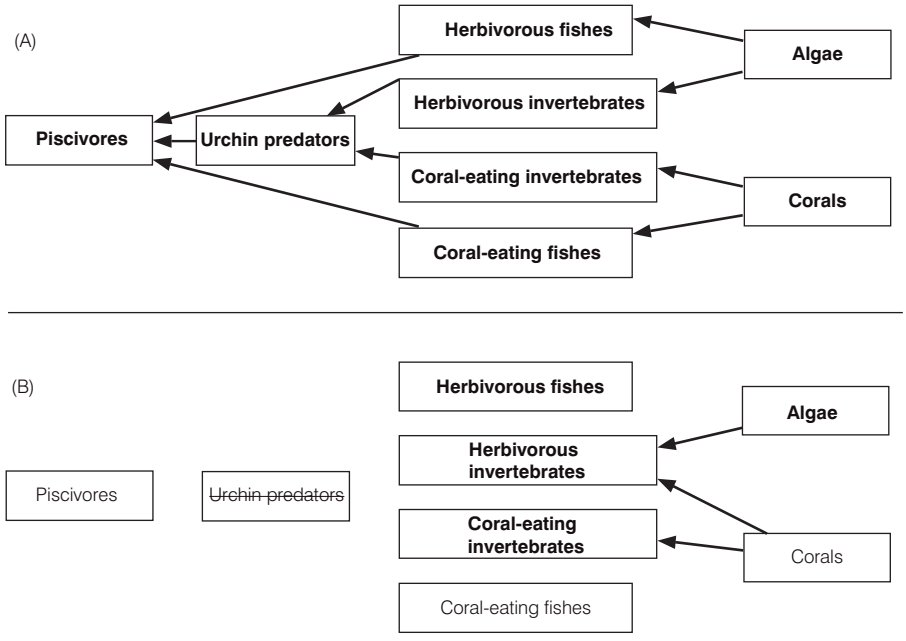


Figure 25.8
Ecosystem level implications of overfishing on coral reefs. Overfishing frequently leads to dominance of invertebrates and algae via a series of interrelated pathways. (A) Unfished or lightly fished reefs house a diversity of fishes in several trophic guilds, as well as abundant coral cover. (B) The removal of large piscivores results in the elimination of fishes that feed both on sea urchins and on invertebrates that feed on corals. Herbivorous and coral-eating invertebrates proliferate, which leads to overconsumption of corals or permits algae to overgrow coral. In either situation, overall fish diversity declines because of strong direct and indirect dependence of many fish taxa on live coral cover. Darkness of lettering denotes changes in relative abundance of trophic or taxonomic group. From Helfman (2007), used with permission.

Turnover rates and the inverted food pyramid

The **biomass** (mass per unit area) of fishes or other animals in a habitat indicates something about the nature of the community. However, biomass is a static depiction, basically a snapshot, of a very dynamic situation for which a moving picture would tell us more. **Turnover**, the ratio of production to standing crop biomass (P : B), provides the added information. Turnover, expressed in units of *mass per unit area per unit time* (e.g., g/m^2/year) is a measure of how productive a population is over time and takes into account life table schedules of birth and death, population density, individual growth rate, and development time (Benke 1993; see Chapter 24, Production). For example, a seeming paradox occurs in many freshwater habitats when prey consumption rates of fishes are investigated. Trout in the Horokiwi Stream of New Zealand consume about 20 times the standing crop biomass of invertebrates annually; trout and stonefly consumption of prey in a Colorado stream is about 10 times greater than standing crop biomass of prey. In some streams, the biomass of predators exceeds that of prey, which would seem to violate laws of ecology and thermodynamics.

Obviously, just looking at biomass tells us little about ecosystem dynamics in such a situation. The paradox of how fish can consume more prey than exist, and how more predators than prey can be maintained in a habitat, is solved when one looks at **turnover rates**, namely how quickly animals reach maturity, how many times they reproduce, and how many young they produce. If benthic invertebrates go through several generations per year (which they do), then their annual production can greatly exceed biomass at any one moment and the invertebrate community can support a much larger fish assemblage than if the fishes were solely dependent on standing crop biomass. Production values three to 10 times greater than biomass are not unusual (Benke 1976, 1993; Allan 1983).

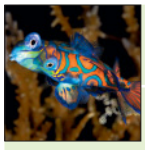
Fishes in the ecosystem

The preceding discussions have focused on the effects that fishes as predators have on trophic levels lower in the food web of the community. Such **"top-down" regulation** of community dynamics can be contrasted with "**bottom-up**" factors affecting plant growth and subsequent plant or animal prey availability, which ultimately determines fish abundance and diversity. From the fish's perspective, top-down processes involve the ways that fishes affect the structure and function of an ecosystem (Table 25.1), whereas bottom-up processes involve the physical and chemical factors that affect food availability for fishes. In addition to these direct interactions, ecosystem function is affected by indirect effects of different trophic levels on one another which are separated by several steps or levels in the **trophic organization** of a community. Fishes function in such interactions as agents that transfer and cycle nutrients, energy, and matter and that link different parts of the ecosystem together. In addition to their interactions with other members of the biotic community, many of the activities and relationships have direct benefits to humans and can be considered as ecosystem services provided by fishes (Box 25.1). Our dependence on fishes for the functional roles

Table 25.1

Top-down effects of fishes in temperate lakes and streams. Whether the same suite of effects and relationships occurs in tropical freshwater systems or marine systems remains largely unstudied. Adapted from Northcote (1988).

Activity	Factors affected	Mechanism and consequence
Direct feeding	Water transparency	• Searching stirs up bottom sediments and lowers transparency • Intense herbivory may increase transparency through removal of phytoplankton; turbidity may increase due to excretion and fertilization
	Nutrient release, cycling	• Benthic food searching increases mud–water nutrient cycling • Littoral vegetation grazing and processing increase nutrient cycling
	Phytoplankton	• Littoral vegetation grazing and processing increase nutrient cycling and water transparency • Heavy grazing commonly increases production
	Periphyton	• Strong cropping leads to increase in biomass
	Macrophytes	• Strong cropping leads to increase in biomass
	Zooplankton	• Strong cropping has an effect on abundance especially of larger forms • Some evidence of increased production
	Zoobenthos	• Strong cropping effect on abundance is common but may vary in lakes and streams • Marked seasonality in effects due to distribution and size of feeding fish • Production is often increased in lakes but not in streams
Selective predation (due to size, visibility, motility)	Phytoplankton Zooplankton	• Shifts in relative abundance of algal size and species composition • Shifts in relative abundance of species reduces algal grazing efficiency and water transparency • Changes in clutch size and timing of maturation
	Zoobenthos	• Heaviest predation on large forms affects their cover selection, activity patterns, and reproductive behavior
	Nutrient release	• Shift to smaller body size of zooplankton increases nutrient release
Excretion	Nutrient release	• Liquid release provides quick, patchy availability • Feces release provides slower patchy availability after remineralization • Epidermal mucous release increases iron availability to algae via chelation
Decomposition	Nutrient release	• Carcass remineralization provides slow, patchy releases
Migration with excretion or decomposition	Nutrient enrichment	• Transport of excreta or body decomposition products from high nutrient to low nutrient regions (sea to inland water, stream lower to upper reaches, lake layers)



Box 25.1

BOX 25.1

Ecosystem services provided by fishes

An aspect of biodiversity loss that affects human welfare involves the role that fishes play in ecosystems. Biodiversity is intimately linked to ecosystem function: healthy ecosystems – those that contain natural assemblages of organisms, habitats, interactions, and processes – can sustain exploitation. Disrupted ecosystems collapse.

Organisms in ecosystems can provide both goods and services, to humans and other members of the ecosystem. Utilitarian **goods** are obvious: we eat fish, we use them in medicines, we worship them in ceremonies, we buy them as curios, and we derive aesthetic pleasure from fish-centered recreation. **Ecosystem services** in contrast are the processes that occur as the result of functioning ecosystems, processes that humans (and other organisms) find useful or necessary (Daily 1997; ESA 2000; see also www.maweb.org). Classically, ecosystem services were defined as processes that benefited humans: plant pollination, water and air purification, seed dispersal and germina-

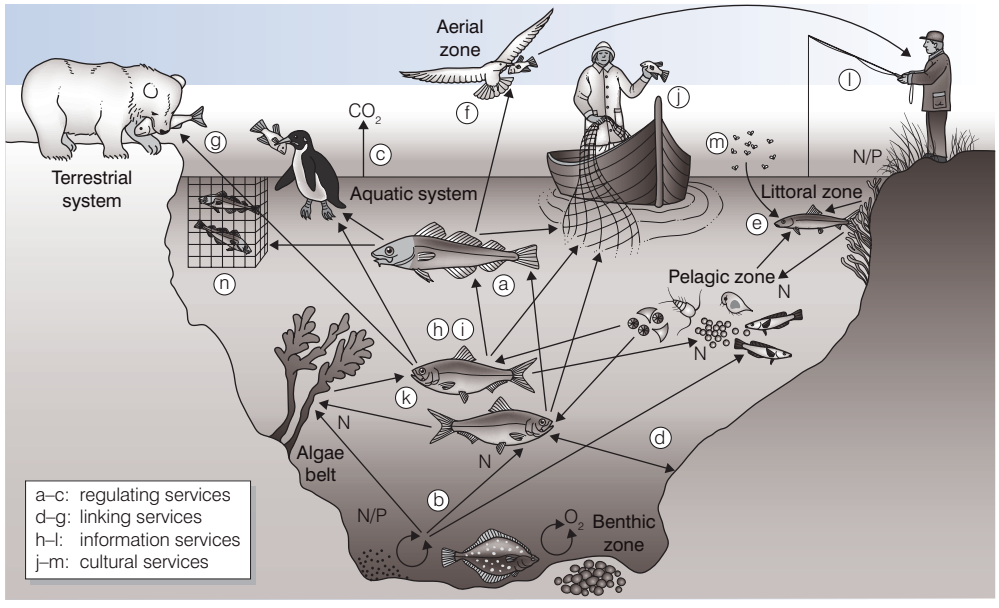


Figure 25.9

A pictorial summary of ecosystem services provided by fishes to humans and other organisms. Services can be classified as: *regulating* populations and processes (e.g., trophic cascades that regulate population dynamics or nutrient cycling, bioturbation of sediments, carbon exchange); *linking* different parts of the ecosystem via transport of nutrients and energy (e.g., open water to benthos, littoral zone, birds, and terrestrial mammals); *informing* (e.g., indicating and recording past and present ecosystem integrity); and *cultural* (e.g., human interactions and direct benefits via exploitation, recreation, water purification, disease abatement, and aquaculture). After Holmlund and Hammer (1999), used with permission; see www.maweb.org for alternative terminology.

tion, drought/flood mitigation, erosion control, nutrient cycling, pest control, and waste decomposition and transformation. These are all products of plant and animal activities. Because of the interconnectedness and co-evolution of living things in ecosystems, one organism's output serves as input to another organism. The essential point here is that "ecosystem services are generated by the biodiversity present in natural ecosystems" (Chapin et al. 2000, p. 240).

Fishes provide a number of such services (Holmlund & Hammer 1999) (Fig. 25.9):

- As a result of short- and long-distance movements, fishes *transport nutrients* between different parts of ecosystems and between different ecosystems. As in the examples of grunts and kelpbed fishes discussed in Box 25.2, nutrients obtained in one habitat and excreted in another stimulate coral or plant growth. Long-distance migrations of salmonids and other diadromous fishes bring nutrients and energy obtained in ocean regions to distant, upriver habitats. This transport forms the base of the food webs in lakes and rivers as well as surrounding terrestrial regions. Fishes, birds, mammals, and riparian vegetation are all dependent directly on these fishes, on the invertebrates that feed on the fishes and their offspring, and on the nutrients released as waste products or from decomposing bodies.
- Some fishes are *ecosystem engineers*, producing and moving sand and gravel; they thus control resource availability by modifying, maintaining, and creating habitat (Moore 2006). Parrotfishes generate sand in the process of digesting coral, and move sand between different reef areas. Salmonids and minnows redistribute gravel and pebbles in the process of nest building. Sockeye Salmon, *Oncorhynchus nerka*, in two Alaskan streams consistently disturbed 30% of the available streambed in the process of building nests. When salmon populations were high (as happened before overfishing), Sockeye dug up the entire streambed more than once, being forced to superimpose new nests on top of old nests. Nest digging affects periphyton growth and may decrease the susceptibility of a stream to flood erosion by sorting sediments into size classes and thus raising the threshold flow level at which bed scouring occurs

(Statzner et al. 2003; Moore 2006). This redistribution and concentration of bottom types creates favorable living conditions for not only the young of the engineers but of many other fishes and invertebrates. Loss of such ecosystem engineers will undoubtedly lead to dramatic changes in ecosystem function, although this remains an area of investigation (e.g., Coleman & Williams 2002).

- Fishes sit at the top of food webs in many habitats, and their feeding activities can *cause trophic cascades*, affecting species lower in the food web. Herbivorous fishes on reefs prevent algae from overgrowing and smothering coral; coral is, in turn, critical habitat for fishes and invertebrates. Reef-dwelling fishes that eat urchins prevent urchin explosions that can denude reefs of both algae and coral. Piscivores in lakes eat smaller fishes that eat zooplankton. Zooplankton feed on phytoplankton. Eliminate the piscivores and lakes experience blooms of algae, some of which are noxious.
- Zooplanktivorous and microcarnivorous fishes feed on larval stages of mosquitoes and other biting flies, some of which carry *human pathogens*. Other fishes feed on snails that are intermediate hosts of human parasites (Stauffer et al. 1997).
- Although no fishes are known to pollinate plants, they do *assist in the germination and transportation* of seeds, as has been shown for piranha relatives in the riparian forests of the Amazon. In another symbiotic relationship, fish deposit eggs in the mantle cavities of freshwater mussels; bivalve larvae attach to the gills of the developing fish and are protected and transported until large enough to survive. In areas where host fishes have been reduced in number, bivalve populations crash.

A fully functional ecosystem is therefore dependent on its biodiversity, on the essential parts being present and functioning in their evolved ecological roles. The ecosystem and its constituent biodiversity are inseparable, and protecting diversity requires an ecosystem perspective.

they play in ecosystems as well as for the calories and nutrients they provide as food underscores the importance of understanding the impacts of overexploitation and biodiversity loss (Allan et al. 2005; McIntyre et al. 2007).

Indirect effects and trophic cascades

The impact of fish predation on both plants and animals extends beyond the direct effects of reduction in biomass and shifts in species and size composition. Indirect effects on other components of the food web have received considerable attention in recent years. Only about half of the variation in annual primary production in lakes can be explained by changes in the amounts and types of nutrients that occur there. The other half results from the indirect but important role that fishes, both piscivores and zooplanktivores, play in determining plant production in lakes. This effect can be described as a **cascade** of influences down through the food web of a lake from secondary consumers to primary producers (Fig. 25.10). A typical trophic cascade involves piscivorous fishes (salmons, Pike, basses) feeding on zooplanktivorous fishes (herrings, minnows), which feed on herbivorous zooplankton, which eat phytoplankton. Increasing the number of piscivores reduces the number of zooplanktivores, which increases zooplankton abundance, which leads to more removal of phytoplankton from the water column. Hence experimental additions of top predators lead to greater water clarity. The previously mentioned increase in average size of zooplankton due to size-selective feeding of fishes occurs as an incidental result of such a manipulation. Fish predators on zooplankton are reduced, favoring larger zooplankton that would otherwise be taken by fishes and that may be too large for invertebrate predators to handle. A reversed chain of events occurs if piscivore abundance is reduced, either experimentally, through overfishing, or from fish kills such as occur during winter deoxygenation. Fewer piscivores mean more phytoplankton because of the reduction in herbivorous zooplankters. In reality, herbivorous zooplankton are never entirely eliminated (Carpenter et al. 1985; Carpenter & Kitchell 1988, 1993; Kufel et al. 1997).

Trophic cascades are not limited to the open water communities of lakes. Benthic communities in shallow water may also be structured by fish-mediated cascades. A fish–snail–epiphyte–macrophyte cascade was found in a Tennessee lake where Redear Sunfish (*Lepomis microlophus*) ate snails that grazed on epiphytes (filamentous blue-greens and diatoms), which normally infest lake weeds (Martin et al. 1992). When fish were excluded, snail abundance increased, snails depressed the epiphyte populations, and macrophyte growth increased. Strong trophic cascades similar to those found in lakes can also develop in lotic ecosystems. During the summer, low-flow conditions create a series of pools in seasonally flowing rivers. In the Eel

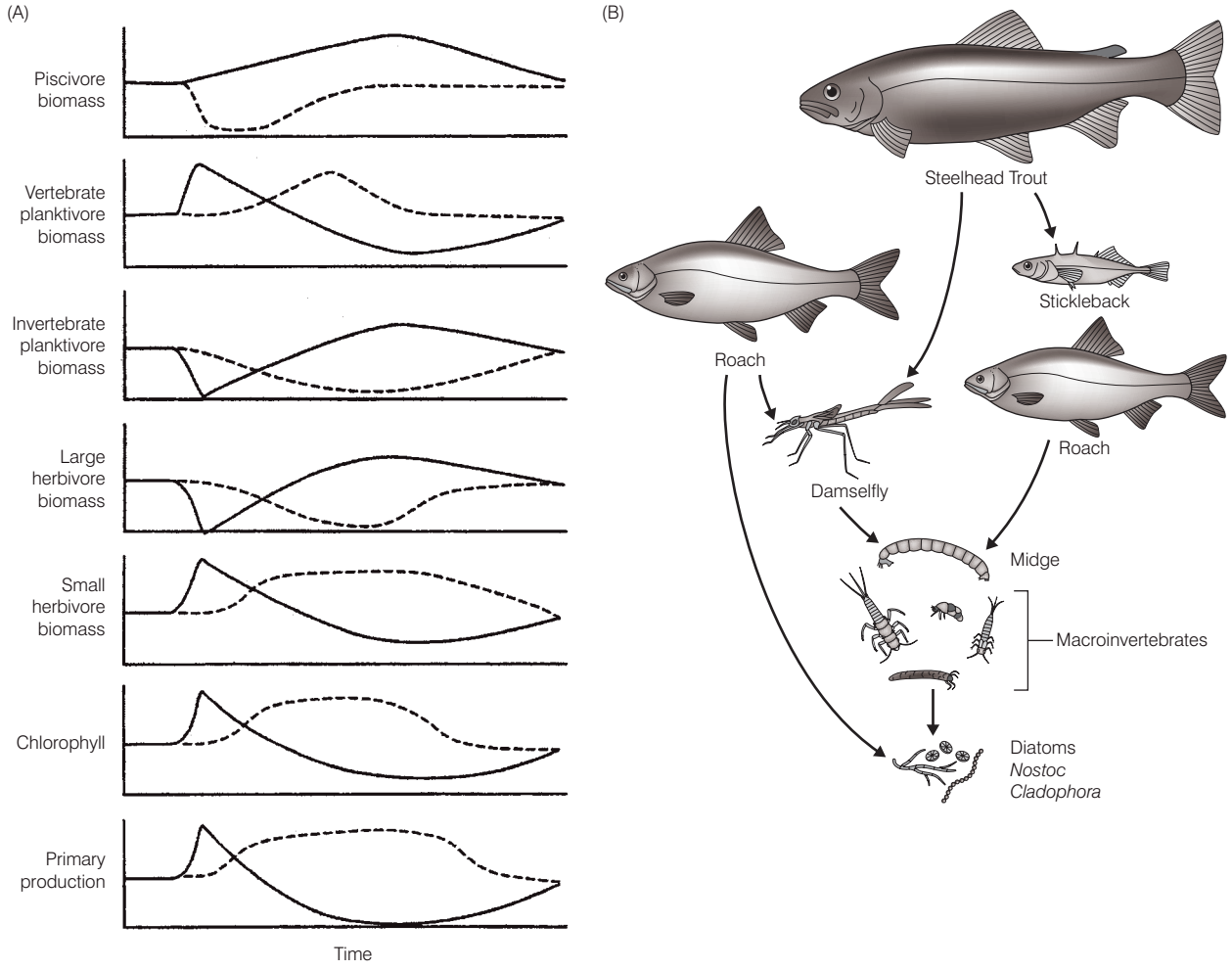


Figure 25.10

Trophic cascades. (A) The various components of a trophic cascade as postulated for a lake or pond over a growing season. Solid lines represent changes in biomass or density resulting from a strong year class or the experimental addition of piscivores; dashed lines show the effects of winterkill or overfishing of piscivores. In North America, piscivores would include salmonids, Pike, black basses, and Walleye; vertebrate planktivores would include herrings, minnows, whitefishes, Bluegill, and Perch; invertebrate planktivores would be copepods and many insect larvae; and most herbivores are crustacean zooplankton. (B) An actual trophic cascade. This is the one producing the outcome in the Eel River, California, depicted in Fig. 25.11. See text for explanation. (A) from Carpenter et al. (1985), used with permission; (B) after Allan and Castillo (2007).

River, California, turfs of filamentous algae up to several meters long and covered with diatoms and blue-green algae cover most of the bottom (Fig. 25.11). Through the summer, these turfs are grazed down to small tufts by midges. The midges are the major prey of predatory damselfly nymphs and the fry of California Roach (*Hesperoleucas symmetricus*) and Three-spined Stickleback (*Gasterosteus aculeatus*). Fish fry and damselfly nymphs are in turn eaten intensively by large roach and Steelhead Trout (*Oncorhynchus mykiss*). When algae are allowed to grow in cages that exclude the trout and large Roach, fry and damselfly nymphs abound, cropping down the midges. This allows the algae to maintain fairly luxuriant growth through the summer. Hence the feeding activities of predaceous fishes cascade down through the food web and eventually determine the growth form and extent of primary producers in the river (Power 1990).

Indirect effects driven by fish predation can cause unexpected physical changes in lakes. Lake Michigan and other high pH, hard water lakes experience milky water during summer months. These "whiting events" result from the precipitation of limestone crystals (calcite = calcium carbonate, $CaCO_3$). Whitings can inhibit zooplankton feeding, increase sinking rates and loss of precipitated nutrients to deeper water, and reduce light penetration and primary production. Whitings result from increased photosynthetic activity of algae at elevated summer temperatures, which removes CO_2 from the water and causes an increase in pH.

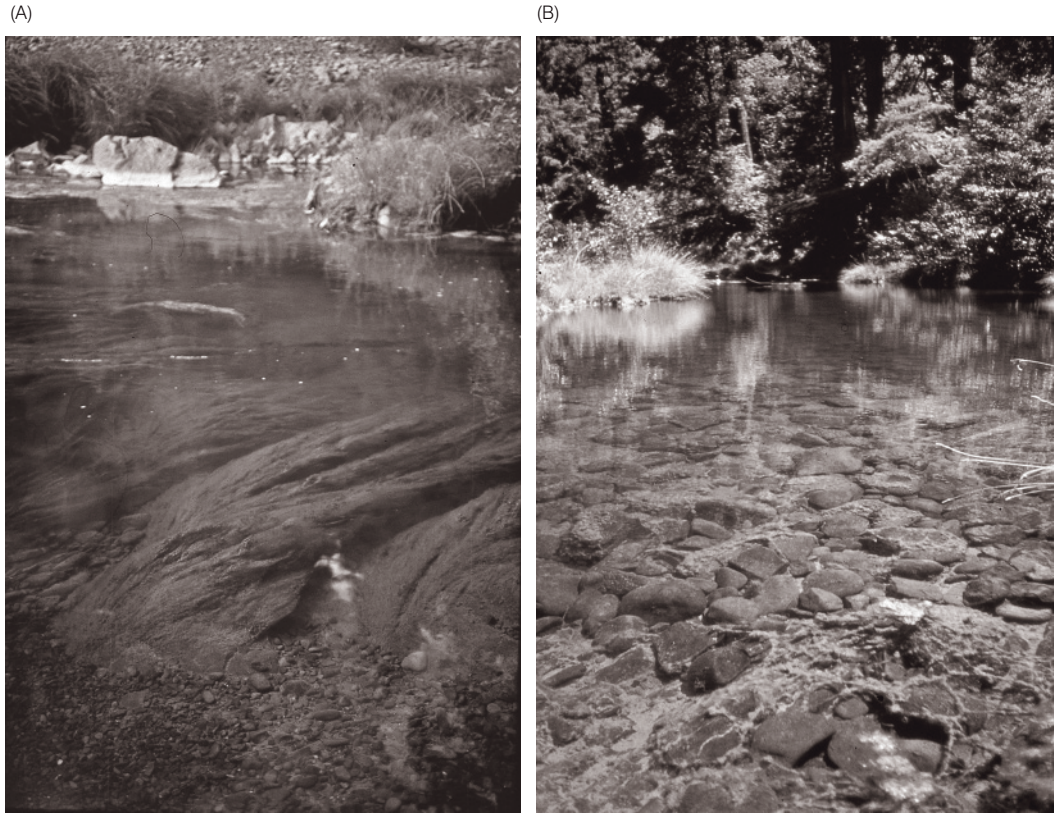


Figure 25.11

Trophic cascades in rivers mediated by fish. (A) During early summertime low flow conditions, filamentous algae develop long turfs on cobble bottoms. (B) By late summer, midges have consumed most of the algae and woven the remainder into small tufts. These midges are eaten by invertebrates and fish fry, which are in turn consumed by larger fish. When large fish are excluded, predators on the midges abound, the midges decline in numbers, and the algae reach abundances more like (A) than (B). Hence algal abundance is determined indirectly by the activities of large predatory fishes. From Power (1990), used with permission.

$CaCO_3$ is less soluble at high pH and thus precipitates out of the water, causing the milkiness. Intensive stocking of salmonids (Coho and Chinook salmon, Lake, Rainbow, and Brown trout) in Lake Michigan during the 1970s led to high salmonid populations in 1983. Salmonids ate huge numbers of zooplanktivorous Alewives, allowing phytoplanktivorous cladocerans to develop large populations, which in turn ate phytoplankton. Lack of phytoplankton kept the pH low and hence no whiting event occurred that year (Stewart et al. 1981; Vanderploeg et al. 1987).

Another physical result of trophic cascades involving fishes is the effect that plankton biomass has on temperatures, thermocline placement, and seasonal mixing depths in a lake. Lakes typically have an upper **epilimnetic** region of warmer water, a lower **hypolimnetic** region of cold water, and an intermediate **metalimnion** or thermocline where temperatures change from warm to cold. In experimental enclosures and small (<20 km^2) lakes that lack zooplanktivorous fishes (and hence have zooplankton that remove phytoplankton), water is clearer, temperatures are 3–13°C higher in the metalimnion, and the greater penetration of light and heat leads to deeper thermoclines and a deeper mixed layer of epilimnetic water. Hence the heat content of a lake and all the biological and physical processes and interactions dependent on that heat may be strongly influenced by the top-down effects of fish predation (Mazumder et al. 1990).

Trophic cascades do not have to be unidirectional, e.g., either top-down *or* bottom-up. Flecker et al. (2002) added nitrogen and excluded grazing fishes from Andean streams. They found that excluding fishes had the strongest impact on algal biomass and composition, but that algae responded more strongly to nutrient addition when exposed to grazing fishes. Hence fishes affect primary producers directly through consumption and indirectly by influencing their response to nutrient availability, thus producing *both* top-down and bottom-up processes.

All of the above examples deal with relatively small- and medium-scale ecosystems involving a few species set in relatively simple food webs. We now know that large, complex, diverse oceanic systems are also driven by bottom-up and top-down, cascading trophic interactions, and that

human disruption of cascades in the form of global warming or overfishing can have far-reaching consequences. In the Northeast Pacific, the abundance and catches of valuable, predatory fish species is closely linked to a trophic cascade involving planktivorous fishes, zooplankton, and phytoplankton productivity. Phytoplankton production declines when warm water masses push into northern Pacific regions, eventually resulting in reduced fish yields (Ware & Thomson 2005). In the North Atlantic, accelerated overfishing of groundfishes (especially Atlantic Cod, but also Haddock, White and Silver Hake, Pollock, Redfish, and flatfishes) occurred in the 1980s and 1990s; these species were the top predators in the benthic and near-benthic communities. Cod stocks were reduced by more than 90%. The removal of these top predators had effects across five trophic levels (Frank et al. 2005). Small pelagic fishes and benthic invertebrates – the primary prey of the top carnivores – increased markedly. Their prey, large-bodied herbivorous zooplankton, decreased. In response, phytoplankton, chlorophyll levels, and nitrate concentrations increased.

Disruption of the trophic cascade has apparently affected ecological interactions within the North Atlantic food web, to the detriment of the ecosystem and its utility to humans. Altered conditions, especially the removal of the top predators, helped to release dogfish and skates from predation by and competition with groundfish species. As (desirable) groundfish decreased through the latter 20th century, (less desirable) skate and dogfish increased (Anderson et al. 1999; Reynolds & Jennings 2000) (Fig. 25.12). Unfortunately, the dogfish and skate increases may be irreversible. Despite bans on fishing, cod are not rebounding (Hutchings & Reynolds 2004; Olsen et al. 2004). The upsurge in their former prey may have turned the tables because these benthic, intermediate-level carnivores are predators on the young of the formerly abundant, top-level predators (although stomach contents analysis indicates that groundfish are uncommon food items of the elasmobranches; Link et al. 2002). Regardless, the prognosis for a rebounding cod fishery is not promising: "the time required for population recovery in many marine fishes appears to be considerably longer than previously believed" (Hutchings 2000a, p. 885).

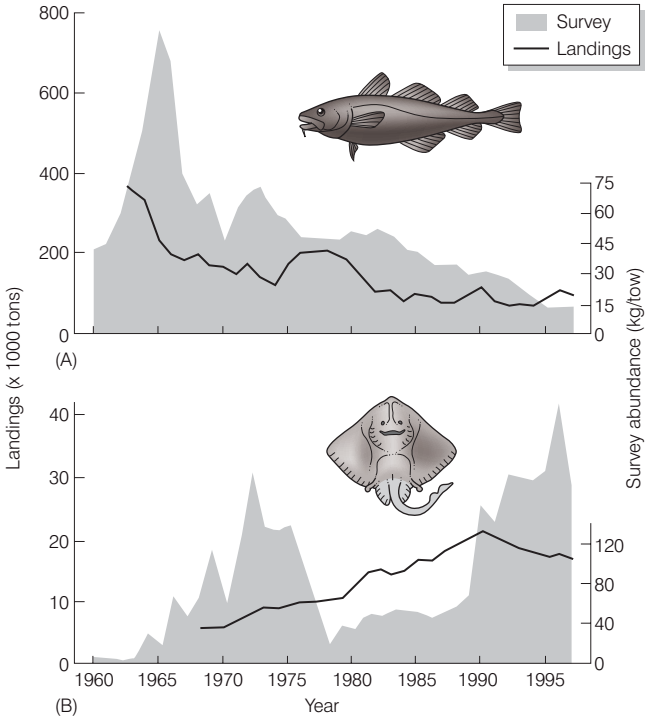


Figure 25.12

Disruptions of large-scale, oceanic trophic cascades can result in major shifts among interacting species. (A) Landings and abundance index for principal groundfishes and flounders off the northeastern USA. (B) Landings and abundance index for skates and Spiny Dogfish, showing increases in these less desirable species while groundfish declined. From Helfman (2007), after Anderson et al. (1999); fish illustrations after Bigelow and Schroeder (1953b).

Trophic cascades applied

Trophic cascades are of interest beyond the insight they give us into the function of aquatic ecosystems. They have been directly applied to problems associated with **eutrophication** in lakes, where excessive nutrient input such as from fertilizers leads to blooms of undesirable phytoplankton (Kitchell 1992; Carpenter & Kitchell 1993). Primary production and turbidity can be reduced by stocking piscivores that eat zooplanktivores or by selectively removing zooplanktivorous fishes. Both practices have the same theoretical result at the end of the trophic cascade: fewer zooplanktivores mean more zooplankton, which means more consumption of phytoplankton and clearer water, assuming that planktivores are not too big to eat and that phytoplankters are edible.

Direct application also occurs in the context of **marine protected areas** (MPAs) on coral reefs. MPAs are created in part to restore large predators, such as groupers. A potential negative outcome of increased predator biomass could be reduced prey numbers, which could be problematic if the prey were herbivores such as parrotfishes that consumed benthic algae that competed with corals for space. However, actual measurements of parrotfish numbers and algal biomass in successful reserves indicates that, despite increases among large predators, parrotfish also increase in size and number. This leads to a doubling of grazing and a four-fold reduction in macroalgal cover, which "highlights the potential importance of reserves for coral reef resilience" (Mumby et al. 2006) (Fig. 25.13).

Finally, failing to understand how trophic cascades function can lead to misapplications and unintended consequences (Fig. 25.14). Concern over shark attacks along South African beaches led to an extensive gill netting effort targeted at large sharks. This netting effort was very

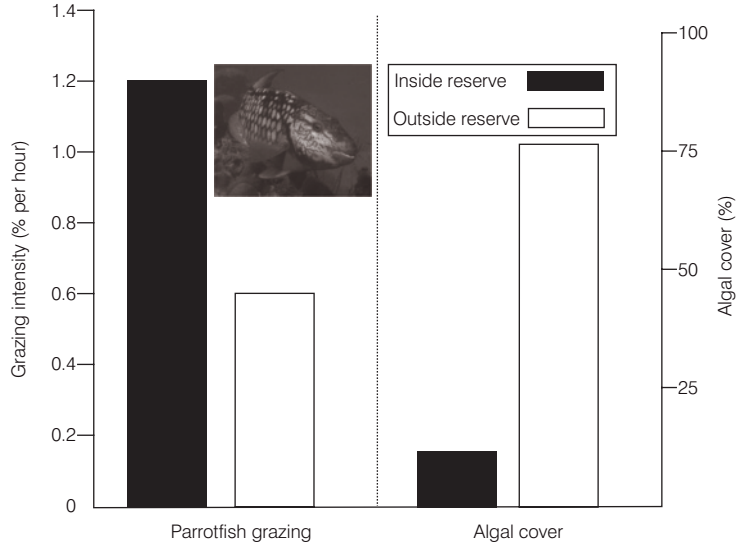


Figure 25.13
The relationship between parrotfish grazing and algal growth in a coral reef protected area, Exuma Cays Land and Sea Park, Bahamas. Left-hand bars show grazing intensity of parrotfishes and right-hand bars show percent cover of macroalgae inside (darkened bars) and outside (open bars) the reserve. Grazing was more intense and algal cover less inside the reserve. Redrawn from Mumby et al. (2006); parrotfish photo by G. Helfman.

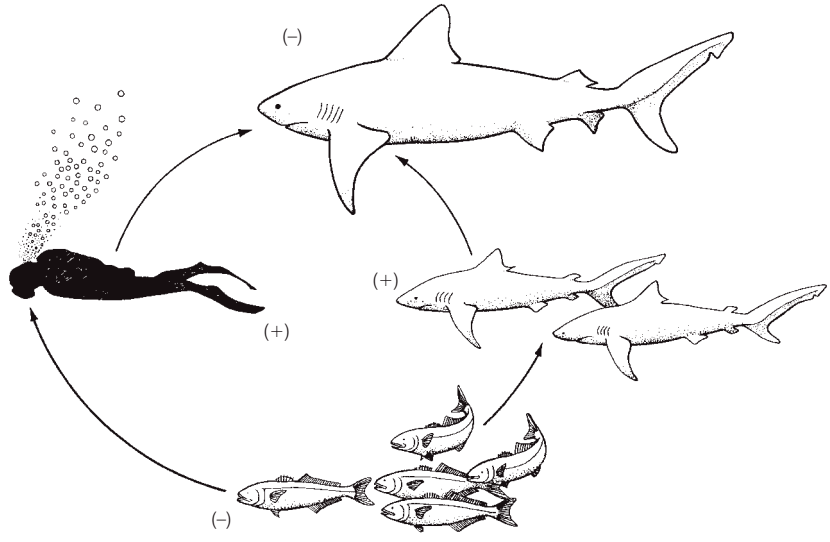


Figure 25.14
A trophic cascade with unexpected results. Extensive gill-netting of large sharks in the Natal region of South Africa removed large sharks, such as the Bull Shark, *Carcharhinus leucas*, a predator on humans. Primary prey of large sharks, such as juvenile Dusky Sharks, *C. obscurus*, increased in numbers. Abundant small sharks consumed sportfishes (e.g., Bluefish, *Pomatomus saltatrix*). (+) increasing population; (–) declining population. Based on data in Van der Elst (1979); drawings after Bigelow and Schroeder (1948b, 1953a).

successful and reduced shark attack frequency, but had a deleterious, cascade effect on sportfishes. Large sharks are predators on smaller sharks, and smaller sharks compete with humans for sportfishes. Hence by reducing the abundance of large predatory sharks, smaller shark species and the young of large sharks experienced a population boom, which in turn strongly depressed the abundance of finfishes in the region (Van der Elst 1979).

Nutrient cycling and transport by fishes

Fishes play an essential role in the **processing**, **transformation**, and **movement** of important nutrients in aquatic ecosystems (e.g., Vanni 2002). Phosphorus is often the nutrient that limits primary production in lakes. Fishes excrete soluble reactive phosphorus (SRP), a form that is readily taken up by algae. Phosphorus excretion by fishes may be the major source of SRP in many lakes, enhancing phytoplankton production and altering algal community composition (Schindler et al. 1993). Although phytoplankton biomass may increase when zooplanktivorous fishes eat phytoplanktivorous invertebrates, nutrient cycling rather than herbivory may be responsible for a significant portion of this trophic cascade-associated increase in phytoplankton (e.g., Vanni & Layne 1997; Vanni et al. 1997).

Fishes also function to move nutrients between different compartments of a lake ecosystem. Benthic-feeding fishes disturb sediments, accelerating the rate of exchange of nutrients between the water and bottom muds. The concentration of dissolved nitrogen and phosphorus is greater in the water and reduced in sediments when more bottom-feeding fishes are active. Vertically migrating fishes serve as

transporters of important nutrients between colder, deeper waters and surface layers where most primary productivity occurs. Peamouth Chub (*Mylocheilus caurinus*) feed on benthic invertebrates at depths greater than 20 m and then migrate to the surface at night during the summer and fall, where excretion and defecation can release nutrients in forms usable by plants. The movement of nutrients across the physical boundary of the thermocline is otherwise limited mostly to periods when the lake turns over, which may occur only once or twice annually in many temperate lakes and rarely in permanently stratified tropical lakes (Northcote et al. 1964; Northcote 1988).

Fishes can represent a major reservoir of nutrients that are essential for primary production and can therefore become part of the bottom-up pathway affecting ecosystem function. In some lentic habitats, 90% of the phosphorus in the water column may be bound up in Bluegill. These nutrients are released through excretion from the gills, through defecation, and through decomposition after death. Approximately 20% of the internal phosphorus entering a large Quebec lake during the spring could have come from decomposing fish that died after spawning (Nakashima & Leggett 1980). Excretion and defecation by Roach (*Rutilus rutilus*) contributed about 30% of the total phosphorus in the epilimnion of a deep Norwegian lake during the growing season (Brabrand et al. 1985). Fish feces and mucus could be important sources of iron in lakes where algal growth is iron-limited (Box 25.2). Fish removal experiments often

Box 25.2

BOX 25.2

Fish feces in the ecosystem: the coprophage connection

Although some fish are converted directly into other fish, squid, jellyfish, birds, and mammals via predation, a major path that energy takes from the organisms on which fish feed to other ecosystem components is through feces (Hobson 1991). For example, on coral reefs, many zooplanktivorous fishes feed on oceanic plankton and produce prodigious quantities of feces during the day that rain down on the reef; the bulk of these byproducts are eaten by **scatophagous** or **coprophagous** (feces-eating) organisms.

Consumers of feces include fishes and various invertebrates such as crustaceans, snails, brittlestars, and corals. Trophically, these organisms are generally considered to be herbivores, omnivores, and detritivores, but a significant proportion of their diet comes from coprophagy, and the fecal component in detritus undoubtedly contributes to its high amino acid and protein content (e.g., Crossman et al. 2001). When zooplankters are particularly abundant, they pass through planktivores' guts so rapidly that they appear basically undigested in the feces that fall to the reef. These conditions raise the possibility that coprophagous consumers gain more energy indirectly from zooplankton than do the planktivores that initially captured the zooplankton. At one Indo-Pacific locale, 45 different species of reef fishes from eight families (primarily sea chubs, damselfishes, wrasses, rabbitfishes, surgeonfishes, and triggerfishes) consumed 5975 fecal particles from 64 species in 11 families (Bailey & Robertson 1982; Robertson 1982).

These coprophages were not indiscriminate consumers. Fecal material from zooplanktivores and other carnivores was preferred, whereas feces from herbivores that ate brown algae (e.g., rabbitfishes) or from corallivores that consumed carbonate skeletal material along with coral polyps (e.g., parrotfishes) were generally avoided. The higher the caloric, protein, and lipid content of the feces, the more likely it was to be consumed. A typical fecal food chain might involve a zooplanktivorous damselfish producing feces that were eaten by a surgeonfish that normally eats red algae and whose feces are in turn eaten by a parrotfish that normally eats small algae and coral. Often, the nutritional value of feces eaten exceeded the value of the usual food of a species. Some fishes actively followed others and fed on their feces, indicating that coprophagy is not just incidental to normal feeding behavior. Interestingly, fish never ate feces from their own species, perhaps because most of the usable nutrition for that species had already been extracted, or due to the risk of parasite transfer.

A time delay may occur in the transfer of fecal material from fishes to other reef components. Following a day's (or night's) foraging, many fishes defecate or otherwise excrete at **resting sites** that are frequently quite distant from the original feeding site. In this way, fishes help exchange energy and nutrients between different parts of the reef. Deposition of feces and other excretory products, particularly of nitrogen and phosphorus, can lead to enhanced growth by corals that live under resting schools of grunts in the Caribbean (Meyer et al. 1983).

Linkages between different parts of marine ecosystems are not restricted to tropical waters. In temperate marine habitats, organic carbon was traditionally thought to either

be produced in situ by reef algae or transported unpredictably to the reef by currents in the form of plankton and detritus. Kelpbed zooplanktivores, such as the abundant Blacksmith (*Chromis punctipinnis*), also feed on oceanic plankton during the day and return repeatedly to the same resting crevices at night where they defecate. Blacksmith produce an average of 180 mg of feces per square meter of resting habitat each night. These feces are taken up by a variety of detritivores (gobies, clinids, shrimps, hermit crabs, amphipods, snails, brittlestars) which are in turn eaten by larger fishes. Blacksmith also excrete ammonium (NH_4^+) through their gills that is taken up readily by growing kelp plants, thus aiding the production of the habitat on which the entire kelpbed community depends. Rather than random arrival with currents, fecal and excretory inputs by fishes are a constant and reliable source of energy, nutrients, and trace metals for detritivores and plants, thus adding an additional pathway for the active capture and transfer of potentially limiting substances in nearshore habitats (Bray et al. 1981, 1986; Rothans & Miller 1991).

The importance of fish feces in the nutrient dynamics of other aquatic ecosystems has been less extensively studied. Little is known about this topic in temperate streams, although large amounts of feces accumulate in pools in some streams and are reworked by minnows (Matthews et al. 1987). Underwater photographs in African lakes that contain large numbers of cichlid fishes often show fecal material intact on the rocks (e.g., photographs on pp. 35, 53–70 of Axelrod and Burgess (1976) and pp. 15, 22, 31–42 of Lewis et al. (1986)). One would be unlikely to make such an observation on a coral reef, implying that the use of fecal material by fishes and invertebrates has not evolved as extensively in tropical lakes (the name of one Indo-Pacific riverine family, the Scatophagidae, implies that tropical coprophages are not unknown in fresh water).

Fecal material may nonetheless contribute substantially to the nutrient budget of lakes. Prejs (1984; and see above) calculated that two minnow species, Roach and Rudd, contribute approximately 133 kg of nitrogen and 12 kg of phosphorus during the 3-month growing season in a Polish lake as a result of the consumption and processing of macrophytes; additional nutrients are released from the digestion of benthic algae. Fishes are efficient consumers of plants but inefficient assimilators of the nutrients contained in the plants; 70–80% of ingested plant material leaves the gut as feces. In situations where high macrophyte biomass supports dense populations of herbivorous fishes, the digestive activities of the fishes can lead to undesirable plankton blooms (Prejs 1984). Where fishes use phytoplankton as a food source, as do many cichlids in African lakes, the redistribution of nutrients that fertilize phytoplankton from macrophytes through herbivores and into the water column may be important in the maintenance of a diverse and abundant fish assemblage. Overharvest of benthic-feeding herbivores could lead, indirectly, to reductions in populations of phytoplanktivores. Food webs are maintained through a complex series of linkages (Lowe-McConnell 1987).

lead to reductions in phosphorus and nitrogen levels in lake waters, whereas fish additions generally lead to increases in nitrogen compounds, except where herbivorous fishes are involved. When macrophytes are eaten, nutrients become available for uptake by phytoplankton (Northcote 1988).

Fishes can act to link different ecosystems together, such as seasonal migrations by characins in Neotropical rivers that make it possible for unproductive, nutrient-poor rivers to house large numbers of piscivores (e.g., Hoeinghaus et al. 2006). Such linkages are illustrated nicely by the life cycles of Pacific salmons and their impact on the energy and nutrient budgets of the different systems they inhabit (Brett 1986; see Chapter 23). Most salmon hatch in low-order (relatively small) headwater streams. After some time in the river or a lake, the fish move downstream and out to sea. Although abundant in numbers, their major impact on the stream or lake ecosystem while en route to the sea is as food for birds and other fishes, including larger salmon. As they move to sea, they represent a relatively minor loss of nutrients and energy from the river; about three times more phosphorus is gained during runs of adults into lakes than is lost when smolts emigrate (Stockner 1987). In the year or more they spend at sea, growth accelerates substantially. The 5 g Sockeye Salmon smolt that left its home river 2–4 years earlier may return as a 3 kg adult. In Babine Lake, British Columbia, 160 tons of smolts leave the lake each year. Despite 95% mortality while at sea, 3400 tons of maturing adults return to the lake. As thousands (historically millions) of these now mature salmon move back to their natal streams, they constitute a large proportion of the animal biomass present. Even Atlantic Salmon, many of which survive spawning at least once rather than dying, contribute significantly and positively to the nutrient and energy budgets of the rivers to which they return (e.g., Jonsson & Jonsson 2003).

Salmon, especially returning adults, also constitute a crucial food source for predators, including seals, sea lions, and killer whales in the nearshore zone, and other piscivores in the river itself (Fig. 25.15). Willson and Halupka (1995) identified 40 species of inland mammals and birds that feed on salmon, including ducks, geese, gulls, dippers, and robins on eggs; loons, mergansers, herons, terns, kingfishers, and

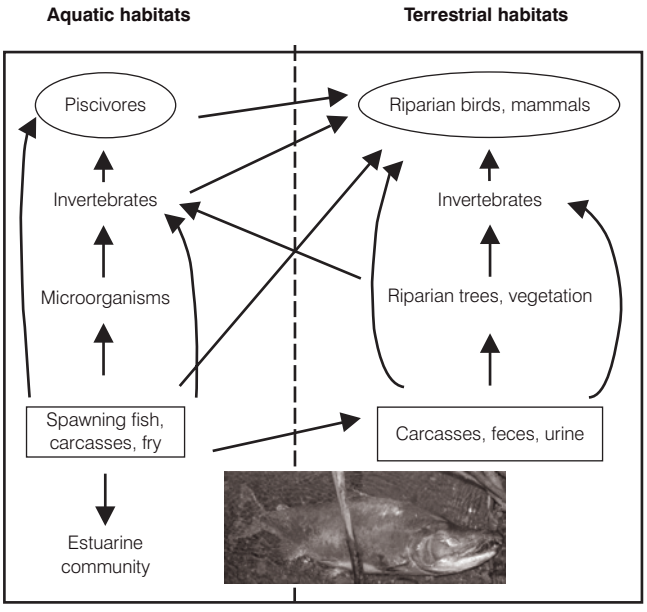


Figure 25.15

Salmon-derived nutrients and food webs based on anadromous fishes. The Pacific salmon ecosystem includes oceanic, estuarine, riverine, and old-growth forest components. Aquatic and terrestrial habitats are linked via predators and scavengers that feed on different life history stages. Inset: a decomposing Sockeye Salmon carcass. After Willson et al. (1998).

crows on juveniles; and eagles, hawks, magpies, ravens, and jays on adults and carcasses. Mammalian piscivores and scavengers include bears, mink, otters, wolverines, wolves, foxes, seals, mice, squirrels, and deer (this does not include eight to 10 riverine fishes that eat eggs and juveniles, numerous stream invertebrates that scavenge salmon carcasses, and a rich community of bacterial and fungal decomposers that recycle salmon-derived nutrients).

It is in the later stages of the spawning migration, and even after the migration, that the major ecosystem impact of spawning adults is felt. Spawning fish, postspawning fish, and spent carcasses floating downstream or decaying in the river and on river banks are crucial to ecosystem processes. As carcasses decompose, they are attacked by microscopic and macroscopic scavengers, releasing carbon, nitrogen, phosphorus, and other nutrients acquired at sea, which leads to significant increases in primary and secondary production. The transfer of energy and nutrients eventually feeds back on the next generation of salmon because of the linkages between ecosystem components (Willson et al. 1998; Schindler et al. 2003). Growth of juvenile salmon is closely linked to the availability of salmon carcasses in a stream (Bilby et al. 1996), in part because young salmon feed on invertebrates that feed on salmon carcasses. But juvenile salmon also benefit because streams with well-developed riparian vegetation provide better salmon habitat for spawning adults and developing fry via temperature-regulating shade, insect inputs, and woody debris inputs that control flow, sediment filtration, and bank stabilization.

Young salmon therefore depend on intact headwater streams embedded in old-growth forests, and the health of these forest ecosystems may be greatly influenced by the spawning migrations of adult fish. Bears and eagles that feed on salmon carry carcasses into the woods and also defecate there. These activities release phosphorus, nitrogen, carbon, and micronutrients that originated in the ocean. These **marine-derived nutrients** are taken up by riparian trees as far as 100 m from a stream (Helfield & Naiman 2001). Sitka spruce, an old-growth species, grows three times faster along salmon-bearing streams, producing the 50 cm trees that are most useful as woody debris inputs almost four times faster than trees along streams without spawning salmon (86 vs. 307 years). Hence, spawning salmon enhance the survivorship of subsequent salmonid generations in many ways besides direct, reproductive activity (Helfield & Naiman 2001).

Although less studied, the potentially important role of fishes in linking different ecosystems is becoming obvious as ecologists focus attention on nonsalmonid migratory species. Nutrients accumulate or are transformed as the result of spawning migrations, metabolic processes, predation, and the death and decomposition of spawning adults of other species, such as clupeids; these inputs can be linked to elevated ammonium concentrations and increased microbial and invertebrate production (Hall 1972; Durbin et al. 1979; Browder & Garman 1994). Alewives, *Alosa pseudoharengus*, migrate up rivers of the Atlantic coast of the USA to spawn. Juveniles spend their first half year of life in headwater lakes, and such lakes often produce trophy-size Largemouth Bass, *Micropterus salmoides* (Yako et al. 2000). Herring were the most important fish prey consumed by bass in such lakes, and bass grew better when herring were a diet component. Yako et al. concluded that juvenile herring were an energetically valuable, potentially key prey for Largemouth Bass. MacAvoy et al. (2000) similarly concluded that anadromous fish such as Blueback Herring, shad, and Alewife may be a significant source of nutrients to freshwater apex predators in tidal and freshwater regions. Garman and Macko (1998) used stable isotope analyses to investigate whether migrating clupeids (*Alosa* spp.) provided an important seasonal subsidy to energy and nutrient budgets of coastal waters. They found that predators in coastal streams derived a substantial proportion of their biomass carbon from marine sources during clupeid spawning runs.

Other reproductive migrations and life cycles may be equally important in transferring nutrients and energy between ecosystems. Catadromous fish migrations by eels and mullet export organic matter and nutrients to nearshore and offshore ecosystem components. Best studied are some fishes that utilize estuaries as part of a complex life cycle (Ray 2005). Gulf Menhaden (*Brevoortia patronus*) are the

numerically dominant fish species in estuaries throughout the Gulf of Mexico (Deegan 1993). These fish spawn offshore in December and January, enter estuaries as larvae in February, spend about 9 months feeding and growing in the estuary, and then migrate offshore in the fall as juveniles, having increased in body mass 80-fold (from 0.15 to 13 g) over that time. Their emigration represents a net export of energy, carbon, nitrogen and phosphorus from the estuary, totaling 930 kJ energy, 38 g biomass, 22 g carbon, 3 g nitrogen, and 1 g phosphorus for every square meter of estuary.

Such calculations indicate that between 5% and 10% of the primary productivity of the Louisiana saltmarshes is exported in the form of emigrating Menhaden. Menhaden may transport half of the nitrogen and phosphorus that leaves these estuaries, the remaining half leaving passively in tidal currents in the form of detritus and dissolved substances. However, the high lipid and protein content of clupeids makes these nutrients much more available to offshore food chains than is the case for the nitrogen, phosphorus, and carbon tied up in detritus. In fact, the estuary's loss is the nearshore environment's gain, as Menhaden are the major prey of many predatory fishes. The carbon contained in Menhaden represents 25–50% of offshore production (Madden et al. 1988). Many other species of fishes, particularly various croakers, have life histories that include larval growth in estuaries followed by offshore migration of juveniles or adults (see Fig. 9.11). Hence fishes link inshore and offshore ecosystems via their role in the exchange of energy, matter, and nutrients. Additionally, nutrient cycles and food webs are seldom limited to the particular habitat in which we find a species at any given moment. Ecosystems are connected to and intimately dependent on one another.

This complex interconnectedness of offshore, nearshore, and upstream habitats underscores the importance of an **ecosystem perspective** when managing fisheries or planning habitat-disturbing human activities. Because of the function of salmon and other migratory species (e.g., lampreys, sturgeons, clupeids, smelt, char, Striped Bass) as connectors and enhancers of ecosystems, Willson et al. (1998) referred to them as **cornerstone species** that provide a resource base that supports coastal and inland ecosystems. Overfishing, habitat destruction, or migration blockage due to dams erodes and eventually removes this cornerstone, which slows tree growth, produces shorter trees, reduces woody inputs, degrades riverine habitat, and eventually accelerates the decline of species important to humans. "The links between ocean and land mean that management of an ocean fishery can have far-reaching effects on distant ecosystems, and vice versa" (Gende et al. 2002, p. 924).

Fishes in food webs

Discussing top-down and bottom-up interactions can imply that linear food chains characterize many aquatic ecosystems. This is, however, a simplification of a much more dynamic situation because few straight line chains ("A eats B who eats C who eats D") exist. Instead, trophic interactions often involve herbivores that eat animals, carnivores that eat plants, cannibalism, reversals in energy transfer (one species eats juveniles of another species but winds up as the prey of the adults of the same species), and fishes that parasitize their predators by eating their fins, scales, and mucus. Most individuals enter a **detrital food loop**, either directly during decomposition or indirectly after falling prey and being processed into feces (see Box 25.2). Hence trophic interactions are more accurately described as **food webs** than food chains, and when disrupted can cause surprising results (Polis et al. 2004; see Fig. 25.14).

A particularly thorough analysis of the role of fishes in a community food web has been conducted for lowland streams in Venezuela and Costa Rica (Winemiller 1990b). The fish assemblages at four different sites included between 20 and 83 species that fed on detritus, plants, seeds, flowers, protozoans, aquatic and terrestrial insects, numerous aquatic invertebrates (worms, crabs, shrimps, clams, snails), fishes, larval amphibians, turtles, lizards, birds, and mammals. Food web analysis of relationships only between fish and their prey indicated between 50 and 100 interacting taxa and 200–1200 **trophic links** (i.e., one fish species might eat a dozen different food types, each one constituting a link) (Fig. 25.16). The pimelodid catfish *Rhamdia* fed at three different trophic levels: seeds, prawns, and fishes. More than a dozen species (mostly characins, catfishes, and cichlids) were omnivores, feeding extensively on both plant and animal matter. Detritus, formed from decaying aquatic and terrestrial vegetation, was a particularly important component, accounting for 30–50% of the food eaten by all species. Species as diverse as characins, catfishes, livebearers, cichlids, and sleepers fed directly on detritus. Reciprocal food loops were common. The trichomycterid catfish *Ochmacanthus* fed on the external mucus of Oscars (*Astronotus ocellaris*); Oscars in turn ate the catfish. A predatory cichlid (*Cichlasoma dovii*) ate juvenile Sleepers (*Gobiomorus dormitor*), while adult Sleepers ate juvenile cichlids.

As complex as the interactions in Fig. 25.16 appear, the actual food web is even more intricate. Different ontogenetic stages of a species were not separated in the analysis; nine dominant piscivorous species fed initially on zooplankton, switching later to invertebrates and eventually to fishes as they grew larger. The food webs at the four sites differed considerably due to varying diversities and species compositions, but differences also occurred within sites during the wet versus dry season. Even this seemingly complex description of interactions simplifies the true complexity of feeding relationships in a natural community, because only the interactions involving fishes are listed; other food items of the prey of the fishes were not considered (i.e., links between shrimp and snails or between

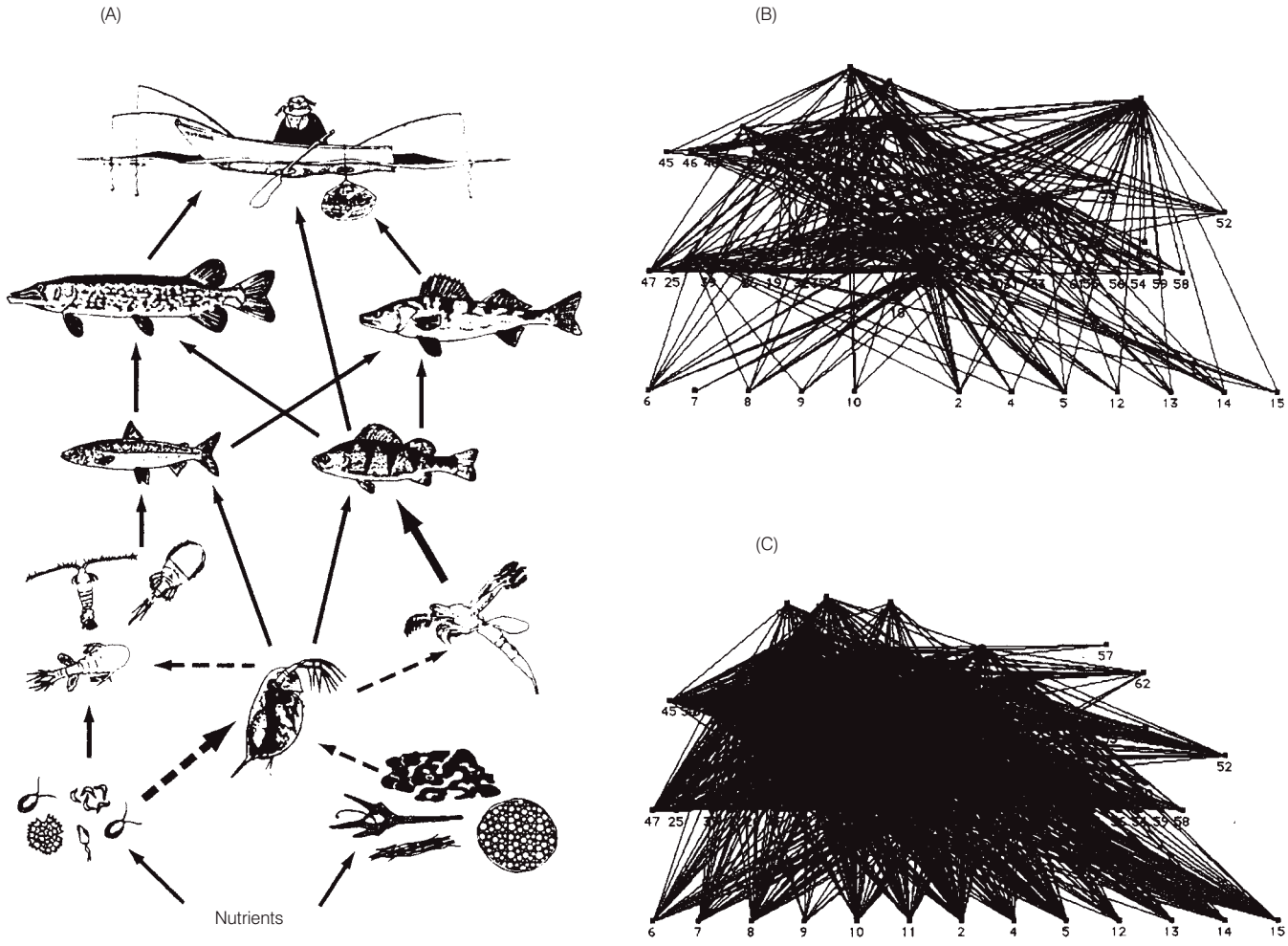


Figure 25.16

Food webs involving fishes. (A) A relatively simple food web in a temperate North American lake involving humans, predatory fishes (Pike, Walleye), planktivorous fishes (Cisco, Yellow Perch), invertebrate plankton, and algae. The thickness of lines reflects the importance of a food item in a species' diet. (B) A small, lowland forest stream in Costa Rica. (C) A swamp creek in Venezuela. Each numbered point in the webs represents a fish species or a prey taxon eaten by fishes. The base of the food webs is at the bottom and includes detritus, plants, and plant parts. Intermediate levels in the webs represent primary consumers (herbivorous fishes and invertebrates), with predatory fishes at the top. Eleven fish species are involved in food web B and 51 species in web C. (A) after Rudstam et al. (1992); (B, C) from Winemiller (1990b), used with permission.

aquatic insects and their prey). An often overlooked component of food webs concerns the placement of **parasites**, which are seldom included. The inclusion of parasites usually increases species richness, number of links, and food chain length plus two additional measures, **connectance** and **nestedness**, all which influence ecosystem stability (Lafferty et al. 2006). The web of feeding interactions in any community is undoubtedly tangled.

Most descriptions of trophic relationships within a community tend to characterize species as either relative specialists or generalists, referring to whether a species feeds predominantly on one or a few food types as compared to a species that feeds on many food types or even at several trophic levels. **Specialist–generalist** characterizations are used in general community descriptions and have also been invoked to explain the relatively high diversity of fishes and other taxa in tropical as compared to temperate communities. Tropical species are thought to be relatively specialized. The relatively narrow niches of specialists make it theoretically possible to fit more species into the resource spectrum of a habitat.

Although usually an accurate description, characterizing a species as either a specialist or a generalist may only apply to its habits under the feeding regime that exists in that habitat at the time of the description. An excellent example of this comes from a study of the feeding habits of two Panamanian toadfishes (Batrachoididae). Both species fed almost entirely (85–100%) on long-spined sea urchins,

Diadema antillarum (Robertson 1987). However, *Diadema* underwent a massive die-off in early 1983 that wiped out 95–99% of the individuals across the Caribbean region. One would have predicted that such feeding specialists as the toadfishes would suffer population declines because of their relatively invariant feeding habits. However, populations of both species changed little, reproduction continued, and food habits shifted to a variety of mobile benthic invertebrates in one species and to fishes and mobile invertebrates in the other species. Hence these classic trophic specialists became relative generalists, sounding a cautionary note for anyone attempting to characterize community feeding relationships.

Fishes as producers and transporters of sand, coral, and rocks

Fishes do not only move energy and nutrients around in aquatic ecosystems. They may also act as ecosystem engineers, contributing to the geological dynamics of an area. Anyone who has snorkeled on a coral reef has probably witnessed the trails of white material vented from the guts of parrotfishes. This excretory material is in part sand produced in the pharyngeal mill of the parrotfish (Fig. 25.17). Live and dead coral and coralline algae are ground up to separate the skeletal rock from algae growing on or in it (Bruggemann et al. 1996; Rotjan & Lewis 2006). Parrotfish also ingest sand trapped in algal turfs, so some sand in their stomachs is newly produced and some sand is recycled sediment. As parrotfish move about the reef, they therefore create new sand, and decrease the particle size of and redistribute old sand (Bellwood 1996).

Estimates of bioerosion vary considerably depending on parrotfish species and depth, but have been measured in excess of 1000 kg sediment/year/m^2 (Bellwood 1995b), with the highest bioerosion rates occurring in shallower reef areas and decreasing with depth (Bruggemann et al. 1996). Rates of sediment turnover can be two to five times higher than bioerosion rates (Ogden 1977; Frydl & Stearn 1978; Choat 1991). The activities of benthic-feeding fishes such as parrotfishes are the major vector of resuspension and movement of sediment on reefs in the absence of storms (Bellwood 1995a; Yahel et al. 2002). Predation on corals by parrotfishes may become an additional stressor with climate change. During the coral bleaching events that accompany temperature increases, corals that have been fed upon contain lower densities of symbiotic algae and may therefore be slower to recover (e.g., Rotjan et al. 2006).

Sand is also produced in the jaws and stomachs of other fishes that feed on corals and coralline algae, as well as those that crush mollusks and echinoderms (e.g., stingrays, emperors, wrasses, surgeonfishes, triggerfishes, puffers) (Randall 1974). Coral is moved around the reef in larger chunks by Sand Tilefish as they dig burrows and then construct piles of coral fragments over them. The mounds can measure 2 m across and several centimeters high and contain hundreds of coral and shell fragments. Frequently, tilefish mounds will be the only accumulations of hard substrate in large expanses of sand. Once abandoned by the tilefish, the mounds may be colonized by large groups of newly recruited damselfishes as well as small drums, butterflyfishes, angelfishes, and surgeonfishes (Clifton & Hunter 1972; Baird 1988).

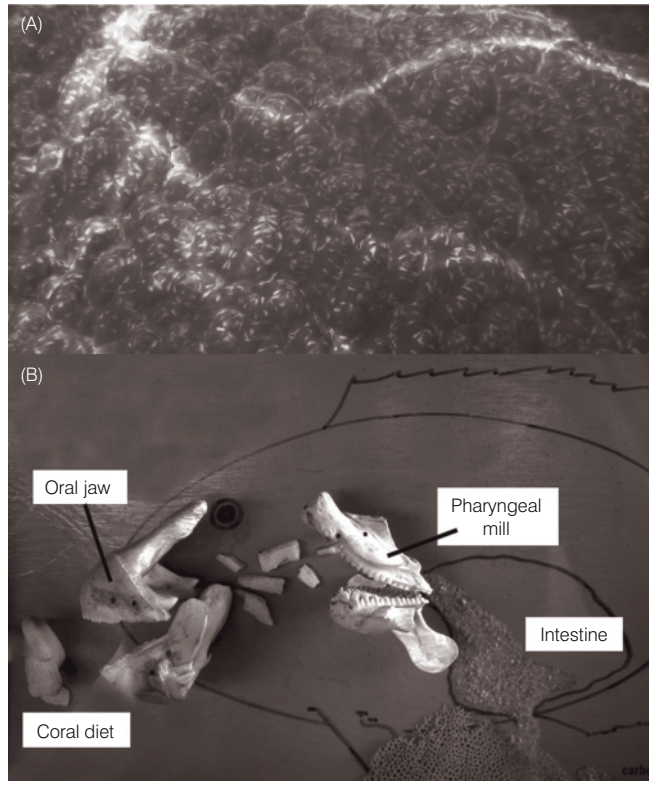


Figure 25.17
(A) Bite marks on a Pacific coral head from parrotfish grazing. (B) A model depicting the processing of coral fragments into sand as they pass through the mouth, pharyngeal mill, and gut of a parrotfish. Photos by G. Helfman.

A similar role is played by nest-building minnows in many North American streams (e.g., *Nocomis*, *Semotilus*, *Exoglossum*). A chub nest can contain thousands of stones as large as 1 cm across brought from several meters distance (Wallin 1989; see Chapter 21, Spawning site selection and preparation). The nest again constitutes hard substrate on an otherwise unstable bottom and is used for spawning by other species and is later colonized by various aquatic insects. The role of fishes as ecosystem engineers that affect the distribution of sediment particles via feeding and spawning activities has become more appreciated the more we investigate the phenomenon (Flecker 1997; Flecker & Taylor 2004; see Box 25.1).

Influence of physical factors and disturbance

Ecosystem ecology is concerned with biological interactions but also with the effects of physical and climatic factors on ecosystem components. Often these effects are most obvious when extreme climatic or other disturbances occur. The **structure** of a community, broadly defined to include species composition, abundance, distribution, and ecological interactions, changes in response to variation in climate and other forms of **disturbance**. Disturbance can lead to short-term changes in the physiology, behavior, or ecology of individuals (e.g., acclimatization, movement, trophic and reproductive adjustments), which result in alterations in community structure, which in turn affect the pathways and rates at which energy and nutrients flow through an ecosystem. Abiotic factors that function as disturbances to fishes and cause alterations in community structure and ecosystem function include but are not limited to reductions in dissolved oxygen, often in concert with increased water temperature; changes in stream and river discharge as the result of storms, floods, dams, and drought; and cyclonic storms in coral and kelpbed habitats. Biological disturbances that have ecosystem-wide repercussions include outbreaks of disease or population explosions of destructive species that affect the food and habitat resources of a system (Karr & Freemark 1985; Karr et al. 1992).

Temperature, oxygen, and water flow

Water holds relatively little oxygen, seldom more than 8 ppm, and levels below 1 ppm are generally fatal to fishes (see Chapter 5, Water as a respiratory environment). Hence periods of *deoxygenation* – due to excessive decomposition of plants and animals, a concentration of fishes trapped in pools during drought or following floods, high summer temperatures leading to thermal and oxygen stratification in lakes, or ice cover – are natural events that strongly affect the distribution and survival of fishes. Species with narrow ranges of tolerance for temperature and oxygen variation will obviously be most strongly affected by extreme conditions. Adult Striped Bass, *Morone saxatilis*, prefer temperatures between 18 and 25°C and oxygen concentrations above 3 ppm. In southern US rivers such as the St. John's in Florida and Flint in Georgia, Striped Bass in summer avoid high water temperatures in the main river and aggregate near inflowing springs that provide cooler, preferred temperatures. By the end of summer, these narrow thermal tolerances result in emaciated fish because of limited feeding opportunities in the springs. Thermal stratification in large reservoirs during the summer can also squeeze stripers into an increasingly small region near the thermocline to the point where mortality occurs if the fish are forced into the relatively deoxygenated but cooler waters of the hypolimnion (Coutant 1985; Van Den Avyle & Evans 1990; see Chapter 7, Thermal preference).

Extreme water flow can constrain fishes in streams and rivers. Small fishes and small species typically cannot hold position in swift water as readily as can larger individuals. Eggs and larvae may be washed out of a system or covered with silt if high flow conditions occur during the breeding season. Juveniles of quiet water species (e.g., many minnows, sunfishes) are frequently flushed out of headwaters during flood conditions (Schlosser 1985; Harvey 1987). Adult stream fishes can also be adversely affected if floods fill pools or riffles with debris (Minckley & Meffe 1987). Upland streams are, however, characterized by recurrent and dramatic fluctuations in flow regime and the fish faunal composition of such areas can return to its original state, probably via recolonization from downstream, within 8 months following even catastrophic floods (Matthews 1986b). In contrast, flooding further downstream is often an important signal inducing spawning in many river fishes because this is the time when riparian zones and gallery forests become inundated and create nursery habitats for juveniles (Welcomme 1985; Lowe-McConnell 1987; see Chapter 23, Reproductive seasonality).

Many species, including relatively small fishes, are of course well adapted to high flow conditions and have little difficulty maintaining position in surf zones (clingfishes, gobies) or swift flowing water (e.g., homalopterid hillstream loaches, Colorado River minnows and suckers, many darters, torrent fishes of New Zealand). Marked differences in adaptation to intermittent and extreme flow can occur between species within a family. The Sonoran Topminnow (*Poeciliopsis occidentalis*) and the Mosquitofish (*Gambusia affinis*) are both small, morphologically similar members of the livebearer family, Poeciliidae. The topminnow has evolved in desert streams of the American southwest that periodically experience flash floods. Mosquitofish are native to southeastern US lowlands where rapidly flowing water seldom occurs. Mosquitofish have been widely introduced into southwestern regions and prey on the young of topminnows, leading to population declines of the desert species. But the speed with which Mosquitofish eliminate the desert native is largely dependent on the extent of flash flooding. In locales where floods occur regularly, Mosquitofish are less successful because they lack the behavioral avoidance and orientation capabilities that topminnows display when flow rate increases. The introduced species gets flushed out of the system because of its inappropriate response to floods (Meffe 1984). The importance of maintaining natural flow regimes in preventing invasions of alien species has been shown repeatedly in studies of the fish fauna of California (e.g., Marchetti & Moyle 2001).

The opposite conditions of *low flow* lead to isolated habitats, desiccation, and deoxygenation. Upland fishes fre-

quently move downstream and floodplain fishes move into the main river as water levels decline. Isolated pools lead to an increased rate of ecological interactions as fishes crowd together. Competition may be reduced if species diverge in their resource use in response to dwindling resource availability. Seasonal shifts of just this type have been observed among Panamanian stream fishes, where the least diet overlap among species occurs during the dry season when resources are least abundant (Zaret & Rand 1971).

Seasonal cycles of changing water levels can lead to complex interactions among community components. The Everglades region of southern Florida experiences seasonally fluctuating water levels that usually include a dry season in the spring. This dry period concentrates fishes in relatively small pools (alligator holes) where they are preyed upon heavily by herons, ibises, and storks. The birds are dependent on the fishes for successful reproduction and eat 76% of the fishes in the pools. Although population sizes of the fishes are reduced, species diversity is highest during low water, with small species of omnivores and herbivores (mostly livebearers and topminnows) dominating. If water levels are high, the fish can escape bird predation (see Fig. 25.1) and bird populations decline. Relaxed bird predation leads to overcrowding if water levels then drop, resulting in 96% fish mortality from deoxygenation and also from predation by piscivorous fishes (bullhead catfish, Largemouth Bass, sunfishes). Overall fish diversity also declines as the predators eat the omnivores and herbivores. Hence *drought conditions* in the presence of predatory birds are beneficial to small fish species, but in the absence of wading birds are beneficial to larger, predatory fishes (Kushlan 1976, 1979; Karr & Freemark 1985).

Extreme weather

Extremes of climate act as disturbances in the marine environment also, although the effects appear to differ between sites and storms. Major tropical (**cyclonic**) storms can generate winds in excess of 200 km/h, creating waves more than 12 m high that break on relatively shallow coral reef environments. The influence of such waves is felt far below the surface, as massive corals are broken off and tossed around at depths exceeding 15 m and tremendous amounts of sand shift, are suspended in the water column, and scour most structure in the area. After a major cyclonic storm (such storms are generally referred to as hurricanes in the Atlantic and eastern Pacific, as typhoons in the northwestern Pacific, and as cyclones in the southwestern Pacific), few live corals remain in shallow water and major destruction can be found down to depths of 30–50 m depending on the nature and direction of the storm, tide stage when it struck, and bottom topography. When Hurricane Allen struck Jamaica's north coast in 1980, much of the shallow water coral and other structure was destroyed or damaged. Damselfish algal lawns were eliminated and the damselfish wandered around for over a week without displaying their usual territoriality. The territories they eventually set up were in deeper water and were associated with different coral types than were used before the hurricane. Parrotfishes formed smaller schools and stopped reproducing for 2 weeks. Normally cryptic and nocturnal species (moray eels, squirrelfishes, hawkfish, blennies) swam out in the open by day, perhaps because their refuges were destroyed. Planktivorous fishes (damselfishes, wrasses, bogas) hugged the reef rather than foraging high in the water column. Large predators (snappers, groupers, grunts) that were previously rare increased in number and swam conspicuously in the open, perhaps capitalizing on displaced and confused prey species. One year after the storm, species distributions and densities remained different, having shifted in favor of fishes associated with low relief habitats (e.g., rubble vs. upright coral). Analysis of coral recovery 6 years after the storm indicated that damselfish caused a decrease in the numbers and sizes of colonies of the dominant coral species (Woodley et al. 1981; Kaufman 1983; Knowlton et al. 1990).

Even moderate storms can have strong effects on reef fishes. A series of three relatively mild (sustained winds of 60 km/h) cyclones struck the northern Great Barrier Reef over a 2-year period. These storms caused little structural damage to corals but had major behavioral and community effects on the fishes (Lassig 1983). Suspended sand, moved by strong surge and currents, forced many otherwise benthic fishes up into the water column and caused visible wounds, apparently from collisions with corals. More importantly, juveniles suffered substantial population losses and subadults were redistributed; 60% of the species surveyed suffered density losses of juveniles following one storm. Poor recruitment in several species was attributed to injury or, more likely, settling juveniles being flushed from the system by strong currents. Hence periodic storms can play a decisive role in the structure of some reef communities.

Analogous events follow storms in temperate marine habitats. A series of severe winter storms occurred off California in 1980, destroying much of the canopy of giant kelp in coastal kelp beds and scouring the bottom. Removal of the kelp eliminated the major food of sea urchins, which switched to a diet of benthic algae and denuded the understory regions of reefs, "transforming the reef from a richly forested site to a barren area" (Stouder 1987, p. 74). The understory turf harbored invertebrates that were the major food types of the abundant, resident surfperches. Differences in microhabitat use and feeding patterns among surfperch species decreased as fish converged on the few areas where prey remained. Although adult surfperches remained in reef areas over the next 15 months, overall fish abundance decreased by 50% as nonresident and subadult fishes abandoned the reefs, probably because of loss of food and

refuge sites and unsuccessful competition with competitively superior, resident surfperches (Ebeling et al. 1985; Stouder 1987).

Not all storms, even major storms, have such clearcut effects on diversity and density of reef fishes. A severe 3-day storm struck the Kona coast of Hawaii in 1980, destroying most of the shallow water coral. Few direct fish mortalities or injuries occurred. Many shallow water species initially fled to deeper water, but returned to former areas after a few weeks or months. Sixteen months after the storm, diversity and density had returned to or surpassed pre-storm levels, with the exception of a few distributional shifts involving species that remained in deeper water (Walsh 1983).

Reduction in diversity and density is reversible if the causative agents do not recur frequently. The Florida Keys were exposed to record cold temperatures in the winter of 1977 that caused an extensive fish kill. Water temperatures fell to 11°C in areas that normally do not drop much below 19°C. Dead and dying reef fishes were found throughout the area; underwater censuses showed significant decreases in both species diversity and individual densities the following summer. However, by the next year, both overall diversity and density were not different from their pre-cold snap levels; in fact, diversity on some reefs was higher than before. These increases were largely the result of successful recruitment of many new individuals, perhaps because potential competitors and predators were eliminated by the cold weather (Bohnsack 1983; see also Thomson & Lehner 1976).

Biological analogs of extreme weather

Violent storms and sudden water temperature shifts create obvious and rapid changes in the physical environment of a habitat. Fishes can experience analogous disruptive effects as a result of the action of biological processes. Major disturbance events include **population explosions** of animals that affect the physical structure of a habitat. One such example is the crown-of-thorns starfish, *Acanthaster planci*, a predator on live corals through much of the Indo-West Pacific Ocean. Normally, the starfish occurs at low densities (2–3 animals/km^2), but periodically and for reasons that remain mysterious, the starfish undergoes population explosions producing densities of several starfish per square meter, with thousands of individuals swarming over a reef. The starfish consumes the live tissue on the surface of the corals; the underlying limestone skeleton first becomes covered with algae but then collapses due to biological and physical erosion. In this manner, 95% of the coral in a large area may be killed and will require 10–20 years to recover (Endean 1973; Wilkinson & Macintyre 1992).

Fishes that are directly or indirectly dependent on corals, either for food or shelter, suffer as a result. Coral-feeding fishes, including butterflyfishes, parrotfishes, gobies, wrasses, and triggerfishes, disappear from affected areas, leading to a 15–35% decline in species diversity on affected reefs. Densities of other coral-dependent fishes (many cardinalfishes, damselfishes, wrasses, gobies, blennies) also decline, leading to an overall reduction in fish density of 55–65% in an area (Sano et al. 1984).

Climate change and fishes

All of the external forces acting on fishes – temperature extremes, oxygen availability, floods, droughts, cyclonic storms, habitat loss – are influenced by climate, and there is little doubt that we have entered a period of human-induced **climate disruption**. The authoritative Intergovernmental Panel on Climate Change (IPCC), in its Fourth Assessment, concluded that climate change has happened and is happening, that it is largely influenced by human activity, that unprecedented warming and sea level rise are occurring ("warming of the climate system is unequivocal"), and that the consequences for humanity and the rest of earth's biota are serious (see IPCC 2007a, 2007b, 2007c, 2007d).

The effects that such unnatural change will have on fishes is in part speculative, but the speculation is scientifically based, and evidence of verifiable impacts grows as we learn where to look. Better studied, more accessible taxonomic groups – birds, mammals, insects, mollusks, plants, phytoplankton, zooplankton – are showing changes in distribution, abundance, physiological performance, and reproductive and migrational timing that are directly linked to documented climatic shifts (Walther et al. 2002; Ahas et al. 2006). "More than 80% of the species that show changes are shifting in the direction expected on the basis of known physiological constraints of species" (Root et al. 2003). Fishes can be expected to respond in similar ways, and the responses will affect all levels of ecological organization, from the genetics of populations, the interactions between fishes and other community components, as well as the roles that fishes play within ecosystems. Details of known and anticipated effects are given in Chapter 26 (Global climate change).

Summary

SUMMARY

1 Fishes interact with non-fish taxa, competing for food and space while eating and being eaten. The distribution of many fish species represents an avoidance of piscine, mammalian, and avian predators; in many streams, fishes are squeezed out of deep water by fish predators and out of shallow water by wading birds.

2 Herbivory among fishes is more common in tropical than temperate habitats; common herbivores include minnows, characins, catfishes, and cichlids in tropical fresh water, and surgeonfishes, parrotfishes, rudderfishes, blennies, and damselfishes on coral reefs. Fishes influence plant biomass, productivity, growth form, energy allocation, and species composition; fishes also disperse seeds. Plants have evolved mechanical and chemical defenses against herbivorous fishes. Damselfishes on reefs "garden" algae within their territories, encouraging edible species and discouraging growth of less palatable species. Damselfish activities thus affect the diversity and distribution of algae and the many invertebrates that live in algal patches.

3 Temperate freshwater herbivores include minnows, catfishes, suckers, pupfishes, and killifishes. During warm months when plants grow quickly, grazing minnows can crop most of the plant productivity. During cold months, temperate herbivores commonly shift to carnivory. Phytoplanktivory also occurs in temperate lakes, where fish such as shad can affect plankton abundance and diversity.

4 Lake fishes prefer to eat large zooplankters, which shifts the size and species composition of the plankton to smaller zooplankton species. Marine zooplanktivores that are active by day also preferentially eat large prey. Avoidance of foraging fishes may be responsible for daily vertical migrations by zooplankters, for day–night differences in zooplankton assemblage composition, and for life history and anatomical traits of zooplankters and other invertebrates.

5 "Trophic cascades" describe the direct and indirect effects that predators at the top of a food web can have on trophic levels several steps below. For example, piscivorous fishes eat zooplanktivorous fishes, which feed on herbivorous zooplankton, which eat phytoplankton. Hence removing the top piscivores has the unexpected effect of increasing phytoplankton density. Complex interactions of this nature indicate that changes in fish populations can ultimately affect water chemistry, calcium carbonate deposition, the distribution of water masses of different temperatures, and ultimately the heat budget of a lake.

6 Fishes can directly affect the transport and cycling of nutrients in aquatic habitats. Phosphorus excretion by fishes is important for algal growth. Benthic fishes disturb sediments, which increases the transfer of nutrients from the mud to the water column. Fish bodies contain a large fraction of the nutrients in many ecosystems; nutrients are released through excretion from the gills, through defecation, and through decomposition after death. Vertical and horizontal migrations by fishes that feed in one area and rest in another influence coral growth on coral reefs and kelp growth in kelp beds; the long-distance migrations of salmons link oceanic ecosystems with headwater streams, even influencing the growth of trees in nearby forests. Fishes can also affect the production and distribution of substrate, as when parrotfishes grind coral into sand, or when tilefishes or breeding minnows pile rocks over their burrows or nests.

7 Physical factors that appear to have the greatest effects on fish assemblages include reductions in dissolved oxygen from drought and ice cover, storm-induced increases in stream and river discharge, and habitat destruction on coral reefs and kelp beds from storm-caused waves. Biological disturbances with ecosystem-wide repercussions include outbreaks of disease or population explosions of species that literally eat the food and habitat resources of a system.

8 The global climate is changing due to human activities, with potentially severe consequences for fishes in almost all ecosystems.

Supplementary reading

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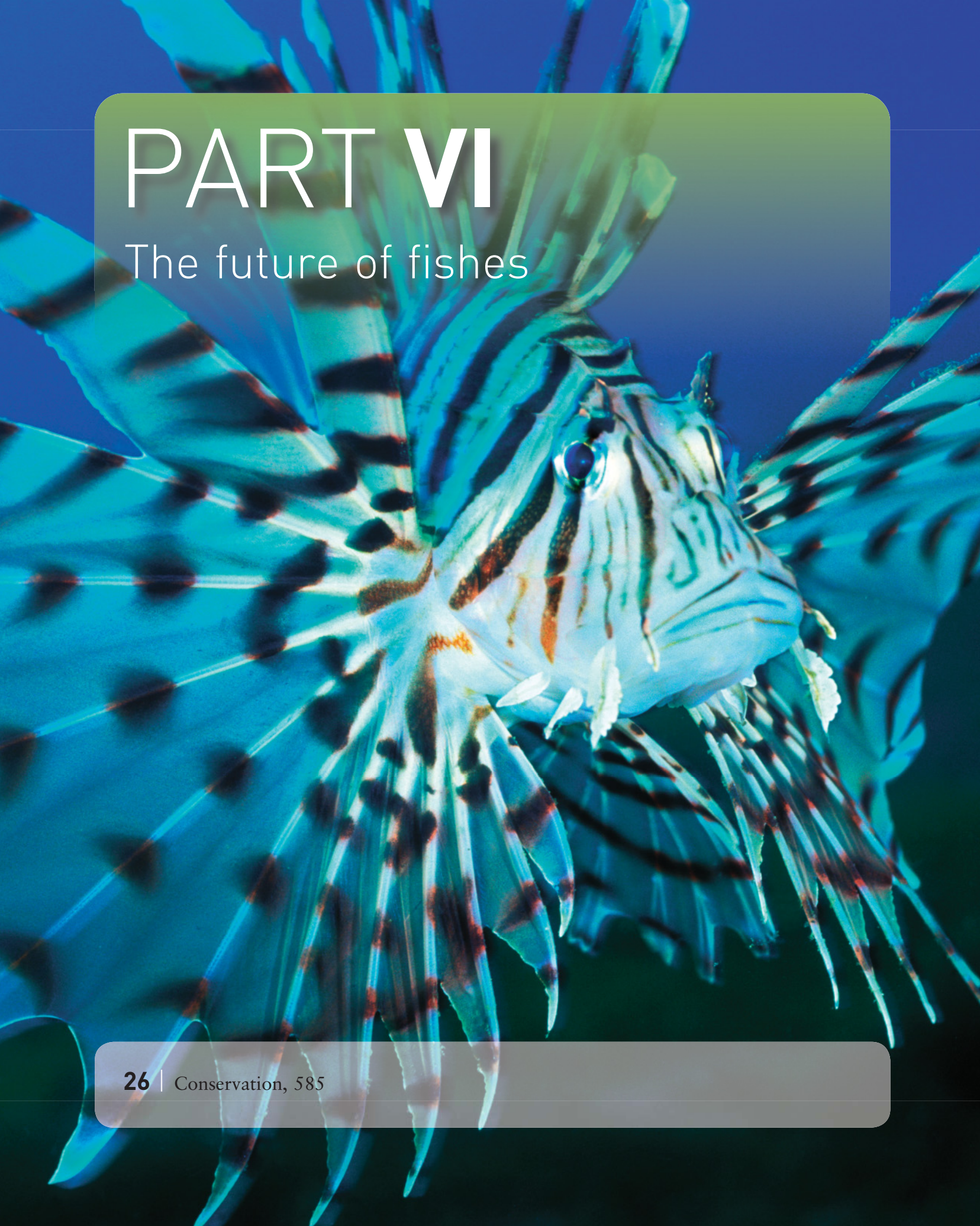
Websites

The Intergovernmental Panel on Climate Change Fourth Assessment (2007) reports are available at www.ipcc.ch.

The Millenium Ecosystem Assessment, www.millenniumassessment.org and www.maweb.org, is a massive, comprehensive overview of human interactions with the biotic world, organized around the topic of ecosystem services.

Figure VI *(opposite)*

Lionfish, *Pterois volitans* (Scorpaeniformes: Pteroidae), are native to the Indo-Pacific region. They have been introduced along the southeastern coast of the USA and the Bahamas, apparently due to aquarium releases. In their native habitats they seldom reach high densities but have undergone a population explosion on Bahamian reefs. Atlantic reef fishes are naive to lionfish predatory tactics, and predation rates by lionfish are high. Photo by D. Hall, www.seaphotos.com.



PART **VI**

The future of fishes

Chapter 26

Conservation

Chapter contents

CHAPTER CONTENTS

Diversity is a major theme of this book. Fishes are objects of wonder in large part because of their incredible diversity, a diversity that makes sense when viewed in the light of evolutionary processes. A major outcome of environmentally destructive human activities is loss of diversity and subsequent homogenization of habitats, genotypes, and assemblages. We conclude this book with a chapter on what we view as a major tragedy of modern times, namely catastrophic, human-caused reductions in the diversity of fishes and other life forms.

Extinction and biodiversity loss

Population declines lead to species declines, local **extirpation**, and eventually to global **extinction** of a species. Extinction is a natural process, and natural processes can be characterized by average rates. These rates have accelerated dramatically during past periods of major environmental change. But never in the history of the earth, as we are able to read that history, have global environmental changes resulted from the actions of a single species, nor have extinction rates approached the pace established in the last decades of the 20th century.

Historically, **extinction rates** for animals average 9% of existing species every million years, or one to two species per year. During the celebrated Permo-Triassic and Cretaceous–Tertiary mass extinctions that marked the ends of the Paleozoic and Mesozoic eras, respectively, extinction rates accelerated to perhaps 50–75% of the marine fauna over a period of 10,000 to 100,000 years (Raup 1988; Jablonski 1991). In stark contrast, extinction rates at the close of the 20th century have been estimated at upwards of 300 species per day or 100,000 per year, about 1000 to 10,000 times background levels and 10 to 100 times greater than the major extinction catastrophes of the past (Wilson 1988; Mann 1991). While the accuracy of such estimates is difficult to verify, there is little argument that extinction rates today exceed any in the past, recent millenia. This astounding loss of **biodiversity**, defined as the variety of life forms and processes, can be directly linked to the activities of an overgrown and overconsumptive human population (Groom et al. 2006). It is the purpose of this chapter to review examples and major causes of decline in fish biodiversity worldwide, and to present some of the solutions that have been suggested for slowing the rate of biodiversity loss. Fishes serve as just one example of the effects on living organisms of human-induced environmental degradation; biodiversity loss is panbiotic, cutting across and into all taxa.

Threatened and endangered fishes

Designation of a fish species as **threatened** or **endangered** is a complicated process influenced by political as well as biological concerns (see Wheeler & Sutcliffe 1991; Helfman 2007). The International Union for the Conservation of Nature (IUCN) publishes catalogs of such species periodically, in which it lists the numbers of plants and animals worldwide that are considered to be Critically Endangered, Endangered, Vulnerable, or otherwise at risk (see Box 26.1). Its Red List for 2006 identified 1170 fish species worldwide that were **imperiled**, and another 93 **extinct**, all of the latter from fresh water. The accuracy of such estimates is constrained by our limited knowledge of the popu-

Box 26.1

International efforts to protect endangered species

Most nations maintain lists of imperiled species, and most have endangered species laws that vary in thoroughness, effectiveness, and enforcement (Helfman 2007). At the international level, two entities deal best with global issues and the implementation of protection for biodiversity.

The International Union for the Conservation of Nature (**IUCN**; now known as the **WCU** or World Conservation Union) is the primary source for comparative information on the conservation status of fishes at national, regional, and global levels (www.iucn.org). The IUCN/WCU is an independent, international organization dedicated to natural resource conservation and the protection of endangered species. It is headquartered in Gland, Switzerland and employs a full-time staff of over 1000 in 62 countries, with a membership of 82 states, 111 government agencies, and more than 800 nongovernmental organizations. It is organized around six commissions, which consist of and are advised by more than 4000 scientists and experts. The **Species Survival Commission** (SSC), which oversees various fish specialist groups (freshwater fish, sturgeon, sharks, etc.), is most relevant to endangered species issues. The SSC maintains and updates the international **Red List** of threatened and endangered species (www.redlist.org). The 2006 Red List included 110 species of elasmobranchs (sharks, skates, rays), two species of lampreys, and 1058 species of bony fishes in its three highest at-risk ranks.

The Convention on International Trade in Endangered Species of Wild Fauna and Flora (**CITES**) is a cooperative, international program designed to protect wildlife from overexploitation and prevent international trade from further threatening imperiled species (www.cites.org). CITES involves 167 signatory countries, bans commercial trade of designated species, and regulates and monitors trade in species that may become endangered. Member countries agree to restrict trade in species listed in the appendices of the convention (www.cites.org/eng/app/appendices.pdf). Species in *Appendix I* are those threatened with extinction and therefore most vulnerable to commercial trading; they cannot be traded commercially between nations, although special permits can be issued for scientific study. *Appendix II* species could be threatened if trade were not restricted or regulated. *Appendix III* lists species that particular nations want to regulate or limit international trade. Inclusion in Appendix I or II requires agreement among signatory parties after often-protracted negotiations. Any country can place a species in Appendix III.

A limited number of fishes are currently (Jan. 2009) listed in CITES. Nine species are protected by Appendix I: both species of coelacanth (*Latimeria chalumnae*, *L. manadoensis*); Shortnose and Baltic Sturgeons (*Acipenser brevirostrum*, *A. sturio*); Golden Dragonfish, *Scleropages formosus*; Julien's Golden Carp (or seven-striped barb), *Probarbus jullieni*; Cui-ui Sucker, *Chasmistes cujus*; Mekong Giant Catfish, *Pangasianodon gigas*; and Totoaba, *Totoaba macdonaldi*. Appendix II includes all remaining 23 sturgeon species, all species of seahorses, and eight other fishes (White, Whale, and Basking sharks; Australian Lungfish, *Neoceratodus forsteri*; Arapaima, *Arapaima gigas*; the Congo Blind Barb, *Caecobarbus geertsi*; Humphead Wrasse, *Cheilinus undulatus, and Pristis* sawfishes). CITES is an invaluable source of information, especially via its relationship with **TRAFFIC**, publishing reports about taxa that are heavily exploited (e.g., on the shark trade, the Whale Shark fishery in Taiwan, the trade in seahorses, sturgeons and caviar, and Bluefin Tuna fisheries) (e.g., Rose 1996; Vincent 1996; Che-Tsung et al. 1997; see www.traffic.org).

CITES affects international trade but not trade within a country's boundaries, which requires passage of separate legislation in each country. It also focuses on wild organisms; endangered species reared in captivity are not controlled. For example, Shovelnose Sturgeon are protected as an Appendix II species, but one can buy young laboratory-reared Shovelnose Sturgeon via the internet in the USA.

lation status of fishes in most parts of the world: 35 (38%) of the 93 extinct taxa are from North America or Europe, and fully 43 of the 58 developing world species are (primarily Lake Victoria) cichlids. This means that only 15 species or 16% of known extinctions among fishes were non-cichlid, third world taxa. Conservatively, 85% of freshwater fishes occur in the tropics (e.g., Berra 2001), making our calculations of extinctions there a vast underestimation that must reflect scientific effort as much as it reflects environmental degradation (Harrison & Stiassny 1999).

Aside from records for certain industrialized nations (Table 26.1), we know comparatively little. North America

Table 26.1

Endangered and threatened freshwater[a] fishes of North America, as recognized and protected by federal authorities under the US Endangered Species Act (ESA), the Canadian Species at Risk Act (SARA), and the Mexican Norma Oficial Mexicana NOM-059-ECOL-2001. "Endangered" species face imminent extinction through all or a significant part of their range. "Threatened" species are likely to become endangered in the near future.

Family	Species native to North America[b]	Number of taxa designated as:					
		Endangered[c]			Threatened		
		USA	CA	MX	USA	CA	MX
Petromyzontidae, lampreys	20	0	1	2	0	1	1
Acipenseridae, sturgeons	8	4	1	1	2	0	0
Polyodontidae, paddlefishes	1	0	1	0	0	0	0
Lepisosteidae, gars	6	0	0	0	0	1	1
Cyprinidae, minnows	298	22	3	22	17	2	22
Catostomidae, suckers	72	6	1	2	2	1	7
Characidae, characins	8	0	0	1	0	0	1
Ictaluridae, bullhead catfishes	46	3	1	2	3	0	2
Pimelodidae, longwhiskered cats	6	0	0	0	0	0	3
Osmeridae, smelts	9	0	0	0	1	1	0
Salmonidae, trouts[d]	46	6	3	0	27	0	1
Amblyopsidae, cavefishes	6	1	0	0	1	0	0
Atherinopsidae, NW silversides	56	0	0	3	1	0	6
Aplocheilidae, rivulines	3	0	0	1	0	0	0
Fundulidae, topminnows	40	0	0	1	0	0	1
Profundulidae, MA killifishes	5	0	0	1	0	0	0
Poeciliidae, livebearers	93	5	0	9	0	0	9
Goodeidae, goodeids	47	3	0	10	1	0	4
Cyprinodontidae, pupfishes	44	7	0	18	0	0	5
Gasterosteidae, sticklebacks	5	1	6	1	0	0	0
Synbranchidae, swamp eels	3	0	0	1	0	0	0
Cottidae, sculpins	121	0	0	0	1	3	0
Cichlidae, cichlids	46	0	0	3	0	0	1
Percidae, perches	189	13	0	2	7	2	2
Gobiesocidae, clingfishes	38	0	0	1	0	0	1
Gobiidae, gobies	101	1	0	0	0	0	0
Totals		72	11	81	63	11	67

Sources queried in July 2007 were, for the USA, http://ecos.fws.gov/tess_public; for Canada, www.sararegistry.gc.ca; and for Mexico, Norma Oficial Mexicana, www.ine.gob.mx/ueajei/publicaciones/normas/rec_nat/no_059_a2f.html.

CA, Canada; US, United States; MA, middle American; MX, Mexico; NW, New World.

[a] Few marine species are listed in any of the three countries: four in Canada, 15 in Mexico, and one in the USA (and another 16 are considered "Species of concern"; www.nmfs.noaa.gov/pr/species/fish).

[b] From Nelson et al. (2004), who list only described species but not subspecies. Includes extinct but not introduced species.

[c] Endangered designation in Canada and Mexico includes extinct and extirpated species (see Helfman (2007) for a rationale).

[d] Many protected salmonids in the USA represent distinct population segments or evolutionarily significant units.

has about 1000 freshwater fish species, of which about 350 (35%) are in need of protection throughout all or part of their range. Of Europe's approximately 350 species of freshwater fishes, about 40% are in serious need of protection. Australia has 200 freshwater species, of which about 15–30% are in trouble. About 60% of South Africa's 100 species are similarly at risk (Lelek 1987; Williams et al. 1989; Kottelat 1997, 1998; ASFB 2001; Skelton 2002; Jelks et al. 2008). In tropical countries, with their thousands of endemic species and rapidly dwindling rainforests (see Chapter 16), faunal surveys are incomplete and we have no way of estimating which species are declining and which habitats need protection. It is estimated that, worldwide, between 20% and 35% of the world's approximately 11,000 species of freshwater fishes and perhaps 5% of 17,000 marine species are in serious decline or already extinct (Moyle & Leidy 1992; Leidy & Moyle 1999; Helfman 2007).

The data from species known to be extinct are sobering. Harrison and Stiassny (1999), using strict criteria and a conservative approach, estimated that between 95 and 171 known fish extinctions had occurred. The former number is close to the 93 extinctions recognized by the IUCN in 2006. Unresolved, problematic, and debatable extinctions raise the number to between 210 and 290, depending on how many cichlids from Lake Victoria are included. In North America, 40 distinct fishes (27 species and 13 subspecies) became extinct in the past century (Miller et al. 1989) (Fig. 26.1A). Ten of these species had apparently viable populations in 1979, reflecting an increasing extinction rate (e.g., 52% of the extinctions occurred between 1900 and 1964, the remaining 48% disappeared in only the next 25 years). The causes of extinction are often discernible, and underscore the environmental problems that form the focus of this chapter (Fig. 26.1B). **Habitat alteration** is the most frequently cited factor, causing 73% of extinctions. Other factors include **introduced species** (68%), chemical alteration or **pollution** (38%), **hybridization** (38%), and **overharvesting** (15%).

Extinction factors often operate in combination. Some reported extinctions represented the elimination of isolated populations, such as the Miller Lake Lamprey, *Lampetra minima*. This unique dwarf lamprey was endemic to one small lake in southern Oregon. Because it parasitized introduced trout, it was poisoned into apparent extinction (Bond & Kan 1973). Although remnant populations were subsequently found in tributary streams, the lamprey has not recolonized Miller Lake (Lorion et al. 2000). Other extinct species were, however, widespread, such as the Harelip Sucker, *Lagochila lacera*, which occurred commonly in large rivers of at least eight eastern states and probably succumbed to siltation of its clear water, pool habitat. The Blue Pike, *Sander vitreus glaucus*, a subspecies of the Walleye, sustained a large fishery in Lake Erie and Lake Ontario until the mid-1950s; in some years, it made up more than half the commercial catch in those lakes. Pollution, introduced fishes, habitat degradation, overharvesting, and hybridization all contributed to its demise (Miller et al. 1989). It was officially declared extinct in 1975.

Certain obvious patterns arise from lists of species at risk. Freshwater fishes account for practically all extinct and compromised taxa, reflecting the sensitivity of, human density near and impact on, and the degraded condition of freshwater habitats. Certain regions and habitat types appear most frequently on the lists. In North America, the

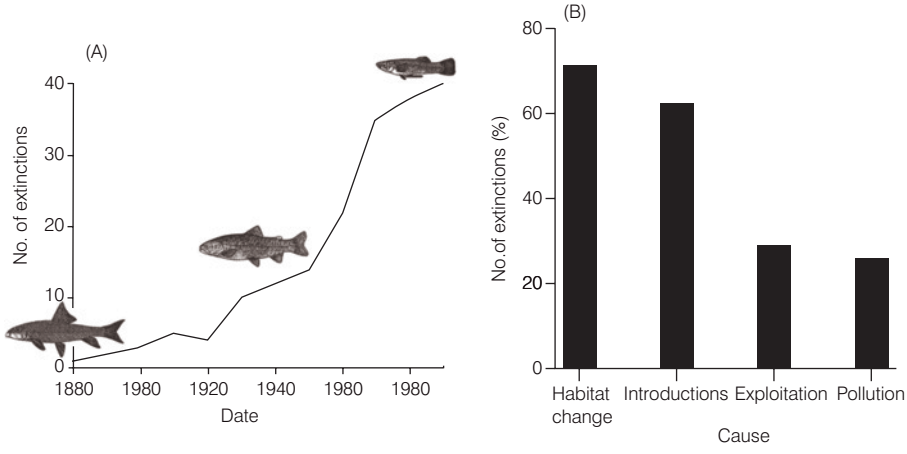


Figure 26.1

Extinction rates and causes. (A) Fish extinctions in North America. Extinctions grew steadily over the past century until the latter part, when they apparently slowed down, possibly indicating improved conditions or early elimination of more sensitive forms. Illustrated left to right are the Harelip Sucker (extinguished *c*. 1900), Alvord Cutthroat Trout (*c*. 1930s or 1940s), and San Marcos Gambusia (*c*. 1980). (B) Major causes of fish extinctions globally. Habitat alteration, introduced species, overfishing, and pollution are the primary agents, but combined factors cause the most extinctions, which is why the summed percentages of all columns exceed 100%. (A) from Helfman (2007), after Stiassny (1999); sucker drawing by J. Tomelleri, trout and gambusia by Sara V. Fink, used with permission of the artists; (B) from Helfman (2007), based on Harrison and Stiassny (1999).

isolated and disjunct aquatic systems of the otherwise arid southwest, such as the spring pools and rivers of the Great Basin and of Mexico, have been centers of evolution and human-induced extinction (Minckley & Deacon 1991; see Chapter 18, North American deserts). Specialist species endemic to small, isolated habitats make up the majority of extinct and endangered fishes because both they and their habitats are exceedingly vulnerable to human activity. An isolated stream or pond can be easily destroyed by the dumping of toxic substances, introduction of predators, habitat modification, or water withdrawal (e.g., the Devil's Hole Pupfish, *Cyprinodon diabolis*, which occupies a 3 × 6 m limestone shelf in a cave, the smallest habitat of any vertebrate).

It is not just small, isolated habitats though that are vulnerable. Big river fishes with special needs for clean water, such as sturgeons, paddlefishes, and some suckers and large minnows, have also been strongly affected. Large rivers are primary sites of human habitation and impact; such habitats have been degraded for centuries due to pollution, siltation, water withdrawal, and damming. Comparatively few marine fishes appear on lists of species at risk (but see Musick et al. 2001). Marine fishes have broad distributions and a greater chance for replacement by neighboring populations (except for the coelacanths, see Chapter 13). Hence, aside from some heavily exploited coastal and pelagic species (e.g., many sharks, Bluefin Tuna) and long-lived, slow-growing forms (Orange Roughy, Patagonian Toothfish), the most vulnerable marine fishes are estuarine species that have been affected because of their dependence on fresh water in their life cycle, such as the giant Totoaba, *Totoaba macdonaldi*, and many salmonids (Moyle & Leidy 1992; Helfman 2007; see below).

General causes of biodiversity decline

The close of the 20th century witnessed a number of well-publicized environmental problems of regional and international scale. Each problem contributed to declines in fish biodiversity (Safina 2001a). In addition to habitat modification, species introductions, pollution, and commercial exploitation, **global climate change** is recognized as a growing threat to aquatic ecosystems and fishes (IPCC 2007d; see Chapter 25, Climate change and fishes). An additional problem is our collective inability to learn from past experiences. We thus repeat our mistakes, as has happened to salmon fisheries in continental Europe, then the British Isles, followed by the northeastern USA and Canada, and finally the eastern Pacfic and Japan (Montgomery 2003). These interacting causes result in direct population losses due to mortality or reproductive failure, or indirect losses due to hybridization or loss of genetic diversity. At the root of each problem is **human overpopulation** and **overconsumption**. Overpopulation is particularly destructive to aquatic ecosystems and to fishes because humans are concentrated along rivers and estuaries.

Habitat loss and modification

Human alteration of aquatic habitats is the most commonly cited cause of declines in fish populations. Habitats are altered via modification of bottom type and above-bottom structure – channelization, dam building, watershed perturbation, and competition for water.

Modification of bottom type

Many fish species are ecologically dependent on bottom topography and above-bottom structure for successful survival. In flowing water, rocks and logs provide shelter from the current and a site of attachment for eggs, algae, and associated fauna. Undersides of rocks are a major refuge for insect larvae and other invertebrates that fishes eat. Aquatic vegetation similarly provides shelter and food attachment sites for lacustrine fishes. In the ocean, rocks and biogenic habitat (corals, sponges, many other sessile invertebrates, kelp beds and other attached algae) are essential habitat for most benthic species. Human activities that disrupt, remove, or cover bottom structure will be detrimental to fishes. Such activities include dredging for navigation and to obtain construction materials, bottom trawling in the ocean, removal of logs and debris dams to aid navigation and as "habitat improvement", and watershed disruption that leads to increased erosion and silt deposition (Fig. 26.2).

Woody debris in streams and rivers exemplifies the effects of habitat disruption on fishes. Woody debris, in the form of debris dams in streams and of logs (= snags) in rivers, plays a critical role in ecosystem function (Wallace & Benke 1984; Harmon et al. 1986; Maser & Sedell 1994). Debris dams retain silt, organic matter, and nutrients, offer a solid substrate for invertebrate attachment, and are a site for transformation and processing of organic matter, thus making it available for invertebrate and fish use. Woody debris also slows the flow of the water, which decreases erosion and increases the time during which nutrients are available to the food web. In coastal, low-gradient (slow moving) rivers, many gamefishes obtain more than half of their food directly from snags. Snags are the most biologically rich habitat in such rivers: although making up only 4% of habitable surfaces, snags contain 60% of the total invertebrate biomass, provide 80% of the drifting invertebrate biomass, and produce four times more prey than mud or sand habitats (Benke et al. 1985). Government efforts at snag removal in navigable rivers of the southeastern USA began in the early 1800s. When rail transportation largely replaced river commerce in the 1850s, snag removal was

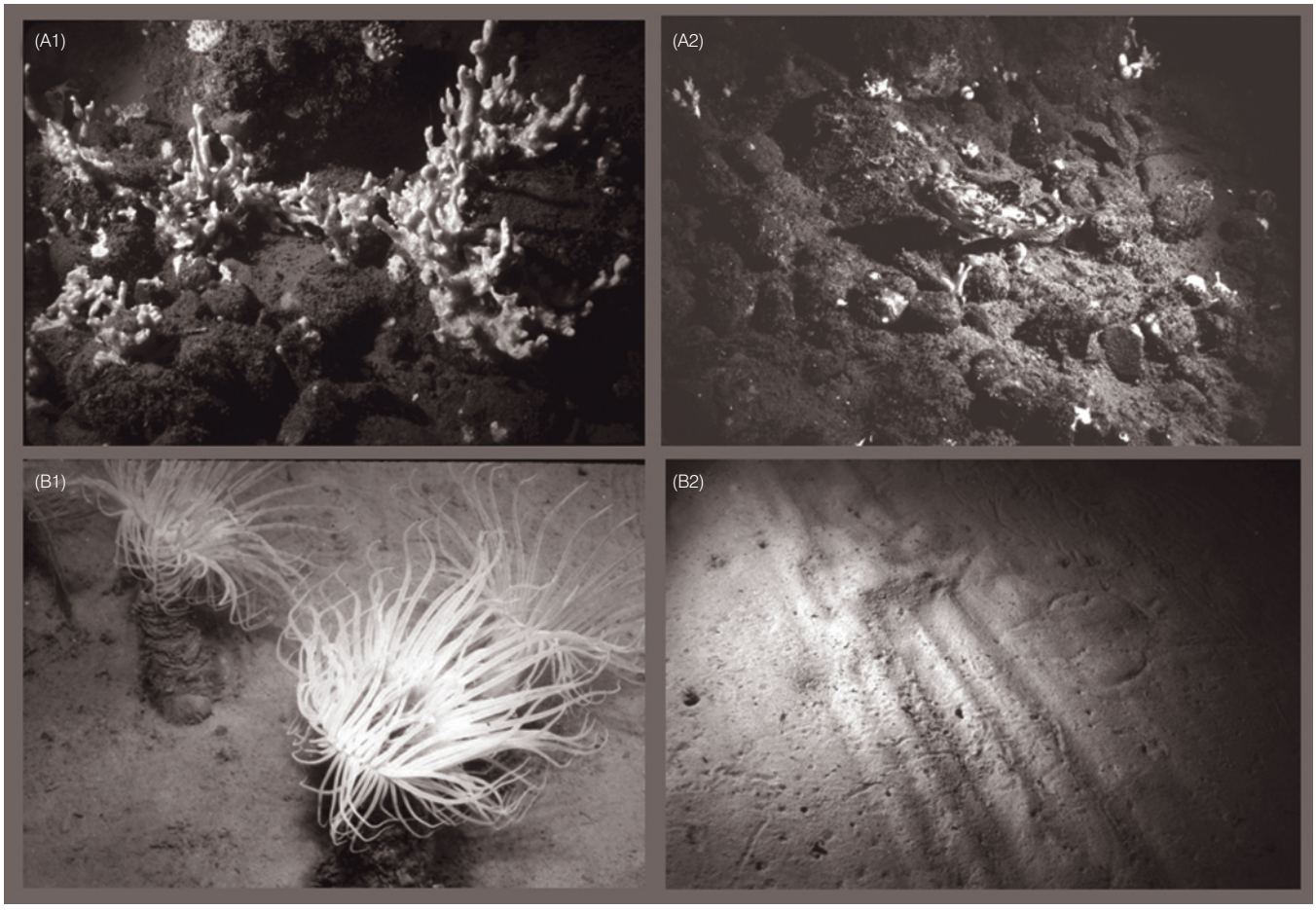


Figure 26.2

Impacts of bottom trawling on gravel (A) and mud (B) habitats, Stellwagen Bank National Marine Sanctuary, Gulf of Maine. Gravel habitats protected from trawling (A1) contain erect sponges; areas open to trawling (A2) lack such biogenic structure (a Longhorn Sculpin, *Myoxocephalus octodecemspinosus*, is visible in the center of photo A2). Mud habitats also contain biological structure such as burrowing anemones (B1), whereas trawled areas (B2) can be devoid of such structure (note trawl gear tracks in B2). Photos courtesy of P. J. Auster, National Undersea Research Center, University of Connecticut.

less important, but the practice was continued by the US Army Corps of Engineers throughout the USA until the 1950s. Many state agencies continued to emphasize removal of woody debris as a habitat improvement tool (Sedell et al. 1982).

In the tropics, catastrophic *deforestation* along rivers and streams adversely modifies both terrestrial and aquatic habitats (Chapman & Chapman 2003). In tropical marine environments, *coral reef destruction* occurs at an equally alarming rate. Coral reefs contain the most diverse fish assemblages on earth, but reefs suffer both directly and indirectly from human activities. Habitats are destroyed by the direct mining and collecting of coral, and inadvertently by harmful fishing techniques (poisons, explosives, bottom trawling), boat anchoring and diver activities, sedimentation and pollution, boat groundings, and changes in coral predator abundance as a result of fishing practices. All these phenomena lead to reductions in fish diversity and biomass because fishes and their prey rely directly on corals for food and shelter (Birkeland 1997).

Coral mining is a particularly deleterious activity. Limestone blocks are cut from the reef surface and then used in road and home building and as landfill. Massive, head-forming corals in shallow (1–2 m depth) water are most frequently targeted. Where heavily practiced, coral cover can change from 50% to 5% both as a direct result of removal and as a byproduct of trampling and sediment production. Recovery is slow, taking more than a decade, if it occurs at all. Fish biomass, abundance, and diversity decline in mined areas through reduction in living coral and also through reduction in substrate rugosity (topographic complexity) (Bell & Galzin 1984; Shepherd et al. 1992).

Coral collecting for the aquarium trade has also taken a significant toll on reef habitat (Derr 1992). Both live corals

and algae-covered or invertebrate-encrusted dead corals are taken. Live coral and "live rock" were removed from the Florida Keys at a rate of 3 tons/day in 1989, with an annual retail value of around U$10 million. Live rock consists of substrate built over 4000–7000 years and does not represent a renewable resource on the reef. Mortality rates for live corals in aquaria exceed 98% within 18 months of collection. Because of the acknowledged difficulties of keeping live coral and reef-building invertebrates in captivity, most large, commercial "public" aquaria use artificial corals; home aquarists should do the same.

Channelization

Channelization, also referred to as "bank stabilization", involves straightening a riverine system and smoothing its sides. Bends in a river are bulldozed into straight lines, levees are built, and banks are covered and heightened with stones and boulders (riprap) or concrete. Rivers and streams are channelized primarily to reduce seasonal inundation of the floodplain (so-called because the floodplain is the natural area that receives overflow during seasonal rains); channelization is basically the process by which a river or stream is converted into a ditch or pipe. Channelized stream segments have low habitat heterogeneity and higher velocities during higher flows. Shallow water and floodplain habitats are eliminated, both of which provide spawning and nursery areas for riverine fishes. Channelized rivers either lack fishes or are dominated by introduced species. Especially affected are big river species, species dependent on sandy areas, and fishes that use the floodplain in their life cycle, including sturgeons, Paddlefish, and darters of the genus *Ammocrypta*. Channelization-induced loss of the floodplain in parts of the Lower Mississippi River has led to a 10-fold reduction in standing biomass of fishes.

Because channelization is often accompanied by deforestation of the floodplain to allow for agriculture and housing development, the entire hydrological regime of a river is altered, with a result that flooding actually increases (Simpson et al. 1982; Moyle & Leidy 1992). The catastrophic flooding of the Mississippi River in 1993 was partly due to decades of channelization (Myers & White 1993); inundation of New Orleans by Hurricane Katrina in 2005 was a result of levee construction that delivered sediment too far downstream thus preventing the development of wave-buffering, nearshore wetlands.

The adverse effects of channelization have been so great in some areas that expensive "dechannelization" programs have been initiated. In southern Florida, the US Army Corps of Engineers channelized the meandering, shaded, productive 165 km long Kissimmee River, turning it into a 90 km long, straight, concrete canal. Channelization resulted in drained wetlands (including desiccation of substantial portions of the Everglades National Park), water pollution and eutrophication, periodic flooding, salt contamination of streams and aquifers, water table lowering and land subsidence, oxidation of peat soils, wind erosion, and marsh fires. Biological effects included a 90% decrease in wading bird populations, the deaths of 5 billion fishes and 6 billion shrimp, and extirpation of six native fishes from the Kissimmee River. In 1976, Florida reconsidered the project. The Corps proposed dechannelization, which began with feasibility studies in 1978–85 and then again in 1990–98. Actual dechannelization is ongoing and will constitute the largest river restoration project ever undertaken in the USA, requiring more than 13 years and costing over $500,000,000 (this number increases regularly). Restoring the river, which has begun, will take several years more and cost perhaps 10 times more than channelization (Koebel 1995; Whalen et al. 2002).

Dam building

Dams provide hydroelectric power, water storage capacity (although evaporation often minimizes water storage benefits in arid regions), agricultural water, recreational opportunities, and lakefront development potential. Drawbacks of dam building include flooding of agriculturally and historically valuable land. Poor watershed management, often brought on by deforestation of the land surrounding newly created reservoirs, leads to rapid **silting-in** of the lake, transforming it into a much less desirable (from a development standpoint) marsh or swamp. In tropical countries, regions around dams become uninhabitable for humans because the altered habitats favor organisms that cause such debilitating parasitic diseases as schistosomiasis and onchocerciasis (river blindness). Increases in these and other diseases are well documented in human populations residing near newly created dams (e.g., Steinmann et al. 2006).

The **altered hydrological conditions** behind dams can cause other, unforeseen problems. Piranha attacks on healthy humans in the Amazon Basin are exceedingly rare (Sazima & Guimaraes 1987). Dam construction created year-round, favorable, still-water conditions for piranha spawning, whereas spawning habitat was previously limited to flooded forest lands during the wet season. Piranhas defend their nest sites against intruders, including waders in the shallow waters of reservoirs. Single bite attacks characteristic of nest defense rose dramatically after dam construction. Bathers in reservoirs in the Parana–Paraguay river systems in southeast Brazil reported more than 85 piranha attacks on humans in 2002; 90% of bites were on the legs and feet, suggestive of defensive attacks on wading bathers by nest-guarding adults (Haddad & Sazima 2003). Wounds were crater-like, 1–2.5 cm in diameter, and bled severely. Several bites required hospitalization and one resulted in amputation of a toe.

Not too surprisingly, fishes adapted to flowing water do not fare well in the impounded regions behind dams. Many productive cold water trout fisheries have been lost behind

dam walls. Stream assemblages, usually rich in native darters, minnows, suckers, and trouts, are usually replaced by sunfishes and catfishes. As is the case in most disturbed habitats, introduced species come to dominate, including Carp, Yellow Perch, Mosquitofish, and lacustrine minnows. The history of the Snail Darter serves as a good example of the biological and political complexities of dam building (Box 26.2).

Two North American examples typify the effects of dams on aquatic faunas. The Colorado River was an ancient, warm, fast-flowing, turbid river that developed a unique fauna of streamlined fishes adapted to high flows and high temperatures. These fishes spawned in response to seasonal changes in water level and temperature. Of 32 fishes native to the Colorado River about 75% are endemic. More than 100 dams were built along this huge desert river for water

Box 26.2

The Snail Darter and the politics of endangerment

Darters belong to the family Percidae, which also includes such large predators as Yellow Perch (*Perca flavescens*) and Walleye (*Sander vitreus*). About 150 species and three genera (*Etheostoma*, *Percina*, and *Ammocrypta*) of darters exist; all are small (<15 cm), benthic, often colorful, and endemic to eastern North America. The region of highest darter diversity is the mountainous areas of the southeastern USA; Tennessee alone is home to about 90 species of darters.

In this center of diversity live several darter species that are restricted to relatively small locales, including headwater streams, springs, and small lakes. Although extensive surveys of the ichthyofaunas of the areas have been made, many areas remain relatively unexplored and uncollected. Hence it was not too surprising when, in 1973, ichthyologists from the University of Tennessee discovered a previously undescribed, small (60 mm) darter in a swift-flowing, gravel shoal of the Little Tennessee River. What was surprising was the uproar the fish created.

Tellico Dam was proposed for construction on the lower Little Tennessee River by the **Tennessee Valley Authority** (TVA) as early as 1936. Its usefulness, beyond the jobs created during its construction, was always a matter of debate; it was the last dam proposed in the area because its construction was difficult to justify. Its environmental impact would be substantial, as the lake created behind it would flood *c*. 7000 ha of valuable agricultural land, several important Cherokee Indian religious and ceremonial sites (including the village of Tanasi, the capital of the Cherokee Nation, from which the state derived its name), and a renowned trout fishery. Proponents of the dam included the TVA, local land developers, and the Army Corps of Engineers. Opponents included conservationists, farmers, local landowners, fishermen, the US Fish and Wildlife Service, Supreme Court Justice William O. Douglas, Tennessee Governor Winfield Dunn, and the Cherokee Indian Nation.

Plans for Tellico Dam were shelved and resurrected repeatedly until the US Congress finally approved the project in 1966. Construction began the next year, only to be halted in 1971 when a Federal Court injunction was issued because the TVA had not filed an environmental impact statement, as required by the National Environmental Policy Act of 1969. The TVA spent 2 years preparing the impact statement, which was approved in 1973 and work recommenced. The Endangered Species Act was then passed in 1973, but no known endangered species were affected by the proposed dam. The ichthyologists chanced upon the Snail Darter in the region to be inundated by Tellico Dam and named it ***Percina tanasi*** (Etnier 1976). When extensive collections by TVA and other fish biologists failed to produce other populations of the Snail Darter, its endangered nature was evident: the Tellico Dam project was one of the chief threats to the species existence. The fish was given *Endangered* status in October 1975.

The TVA meanwhile was not idle. The authority undertook a massive, unauthorized 8-month transplantation program, moving 700 Snail Darters from the Little Tennessee River to the nearby Hiwassee River. Construction on the dam accelerated in an apparent attempt to complete the dam before other complications arose. In February 1976, TVA was sued for violating the Endangered Species Act, but the suit was not upheld. Construction continued. The court decision was appealed and in February 1977, a US Court of Appeals decided in favor of the fish and issued a permanent injunction against any further dam construction.

The TVA appealed on the somewhat ironic grounds that the Little Tennessee River was no longer suitable habitat for the Snail Darter because of the Tellico Dam: the existing construction was blocking the upstream spawning migration of the fish. TVA proposed transplanting all Snail Darters to the Hiwassee. The US Supreme Court denied the TVA appeal, which was good news for the conservationists. The

catch was that the Supreme Court recommended that the US Congress, which had passed the Endangered Species Act in the first place, become the ultimate arbiter of the situation. Congress, amidst much press coverage of the Tellico project, amended the Endangered Species Act and created an exemption committee, which consisted of Secretaries of major federal agencies and was later referred to as "**the God Squad**" and "the Extinction Committee". This panel had the power to exempt certain activities despite their threat to endangered species if the economic consequences of species preservation were substantial. In this situation, it was the darter *or* the dam. The committee met in February 1979 and voted unanimously in favor of the darter! The environmental coalition rejoiced.

The celebration was short-lived. A few months later, in a deft political maneuver, a special exemption for the Tellico project was hidden in more general energy legislation and passed Congress without debate. Many members of Congress did not even realize what they were voting on. President Carter reluctantly signed the legislation, apparently trading the Snail Darter for conservative votes on his Panama Canal legislation. This vote "sentenced the Little T and its snail darters to death beneath the murky waters behind Tellico Dam" (Ono et al. 1983, p. 185). Fifteen years after construction began, the Tellico Dam was completed.

Although the Endangered Species Act was weakened during the legislative battle that ensued over the Snail Darter, the process strengthened the species preservation movement in the USA. Never before had so much public interest and sympathy been generated for a comparatively small, economically unimportant, cold-blooded vertebrate. Fortunately, although extirpated from the Little Tennessee, the darter managed to survive the battle. The transplanted population in the Hiwassee River is viable, and additional transplants to the Holston, Elk, and French Broad rivers are apparently successful. Additional, nontransplanted populations were later discovered in four other locales in Tennessee, Georgia, and Alabama. In fact, thanks to the concern of and efforts by the ichthyological community and an enlightened public, the Snail Darter's status improved from Endangered to Threatened as of 1984 (Etnier 1976; Ono et al. 1983; D. A. Etnier, pers. comm.).

retention, flood control, and agriculture; less than 1% of the virgin flow now reaches the river's mouth. The deep reservoirs formed by many dams became thermally stratified, and water released periodically from the cold, lower portions of the reservoirs chilled downstream habitats, disrupting natural spawning cycles and killing native fishes while promoting the survival of introduced cold water predators such as Rainbow Trout. Of the 80 fish species that now occur in the Colorado River, only about one-third are native. Of the remaining native fishes, most are Threatened or Endangered, including the Humpback Chub (*Gila cypha*), the Bonytail Chub (*G. elegans*), the Razorback Sucker (*Xyrauchen texanus*), and the Colorado Pikeminnow (*Ptychocheilus lucius*), the largest minnow native to North America (Fig 26.3). The modified environment created by the dams and the success of introduced fishes are chief contributors to the decline of native fishes (Ono et al. 1983; Minckley 1991; Wydoski & Hamill 1991).

Hydroelectric dams also block movements of fishes that migrate upriver to spawn, and pulverize juveniles during their downstream movements (Lucas & Baras 2001). Fishes that make it past tailwaters or through turbines often suffer from gas-bubble disease, brought on because the agitated waters below a dam are often supersaturated with gas (e.g., Raymond 1988). Habitat destruction, water flow reduction, and other dam effects are considered major factors causing the decline of salmonid stocks in western North America. The Columbia River system, including its large tributary Snake River, has a gauntlet of 28 dams that must be run by spawning adult salmonids and oceanbound juveniles. Upstream mortality is estimated at 5% and downstream mortality at 20% *per dam* (Booth 1989); four of the Columbia and Snake river dams lack any fish bypass structures such as fish ladders.

Commercial catches of salmon in the Columbia have declined dramatically (Fig. 26.4). For related reasons, approximately 106 major West coast salmon and steelhead stocks (*Oncorhynchus* spp.) have already been extinguished and an additional 214 native, naturally spawning stocks of Pacific salmons, Steelhead, and sea-run Cutthroat Trout are at risk in Oregon, California, Washington, and Idaho. Some analyses put the numbers as high as 280 stocks extinguished and another 880 stocks at high risk of extinction (Nehlsen et al. 1991; Huntington et al. 1996; Slaney et al. 1996). Overfishing, deforestation, hatchery introductions, aquaculture escapes, introduced pathogens, and agricultural and industrial pollution also contribute to the problem (NRC 1996b; Lichatowich 1999; Williams 2006; among many others).

Retention of sediments in reservoirs, combined with elimination of flood cycles, can have far-reaching consequences for fish production. Nutrients that would have been delivered to estuaries or dispersed over many kilometers of downstream floodplain during seasonal inundation remain trapped behind a dam. Construction of three dams in northern Nigeria led to a 50% reduction in downstream fish landings. Similar effects of dams have been reported in Zambia, South Africa, Ghana, and Egypt. In Egypt, con-

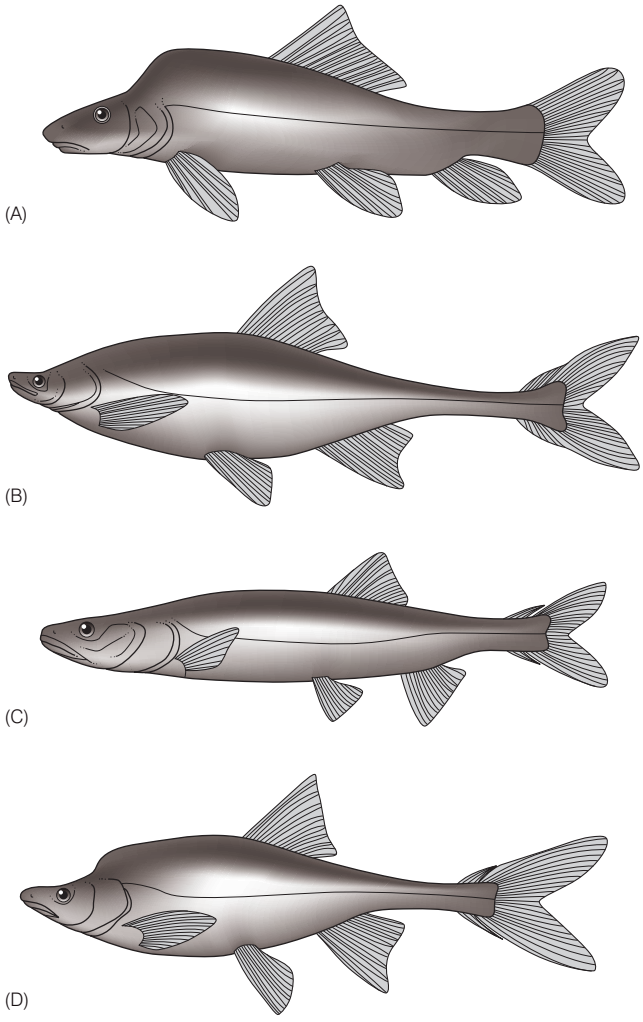


Figure 26.3

Endangered fishes of the upper Colorado River. Prior to impoundment, the Colorado River experienced exceptionally high flows, >9000 m^3/s during winter and spring floods, which redistributed sediments critical to spawning and larval rearing. Several Endangererd Colorado River endemics evolved reproductive habits attuned to this flood cycle. Large native Colorado River species also show marked convergent morphologies, having long, tapered bodies with elongate caudal peduncles, small depressed skulls with predorsal humps or keels, winglike fins that have hardened leading edges, and tiny or absent scales. Humps have been interpreted as providing a hydrodynamic advantage or as a response to gape-limited native predators such as Colorado Pikeminnows. Four of the large, Endangered cypriniforms of the Colorado exemplify these traits: (A) Razorback Sucker (*Xyrauchen texanus*); (B) Bonytail chub (*Gila elegans*); (C) Colorado Pikeminnow (*Ptychocheilus lucius*) and (D) Humpback Chub (*G. cypha*). After Portz and Tyus (2004), used with permission.

struction of the Aswan High Dam, which impounds 50–80% of the Nile River's flow, caused a 77% reduction in annual landings of sardines, *Sardinella aurita*, in the southeastern Mediterranean (Smith 2003). In eastern Europe, dams along the Volga River contributed to a 90% reduction in fish catches in the Caspian Sea. Similar, or worse, scenarios have been created in the Azov, Black, and Aral seas (Welcomme 1985; Moyle & Leidy 1992; Pringle et al. 2000; see below).

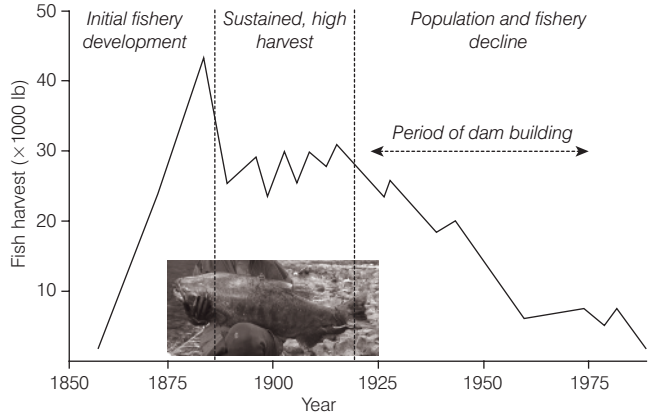


Figure 26.4

Commercial catches of Chinook Salmon and Steelhead Trout in the Columbia River over the past century. Soon after commercial exploitation began, catches rose to sustained levels of 20,000 tons annually. After dam construction, catches declined regularly and have been as low as 550 tons. After Williams (2006); inset photo courtesy R. Carlson.

Many options exist that will prevent, minimize, and reverse the negative impacts of dams. Dam construction, which is costly in addition to being environmentally destructive, can be avoided via conservation measures such as improving irrigation methods and other practices that reduce water loss, and conserving energy and developing alternative energy sources. Activities that reduce the impacts of existing dams include dam operation schedules that restore natural flows in river ecosystems, correcting sediment transport and deposition problems, correcting fish passage and entrainment problems, and, ultimately, removing dams that have outlived their usefulness (Heinz Center 2002). Dams modify entire ecosystems, more so than many of the other insults that humans visit on aquatic habitats and fishes (Dudgeon 2000). Correcting the damage requires an ecosystem perspective and ecosystem-level management actions.

Watershed perturbation

Aquatic systems include not only the water in which fishes live but also the groundwater and the surrounding **landscape** or terrestrial area through which water must flow. Many activities have an adverse effect on a river's **watershed** (the land from which water drains into a river), including logging or burning of vegetation, bulldozing for construction and development, groundwater and surface water withdrawal and contamination, overgrazing and trampling of streamside vegetation, and erosion caused by wind, water, or the movements of livestock.

Much has been written about deforestation in tropical and temperate regions. **Riparian** trees, those that grow along stream and river banks, interact intimately with nearby water courses. Obvious consequences of tree removal include a rise in water temperature from loss of shade (from direct heating of a stream and transfer of heat to groundwater by irradiated soil), increased variation in flow rates because water uptake by plants is lost, intensified erosion leading to turbidity, siltation and stream bank collapse (particularly where logging operations occur on steep slopes), and loss of nutrient inputs from falling leaves and fruit.

Shade also reduces **ultraviolet (UV) radiation**. Fishes can suffer directly from UV exposure, including being sunburned (see Blazer et al. 1997), and some sun-dwelling fishes are even protected by mucus that has a sunscreen function (Zamzow & Losey 2002). Eggs, embryos, and larvae of marine and freshwater species suffer higher mortality when exposed to high but natural levels of solar UV-B (reviewed in Häkkinen et al. 2002). Excessive exposure to solar radiation induces cataracts in Rainbow Trout lenses (Cullen & Monteith-McMaster 1993), which diminishes a trout's ability to focus images on the retina. Young of several fish species avoid UV light if refuges are available (Kelly & Bothwell 2002; Ylonen et al. 2004).

Siltation of streams is a major problem – it hinders productivity because of light reduction; eliminates refuge sites; decreases water clarity which makes sight feeding more difficult; depresses spawning activity; and smothers eggs, sessile invertebrates, and plants (Sutherland 2007; Sutherland & Meyer 2007). Silt and sediment are highly abrasive and cause loss of gill function, especially in juvenile fishes (Fig. 26.5). Siltation has been directly linked to native fish declines in many habitats, including Sri Lankan streams and South African estuaries (Moyle & Leidy 1992). Sedimentation is the largest source of contamination in North American streams and rivers (Waters 1995; USEPA 2000) and is the most important factor limiting the availability of fish habitat. Waters (1995, p. 79) stated that fine sediments constituted "perhaps the principal factor . . . in the degradation of stream fisheries".

Another adverse effect of deforestation on aquatic systems involves the cessation of inputs of woody debris, in the form of branches and trunks that normally fall into a water course. Such structure is crucial to the productivity of many low-gradient rivers along coastal plains (see above). Many species use the exteriors and hollowed interiors of logs as spawning sites (e.g., catfishes, Ictaluridae) or as resting sites (Lowe-McConnell 1987). The gallery forests that line lowland rivers are also major spawning sites for fishes that migrate into their flooded zones during winter or spring floods at high latitudes and during rainy seasons at low latitudes (see Chapter 23, Reproductive seasonality). The strong dependence of Amazonian fishes on seasonally inundated floodplains underscores the more general problem of wetland loss through logging and filling (Goulding 1980; see Fig. 23.8).

Logging along stream courses can have quite unexpected, complicated impacts on fish populations. Clearcutting in the Carnation Creek watershed of British Columbia raised stream temperatures 1–3°C. Elevated temperatures caused early emergence and accelerated growth of young Coho Salmon, *Oncorhynchus kisutch*. Smolts migrated earlier than normal and then experienced poor ocean survival, probably because their early arrival in the ocean placed them out of synchrony with prey cycles (Holtby 1988). Logging operations high in a watershed can affect ecosys-

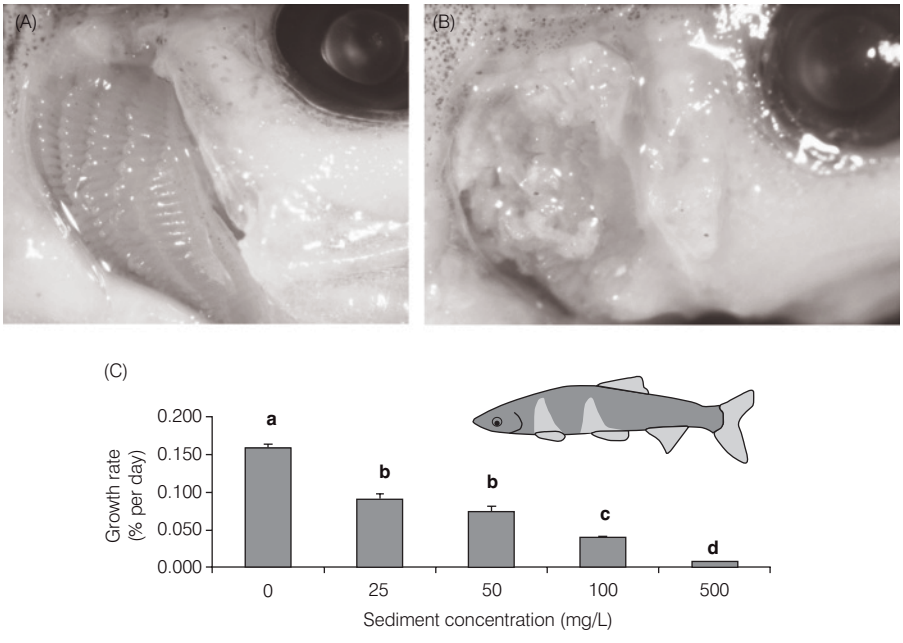


Figure 26.5

Effects of suspended sediments on young fishes. Threatened Spotfin Chub, *Erimonax monachus*, were raised at various sediment concentrations to study the effects on gill morphology and growth. (A) Gill arches and filaments of a young Spotfin Chub reared for 21 days at low (0 mg/L) sediment concentrations. (B) Gills from a similarly aged chub reared at high (500 mg/L) sediment concentrations; note the thickening and fusion of filaments and clogging with mucus. (C) Growth rates of young Spotfin Chub relative to sediment concentration, showing decreased growth at higher sediment loads. The growth rate at the highest sediment level was 1/15th that in clean water. High sediment concentrations tested (500 and 100 mg/L) occur regularly in the wild due to watershed development. Bars with the same lower case letter are not significantly different. From Helfman (2007), after Sutherland (2005), used with permission; chub drawing by A. Sutherland.

tem processes at distances far removed from the actual site of disturbance, such as when increased erosion causes unnaturally high levels of sediment deposition in coastal lagoons and estuaries (Moyle & Leidy 1992).

Competition for water

Humans use water for drinking, agriculture, recreation, fishing, and waste disposal. All these activities have adverse effects on aquatic organisms. Consumption and irrigation necessitate water withdrawals, leading to flow reductions in aquatic systems. Pumping of groundwater lowers water tables, which reduces the output of springs and seeps that are often necessary for maintaining year-round flow in many systems. Habitats subjected to withdrawals shrink, progressively losing heterogeneity and species. Downstream systems from which water is diverted evaporate, concentrating salts and pollutants. The universal use of waterways and waterbodies as dumping grounds for human waste creates environments toxic to fishes and humans.

Water withdrawal for irrigation of arid regions has created numerous ecological disasters, leading to species extinctions among fishes and other biota, and eventually producing salinated croplands and contaminated water supplies for humans. The history of species extinctions in the desert southwest of North America, summarized briefly above, serves as one example. At a larger scale are the events surrounding desiccation of the Aral Sea in the Uzbekistan/Kazakhstan region of the former Soviet Union. In 1960, the Aral Sea was the fourth largest lake in the world, covering 68,000 km^2; it supported large commercial fisheries as well as extensive hunting in its wetlands. Inputs are primarily from river flow, losses are due to evaporation. Construction of diversion canals and withdrawal of water from its two major input rivers for irrigation purposes shrank the lake to only 41,000 km^2 in 1987. By 1998, lake volume was reduced 80% from its original size. Lake salinity rose to 50 ppt in the 1990s, well above that of sea water, which is only 37 ppt. An original native fish fauna of 24 species has been reduced to four introduced species (Zholdasova 1997); commercial fisheries fell from 48,000 metric tons in 1957 to zero by the early 1980s.

Impacts have extended far beyond the ichthyofauna. Dust and salt storms, detectable on satellite imagery, originate on the dry lake bed and distribute 43 million metric tons (mmt) of crop-destroying salt annually over a 200,000 km^2 area. Reduced river flow, salinization, pollution of remaining water, and lowering of the water table have led to a high incidence of intestinal illnesses, throat cancer, tuberculosis, and anemia, high infant mortality, and a death rate from respiratory ailments that ranks among the highest in the world. Economic losses of approximately 2 billion rubles (= U$3.2 billion) annually have been estimated for the Aral Sea region as a result of its desiccation (Micklin 1988). The Aral Sea disaster has been called "perhaps the most notorious ecological catastrophe of human making" (Stone 1999, p. 30).

Species introductions

Movement of species into new areas is a natural zoogeographic phenomenon. When such range extension occurs as a result of human actions, it is considered an **introduction**. Natural dispersal is limited by a species' mobility and by physical barriers. Under natural conditions, species are constrained by co-evolutionary processes; species have natural parasites, predators, and competitors that control population growth, and organisms typically exploit prey taxa that have evolved defense mechanisms against the predator's foraging tactics. When individuals of a species are introduced suddenly into an alien environment, they may find the new physical and biological factors inhospitable or even lethal. Alternatively, freedom from natural biotic control may remove all checks on population growth. It is these liberated aliens that cause the greatest problems. Many such introductions have become well-known pests: rabbits, cane toads, and prickly pear cactus in Australia; starlings, English sparrows, gypsy moths, and zebra mussels in North America; mongoose and mynah birds in Hawaii; feral goats in the Galápagos and on many other islands, to name a few. These catastrophic introductions have their counterparts in fish assemblages as well.

Introductions go by a great variety of names, including alien, allochthonous, exotic, feral, introduced, invasive, naturalized, nonindigenous, non-native, transplanted, and translocated. Official US terminology under the Nonindigenous Aquatic Nuisance Prevention and Control Act of 1990 refers to **nonindigenous** organisms, but increasingly acceptance is leaning to simply **alien** (see Lever 1996, and especially Fuller et al. 1999). Sometimes a distinction is made between **transplants** that are moved within their country of origin but outside their native range, versus **exotic** species that are introduced into a new country. In terms of ecological impact, such geopolitical distinctions are meaningless (Fuller et al. 1999). Introductions may occur through deliberate actions (gamefish stocking, vegetation control, aquaculture, aquarium releases) or inadvertent mishaps (ballast water introductions, aquaculture escapement, bait fish release).

Untold hundreds of species of fishes have been deliberately transported among different countries. In the USA alone, approximately 536 alien fish taxa (species, hybrids, and unidentified forms) have been introduced, 35% imported from foreign countries and 61% translocated within the nation (Fuller et al. 1999; Nico & Fuller 1999; http://nas.er.usgs.gov). Half of the foreign exotics have established breeding populations. Most of these fishes represent deliberate introductions by government agencies and individuals (e.g., Grass Carp, *Ctenopharyngodon idella*, for vegetation control; Peacock Cichlid, *Cichla ocellaris*, as a

Table 26.2

Ten commonly introduced but controversial fish species. Species listed have often been effective in terms of the original purpose for which they were introduced, but have subsequently posed serious ecological problems. From Helfman (2007), based on Courtenay et al. (1984), Welcomme (1984, 1988), Lever (1996), and Fuller et al. (1999). The number of countries and island groups where established is from Lever (1996), the number of US states where introduced is from Fuller et al. (1999). Adapted from Helfman et al. (1997), and presented in roughly phylogenetic order.

Species	Number of countries where established	Number of states where introduced	Native area	Original purpose of introduction
Cyprinus carpio, Common Carp	49	49	Eurasia	Food, ornamental
Carassius auratus, Goldfish	>40	49	East Asia	Ornamental
Ctenopharyngodon idella, Grass Carp	9	45	East Asia	Vegetation control
Oncorhynchus mykiss, Rainbow Trout[a]	56	48	Western North America	Gamefish, aquaculture
Gambusia spp., Mosquitofish	67	35	Eastern North America	Mosquito control
Poecilia reticulata, Guppy	34	15	Northern South America	Mosquito control
Micropterus salmoides, Largemouth Bass[b]	53	43	E. North America	Gamefish
Lates niloticus, Nile Perch[c]	3	1	East Africa	Food
Tilapiine cichlids[d]	94	13	East, Central, and South Africa	Aquaculture, vegetation control
Cichla ocellaris, Peacock Cichlid	6	2	Amazon Basin	Gamefish

[a] Related species: Eurasian Brown Trout, *Salmo trutta* (28 countries, 47 states), and North American Brook Trout, *Salvelinus fontinalis* (31 countries, 38 states).
[b] Related species: *Micropterus dolomieu*, Smallmouth Bass.
[c] *Lates longispinus* or *L. macrophthalmus* may have also been introduced into Lake Victoria (see Ribbink 1987; Witte et al. 1992).
[d] Numbers are for *Oreochromis mossambicus* and *O. niloticus*; other widely introduced tilapiines include *O. aureus*, *O. macrochir*, *O. urolepis* ssp., *Tilapia rendalli*, *T. zilli*, and others, including hybrids.

gamefish), escapees from aquaculture facilities (*Tilapia* spp., Atlantic Salmon), or inadvertent bait or aquarium releases (Rudd, *Scardinius erythrophthalmus*; Walking Catfish, *Clarias batrachus*; Redeye Piranha, *Serrasalmus rhombeus*; suckermouth catfishes, *Hypostomus* spp.). Florida, California, and Hawaii have the largest number of established exotics (90, 60, and 50, respectively), followed by other southwestern states. The aquarium industry and lack of freezing weather facilitate the establishment of many tropical species.

Depending on one's perspective, the same introduction can be claimed as a success story or reviled as a disaster (Fuller et al. 1999) (Table 26.2). Eight fish species are included among "100 of the world's worst invasive species" as recognized by the Global Invasive Species Database of the IUCN's Invasive Species Specialist Group (www.issg.org/database). These eight are the Walking Catfish, *Clarias batrachus*; Common Carp; Rainbow and Brown trout; Mosquitofish; Largemouth Bass; Nile Perch; and Mozambique Tilapia (see Table 26.2 for details on most of these). Many of these species have been spread around the world and their ecological impacts vary from minor to catastrophic (Tilapia supply significant protein to humans in need, although alternative, edible native species exist, or existed, in many locales). These fishes are listed by IUCN alongside such known bad actors as chestnut blight, water hyacinth, prickly pear cactus, kudzu, fire ants, malaria mosquitoes, gypsy moths, zebra mussels, cane toads, brown tree snakes, starlings, rats, rabbits, pigs, and goats.

One outcome of this enthusiasm for moving fishes around the globe is **homogenization** of previously unique assemblages that evolved at particular locales. As can be seen in Table 26.2, the same fishes have been introduced repeatedly in different places: six of the 10 listed species have been introduced into 40 or more different countries. Not coincidentally, considerable overlap exists among the receiving nations, hence most countries contain established populations of several of the species listed. Introductions are often most successful in **degraded habitats** that are no longer suitable for local endemics, which means that alien species are replacing and displacing native species. When we total up the introductions and losses, we find that widely separated locales have similar faunal lists that are dominated by alien species. This repeated observation, which includes not just fishes but birds, mammals, insects, and plants, amounts to homogenization of the earth's

fauna and flora: everywhere looks the same (Lockwood & McKinney 2001). The process is so widespread, its outcome so ubiquitous, and the disruption so thorough that Williams and Meffe (1998, p. 118) declared that, "The continued homogenization of the world's flora and fauna . . . is an ecological holocaust of major proportions". Gordon Orians of the University of Washington refers to the era in which we live as the **Homogocene**.

Homogenization of fish faunas is especially prevalent in temperate, developed nations where introduction "efforts" have been ongoing. In Europe, Cowx (1997) listed 166 introduced or translocated fishes, which amounts to about 46% of Europe's 358 native species. Fifteen species have been introduced into 10 or more countries, including Carp (24 countries), Brook Trout (23), Grass Carp (20), Pumpkinseed Sunfish (19), and Rainbow Trout (nine). Other countries with low native diversity or high numbers of introduced species – where extensive homogenization would be expected and where its impacts should be monitored – are New Zealand, Australia, and South Africa.

Homogenization of US fish faunas has happened on a grand scale (Fuller et al. 1999; Rahel 2000, 2002). Of the 76 species introduced into 10 or more states, 32 have been placed in 25 or more states and 13 have gone into more than 35 states. Eight of the latter 13 are relatively large piscivores that continue to be stocked as game species in many places. Three (Common Carp, Goldfish, and Tench) stocked extensively during the late 19th century are now generally regarded as nuisance species.

How have stocking efforts affected fish diversity? Rahel (2000) compared historical lists with current species lists and found that state faunas have grown significantly more similar over time. In the past two centuries, similarity among fish faunas of states has increased by an average of 15 species, with almost 20% of states sharing 25 or more additional species. Over half of the fish faunas of Nevada, Utah, and Arizona are non-native, containing species brought in primarily from the eastern part of the country to improve angling. At the same time, and in combination with the habitat degradation that makes regions hospitable to aliens and inhospitable to local endemics, the list of imperiled US fishes has grown.

Homogenization is generally discussed with regard to exotics displacing natives, but the process also involves movement of widespread, generalist native species into areas or habitats previously occupied by local endemics. As is occurring in the southern Appalachian mountains of the USA, **localized endemics** adapted to clear, cool, low-productivity streams in upland regions are progressively replaced by **widespread**, **generalist** species more common in lower, more productive portions of river networks (Scott & Helfman 2001) (Fig. 26.6). The factors responsible for this replacement scenario include upland and riparian deforestation. Subsequent erosion of the uplands causes infilling of rapid and riffle habitats due to increased sediment loads; streams also become broader, deeper, and warmer. Cool water, endemic specialists in shallow, fast-flowing habitats (darters, sculpins, benthic minnows) are replaced by warm water generalists that can live in a variety of habitats but especially in slower flowing habitats (sunfishes, pool-dwelling minnows, suckers) (Jones et al. 1999a, Walters et al. 2003). Because the endemics were localized and the generalists were widespread, faunas of different drainage basins increase in similarity. Habitat homogenization promotes biotic homogenization (e.g., Boet et al. 1999; Marchetti et al. 2001), and homogenization occurs even though almost all species involved are technically native to the area.

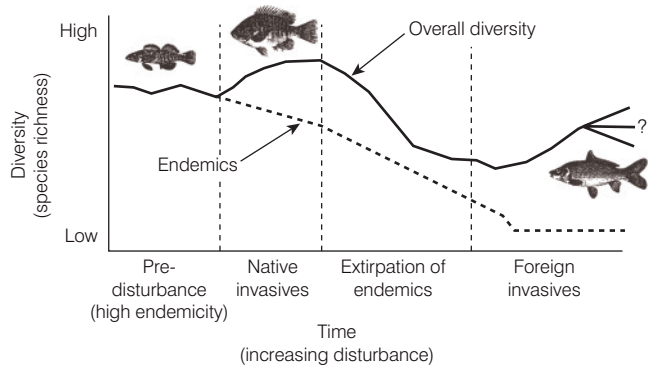


Figure 26.6
Natives as well as aliens are involved in faunal homogenization. The progressive changes expected in southern Appalachian streams are depicted, showing how habitat disruption (deforestation, siltation) first favors native generalists over endemic specialists. As habitat disruption continues, even these native invaders are replaced by highly tolerant aliens. From Scott and Helfman (2001), used with permission.

Introduced predators

> What havoc the introduction of any new beast of prey must cause in a country, before the instincts of the indigenous inhabitants have become adapted to the stranger's craft or power.
>
> Charles R. Darwin (1871)

Introductions can lead to population reduction or extermination of native fishes, either directly through predation on adults, eggs, and young, or indirectly through superior competition, hybridization, or transmission of pathogens (Balon & Bruton 1986; Fausch 1988; Ross 1991). Some catastrophic introductions are inadvertent, as with the spread of the Marine Lamprey, *Petromyzon marinus*, into the North American Great Lakes probably via manmade canals; Lake Trout, whitefishes, pike-perch, and other species declined precipitously in the wake of the lamprey (Daniels 2001; see Chapter 13, Petromyzontiforms). Predatory species that have been widely introduced to provide

sportfishing are the Peacock Cichlid (*Cichla ocellaris*), Largemouth Bass (*Micropterus salmoides*), and Rainbow and Brown trout (*Oncorhynchus mykiss* and *Salmo trutta*). Such introductions often decimate native fish faunas, including reduction of important food fishes. Peacock Cichlids escaped from an impoundment and into the Chagres River, Panama. The cichlid invaded Gatun Lake and progressively eliminated seven local fish species, including an atherinid, four characins, and two poeciliids; vegetation increased and fish-eating birds were displaced (Zaret & Paine 1973; Swartzmann & Zaret 1983).

Largemouth Bass have been responsible for similar community disruptions in Lago de Patzcuaro, Mexico; in Lake Naivasha in Kenya; in northern Italy; in Zimbabwe and South Africa; and in Lake Lanao, Philippines. Rainbow and Brown trout have led to the decline of endemic fishes in Yugoslavia, Lesotho, Colombia, Australia, New Zealand, South Africa, and in Lake Titicaca in Bolivia and Peru (McDowall 2006). In Lake Titicaca, the world's highest lake, a species flock of numerous cyprinodontids (*Orestias*) has been decimated, first through direct predation and later via competition for invertebrate prey (see Box 15.2). Brown Trout in particular have been identified as an effective predator on native fishes, including other salmonids. Brown Trout have contributed to the decline of several threatened salmonids, including Gila Trout (*Oncorhynchus gilae*), McCloud River Dolly Varden (*Salvelinus malma*), and Golden Trout (*Oncorhynchus mykiss aguabonita*), the latter being the official state fish of California. Introduced salmonids have been particularly destructive to galaxioid fishes through much of the geographic range of this group of southern hemisphere fishes (McDowall 2006).

One of the most dramatic examples of the effects of an introduced predator involves the stocking of the latid Nile Perch, *Lates* cf. *niloticus*, in Lakes Victoria and Kyoga, east Africa (Ogutu-Ohwayo 1990; Kaufman 1992; Witte et al. 1992; Lowe-McConnell 1997; Ogutu-Ohwayo et al. 1997); debate rages over exactly which *Lates* species was introduced and how often (Pringle 2005). Lake Victoria is, or was, a showcase of evolution and explosive speciation among fishes, having given rise to a **species flock** of perhaps 300 haplochromine cichlids, as well as three dozen other fishes. The lake is thought by many to have contained the richest lacustrine fish fauna in the world (see Box 15.2). Against the advice of ecological experts, Nile Perch were stocked in the lakes in the early 1960s, "to feed on 'trash' haplochromines . . . [and convert them] into more desirable table fish" (Ribbink 1987, p. 9).

This predator, which can attain a length of 2 m and a weight of 200 kg, spread slowly through both lakes, effectively wiping out native fishes by feeding preferentially on abundant species, then shifting to other species as the density of the initial prey declined, and finally turning to cannibalism. Commercial landings of cichlids went from 27 to 0 kg/h and fell from 32% to 1% of the catch between 1977 and the early 1980s. Nile Perch landings increased to 169 kg/h (Seehausen et al. 1997b). As species were eliminated, food webs in the lakes were substantially disrupted and simplified (Fig. 26.7); elimination of herbivorous cichlids led to algal blooms and attendant oxygen depletion in deep water, which caused periodic fish kills. In Lake Kyoga, the catch changed from a multispecies fishery dominated by several haplochromines to one dominated by two introduced species (Nile Perch and a tilapia) and a native cyprinid (*Rastrineobola argentea*).

Just how many of the endemic cichlids have actually been exterminated is difficult to say: perhaps only 50% of the species have been described and rare fishes are difficult to sample (Goldschmidt 1996). However, decreasing catches indicate that populations are shrinking and the continued threat of predation by Nile Perch and commercial fishing will only exacerbate the situation. Based on comparative samples taken in 1978 and 1990, approximately 70%, or 200 species, of haplochromines are extinct or threatened with extinction (Witte et al. 1992). Given present trends, "probably more vertebrate species are at imminent risk of extinction in the African lakes than anywhere else in the world" (Ribbink 1987, p. 22). Events in Lake Victoria call into question recent proposals for introduction of Nile Perch into Lakes Malawi and Tanganyika and point out the ecological consequences of introducing predators into any aquatic system (Witte et al. 1992).

The scenario played out in Lakes Victoria and Kyoga is one of reduced biodiversity and simplified community interactions as a cost of production of animal protein for human consumption. Successful fisheries for introduced Nile Perch and Tilapia have been established in those lakes, replacing the previous fisheries for smaller, native haplochromines. The impacts of these introductions are not, however, limited to the aquatic ecosystems. Nile Perch have a relatively high oil content. Traditional preparation methods, such as air drying, are less effective for processing Nile Perch. Instead, the flesh is often smoked over wood fires, which leads to deforestation of hillsides in the Lake Victoria basin, runoff of sediment and nutrients into the lake, reduced light transmission affecting reproduction of cichlids, and eutrophication leading to deoxygenation of deeper waters, to which Nile Perch are intolerant (Seehausen et al. 1997a, 1997b; Kitchell et al. 1997); low oxygen areas may serve as refuges for native cichlids (Schofield & Chapman 2000). An unexpected result of combined ecological and socioeconomic influences is that condition factors of Nile Perch in Lake Victoria have declined to the lowest values known for the species anywhere (Ogutu-Ohwayo 1999). Similar introductions, for similar purposes and with similar results, could be cited. For example, Contreras and Escalante (1984) identified nine instances in Mexico where, after the introduction of potential food fishes, the number of native, often endemic species declined by an average of 80%.

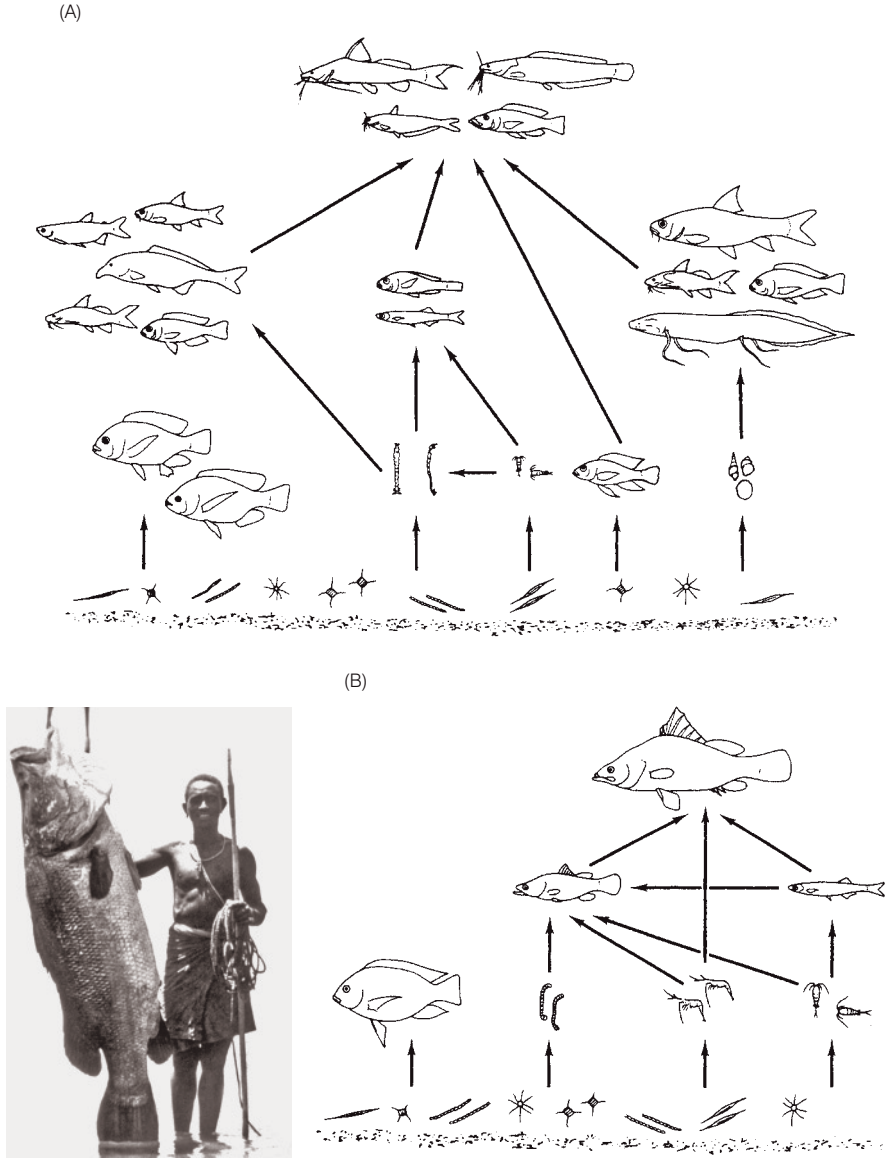


Figure 26.7
Effects of Nile Perch introduction on the food web of Lake Victoria. (A) The food web prior to the introduction of *Lates*. The top predators included piscivorous catfishes and haplochromine cichlids which fed on a variety of prey (including characins, cyprinids, mormyrids, catfishes, haplochromine and tilapiine cichlids, and lungfishes), which in turn fed on a variety of invertebrate prey and algae. (B) The food web after *Lates* eliminated most other fish species. *Lates* feeds on juvenile *Lates*, a cyprinid (*Rastrineobola*), and an introduced tilapiine cichlid. Inset: a large Nile Perch. (A, B) from Ligtvoet and Witte (1991), used with permission; inset photo courtesy of L. and C. Chapman.

Competition

Predation of new fishes on old is the most obvious effect of introduced species. Less well documented, but of potentially serious consequence, is the threat of competition, disease, and hybridization that can occur from introducing foreign species (Taylor et al. 1984). Competition is difficult to prove even under the best controlled, experimental conditions (Ross 1991; see Chapter 24). Evidence of competitive depression of native fishes usually takes an inferential form, in terms of overlap in use of potentially limiting resources, or decline in native fishes correlated with the introduction of a nonpredator. Diet overlap with native fishes in North America has been documented for such introduced species as Brown Trout, Common Carp, Pike Killifish (*Belonesox belizanus*), numerous cichlids, and two Asiatic gobies (*Acanthogobius flavimanus* and *Tridentiger trigonocephalus*). Blue Tilapia (*Oreochromis aureus*) overlap extensively in diet with Gizzard Shad and Threadfin Shad (*Dorosoma cepedianum* and *D. petenense*, Clupeidae). Blue Tilapia reproduce rapidly, forming dense populations (>2000 kg/ha) of stunted individuals. Introductions of Blue Tilapia in Texas and Florida have resulted in concomitant population declines of shad, particularly of the benthic-feeding Gizzard Shad. Overcrowding by tilapia also inhibits Largemouth Bass spawning behavior, although the actual mechanisms involved (competition, chemical suppression, behavioral interference) are poorly understood (Taylor et al. 1984). Competition for food probably explains the negative impact of introduced Guppies (*Poecilia reticulata*)

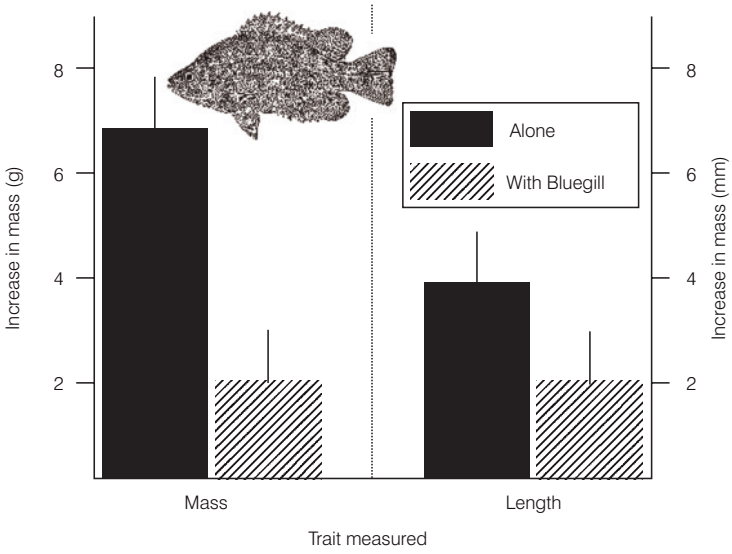


Figure 26.8

Experimental evidence of competitive displacement of a native by an introduced species. Sacramento Perch, an imperiled native sunfish of California, alone in aquaria (dark bars) grew more in mass and showed a trend toward greater length increase than when kept with introduced Bluegill Sunfish (shaded bars). After Marchetti (1999); fish drawing by A. Marciochi, in Moyle (2002), used with permission.

on the endemic White River Springfish (*Crenichthys b. baileyi*) in Nevada. Competition for nursery grounds led to a decline in catches of native *Tilapia variabilis* after transplantation of Redbelly Tilapia to Lake Victoria. Competitive impacts on rare, native Atlantic Salmon, *Salmo salar*, from abundant, escaped and released, cultured fish are a genuine concern (Jonsson & Jonsson 2006).

Our understanding of how aliens displace natives can be improved via laboratory manipulations of species and resources (e.g., Fausch 1988; Ross 1991). Marchetti (1999) looked for competitive interactions as a cause of population declines and extirpations of Sacramento Perch, *Archoplites interruptus*, a native California centrarchid. Sacramento Perch are least abundant where introduced sunfishes are most numerous. In lab aquaria, Marchetti found that Sacramento Perch placed with Bluegill Sunfish, *Lepomis macrochirus*, grew less and shifted habitat use to less natural habitats. Bluegill fed more actively and harassed the perch (Fig. 26.8).

Hybridization

Hybridization and **introgression** (crossing of hybrid offspring with parental genotypes) has caused rapid losses of native fishes over extensive geographic areas (Echelle 1991). Hybridization can result from habitat alterations that reduce physical and behavioral barriers between populations (e.g., Lake Victoria cichlids; Seehausen et al. 1997a). Hybridization also occurs when numbers of one species fall to the point where conspecifics are rare during mating periods, leading to interspecific matings (Hubbs 1955). Rare species have fallen victim to hybridization in the US southwest, including hybridization between the threatened Clear Creek Gambusia (*Gambusia heterochir*) and introduced Mosquitofish (*G. affinis*), between the endangered Humpback Chub (*Gila cypha*) and the more common Roundtail Chub (*G. robusta*), and between June Suckers (*Chasmistes l. liorus*) and Utah Suckers (*Catostomus ardens*). June Suckers were at one time exceedingly abundant. As their numbers decreased, in part because of water drawdowns for irrigation, June Suckers became increasingly vulnerable to genetic disruption via hybridization with abundant Utah Suckers (Echelle 1991).

Human-caused hybridization is particularly threatening where stocking programs bring hatchery or other strains of fishes into contact with native conspecifics (Utter & Epifanio 2002). Native strains disappear as they interbreed with introduced fishes, as has happened when Rainbow Trout were stocked with threatened Cutthroat, Gila, and Apache trouts (*Oncorhynchus clarki* ssp., *O. gilae*, and *O. apache*) in western North America (Echelle 1991). Hatchery fishes often originate from a limited gene pool or from inbred lines and have reduced genetic variability compared with wild populations. **Low genetic variability** correlates with lower fecundity, poorer survivorship, and slower growth, as found in different populations of endangered Sonoran topminnows (*Poeciliopsis occidentalis* ssp.; Quattro & Vrijenhoek 1989).

When hatchery transplants breed with wild fish, resulting offspring will often be less diverse genetically than the wild strains. Hybrid offspring may continue to breed with and eventually eliminate native stocks, as has occurred with Rainbow Trout stocked widely throughout North America. Threats from transplanted and cultured fish have caused considerable concern over the genetic integrity of wild Atlantic Salmon (*Salmo salar*) stocks, prompting programs to minimize the effects of sea ranching and stock enhancement programs (NASCO 1991; NRC 2004a). Even the genetic integrity of Common Carp, *Cyprinus carpio*, is threatened by introgressive hybridization with introduced,

cultured strains. Very few wild-type carp remain in the native habitat of this widely introduced species, and the wild genetic strain has endangered status in such large river systems as the Danube (Balon 1995).

The creation of intergeneric hybrids, initially considered unlikely, has also proven troublesome. European Brown Trout (*Salmo trutta*) hybridize with North American Brook Trout (*Salvelinus fontinalis*), producing a cross known as the tiger trout (e.g., Brown 1966). The widely introduced European Rudd, *Scardinius erythrophthalmus* (Cyprinidae), is a hardy, colorful baitfish cultured in the southern United States. Rudd hybridize with native Golden Shiner, *Notemigonus chrysoleucas*. Rudd are known to be established in eight states and could potentially hybridize with Golden Shiners in 26 states in the Mississippi River basin, with unknown consequences for the fish assemblages or ecosystems of those areas. Such risks are unnecessary given that several acceptable native bait species, including the Golden Shiner, already exist throughout the region (Burkhead & Williams 1991).

Parasites and diseases

A major threat from introductions, whether exotic or transplanted, is transmission of bacterial and viral diseases and parasites to which native fishes were previously unexposed (Hedrick 1996). **Furunculosis**, a fatal bacterial disease caused by *Aeromonas salmonicida*, was originally endemic to western North American strains of Rainbow Trout. When the trout was introduced into Europe, the disease became widespread among Brown Trout populations and now occurs wherever salmonids are cultured (Bernoth et al. 1997). **Whirling disease**, caused by the protozoan *Myxosoma cerebralis*, is native and originally nonpathogenic to European salmonids (Hedrick et al. 1999). It causes swimming in tight circles, followed by postural collapse and immobility. The parasite inflames cerebrospinal fluid, deforms the brainstem, and causes degeneration of nerves connecting the medulla and spinal cord (Rose et al. 2000). Whirling disease was transmitted from Europe to North America in the late 1950s, has proved extremely pathogenic to Rainbow and Brook trout, and is considered the single greatest threat to many US wild trout populations (MWDTF 1996). It has subsequently spread with exportation of North American salmonids, including back to Europe, where it has increased in pathogenicity. "**Ich**", a debilitating gill and skin infestation caused by the ciliated protozoan *Ichthyopthirius multifiliis*, originated in Asia and has spread throughout temperate regions via introductions (Hoffman & Schubert 1984; Welcomme 1984; Dickerson & Clark 1998).

An interaction between genetic disease resistance and the dangers of transplantations is exemplified by fall Chinook Salmon, *Oncorhynchus tshawytscha*. Salmon raised from eggs taken from streams where the protozoan *Ceratomyxa shasta* is endemic show mortality rates of less than 14% when exposed to the pathogen. Salmon taken from streams where the pathogen is not native exhibit mortality rates of 88–100% upon exposure (Winton et al. 1983). The introduction of infected fishes into areas where specific diseases do not occur naturally, such as might occur during pen-rearing operations or a "supplementation program", could have catastrophic consequences for endemic stocks of fishes.

Infestation problems involving native parasites can also be aggravated. Juvenile Pacific salmon (Pink and Chum, *O. gorbuscha* and *O. keta*) migrating past net pens holding Atlantic Salmon suffered mortality rates of 9–97% as a result of infestations of external copepod parasites. Infestation rates were significantly lower on juveniles that did not swim past net pen operations (Krkosek et al. 2006, 2007). Copepods (sea lice) on adult salmon are seldom fatal (see Chapter 22, Mutualism and commensalism), but a single copepod can kill a juvenile salmon (Box 26.3).

Ballast water introductions

A significant source of introductions receiving increasing attention is the ballast water of large ships (NRC 1996a). Water is pumped into special ballast tanks or empty holds of ships to stabilize them; this water is then pumped out when cargo is taken on board at another port. Ballast water sampled from five vessels in Hong Kong Harbor contained 81 species in eight animal and five protist phyla (Chu et al. 1997). Extrapolating from the international extent of shipping, Carlton (1999) estimated that >7000 species are transported daily in ballast water, including serious human pathogens. Hundreds of species of fishes and invertebrates have become widely established as a result of such ballast water introductions, including such well-known pests as the zebra mussel, *Dreissena polymorpha*, and the predatory cladoceran, *Bythotrephes cederstroemi*, in the Laurentian Great Lakes.

These and other invertebrates can drastically alter the food resource base for fishes via competition for or elimination of natural prey. An American export, the ctenophore, *Mnemiopsis leidyi*, was introduced via ballast water into the Black and Azov seas of Asia, where it reached densities of 180 individuals/m^3. It competed with and ate native fish larvae and has been linked to loss of a $250 million anchovy fishery (Ruiz et al. 1997; Shiganova & Bulgakova 2000). Globally, at least 32 introduced fish species in 11 families are thought to have been transported by ballast tanks; 31 species have actually been collected from ballast tanks.

Gobies and blennies are the two families most commonly associated with ballast water (Wonham et al. 2000). The Yellowfin Goby, *Acanthogobius flavimanus*, an east Asian native, has become one of the most common benthic fishes in the San Francisco Bay–Sacramento River area. Round Goby, *Neogobius melanostomus*, and Tubenose Goby,

Box 26.3

BOX 26.3

Should we eat farmed salmon?

> Aquaculture will do no more to save wild fish than poultry farms do to save wild birds.
>
> Safina (2001a, p. 791)

The transmission of parasites from fish held in sea pens to migrating juveniles is just one of the complications surrounding the practice of raising salmon on farms. The process of growing out salmon in net pens until they reach marketable size, commonly called **sea ranching**, is a study in the costs and benefits of attempts to supplement or enhance the human food supply. Different costs and benefits are emphasized and interpreted depending on whether one is an adherent or detractor of sea ranching.

The economic benefits of sea ranching are difficult to dispute. The practice is international in scale and truly characterizes an increasingly globalized economy. The most commonly ranched species is Atlantic Salmon, *Salmo salar*, but much of the enterprise takes place far from the native range of the species. Global production of farmed salmon in 2005 was 1.3 mmt, 90% of which was Atlantic Salmon (Jonsson & Jonsson 2006). Norway, Chile, and Canada, in that order, accounted for about 85% of global production. Farmed salmon were worth about US$4 to $5 billion in 2005, although that number varies depending on source and calculations. Regardless, "farm fresh salmon" are a large industry, and proponents of salmon farming point to this economic activity as a major benefit. Their other arguments focus on providing healthful animal protein at a reasonable price and taking pressure off wild stocks, many of which are overfished.

The arguments against farmed salmon are numerous and diverse, based on empirical observations as well as speculation. The claim that farmed salmon will provide much-needed human protein and reduce fishing pressure on wild stocks is not supported by calculations of **ecological efficiency**. Salmon are a predator, and raising salmon requires feeding them nutritionally complete fishmeal- and fish oil-based diets, often in the form of small fishes that could themselves provide food for people. On average, it takes 2.5 kg of feed to produce 1 kg of salmon flesh (Tacon 1996; Naylor et al. 2000). Culturing species lower in the food chain, as is done in China and Africa, would reduce the depletion of fish stocks for feed production. Salmon farming also creates socioeconomic hardships because fishers who exploit wild stocks, such as the comparatively well-managed salmon fisheries of Alaska, cannot meet their overhead expenses of boat payments, fuel costs, and equipment and crew expenditures when competing with farmed salmon that sell for $4 a kilo.

Pollution is also a factor arguing against salmon farming. Farmed fish are kept at artificially high densities, which leads to nutrient pollution around farms from uneaten feed and excreted waste. Forty salmon produce as much organic sewage as one person; salmon farms along the British Columbia coast discharged as much organic sewage as 500,000 people (Ellis and Associates 1996; Naylor et al. 2000). Controlling parasites and disease requires the extensive use of pesticides, antifoulants, algicides, and antibiotics, which leach from the pens or become concentrated in the flesh of the fish (Herwig et al. 1997; Haya et al. 2001). The use of antibiotics to curtail disease has led to concerns over the production of **antibiotic-resistant strains of bacteria** near salmon pens (McVicar 1997). The claimed dietary benefits of eating farmed salmon are compromised by contaminants such as **organochlorines** that occur in higher levels than is found in wild salmon (e.g., Jacobs et al. 2002; Hites et al. 2004), although contaminant levels vary by species and the health benefits of eating farmed salmon may outweigh the risks (Mozaffarian & Rimm. 2006; Ikonomou. et al. 2007).

The **escape** of salmon from facilities presents a number of problems. Literally millions of salmon escape from sea pens annually as a result of net destruction by sea lions or during storms (McKinnell & Thomson 1997). These "introduced" fish have negative impacts on wild fish, including competition for food and spawning sites, transmission of diseases (net fish are kept in crowded conditions that promotes disease spread), and hybridization and subsequent loss of genetic uniqueness. When planktonic food for juvenile salmon is scarce, such as during strong El Niño years, abundant escapees or fish released from hatcheries compete with rarer wild fish and overwhelm them, driving them to even lower densities (Levin et al. 2001). Escapees tend to arrive later in spawning rivers, and their courting and digging activities displace the eggs of wild fish that spawned before them (Webb et al. 1991). In addition to the problems of sea lice discussed earlier, crowding leads to outbreaks of other parasites and bacterial and viral diseases such as infectious salmon anemia, infectious hematopoietic necrosis, infectious pancreatic necrosis, furunculosis, coldwater vibriosis, and rickettsia, all of which can be transmitted to wild fish (McVicar 1997). Concerns over genetic introgres-

sion of domesticated, hatchery/farm genomes into wild fish populations are considerable. Escaped farm fish accounted for 22–100% of the runs in various rivers in Maine. Genetic tests confirmed hybridization between Endangered wild and superabundant aquacultured fish, the latter largely derived from European genetic strains (Colligan et al. 1999; NRC 2004a).

A major problem with escapees, along with deliberate hatchery releases, is that these introductions elevate overall salmon populations at a cost to wild strains. Such large numbers supplement the diet of and therefore help maintain large populations of natural predators such as piscivorous birds, seals, sea lions, and orcas, thereby depressing wild fish stocks (Utter 1998; Bayer 2000). Abundant escapees, along with deliberate releases from hatcheries, also create a mixed stock fishery that increases harvest pressure on wild populations (e.g., Naish et al. 2007). Approximately one-half of the Pacific salmon stocks considered at risk suffer from excessive fishing pressure due to such mixed stock fisheries (Nehlsen et al. 1991).

Finally, farmed salmon suffer from a number of **aesthetic liabilities**. Salmon farms need to be located nearshore, often in bays and other protected areas. These "ocean view" locales are also prized for real estate development, demanding high prices. Homeowners investing in such parcels are unlikely to want a commercial salmon farm in their viewscape (Stead & Laird 2002). Other aesthetic issues focus on the taste and appearance of farmed versus wild-caught salmon. It is widely stated that food quality authorities consider the taste of wild salmon as superior to that of farmed fish (e.g., cnnstudentnews.cnn.com/2000/NATURE/06/22/salmon.enn). Also affecting consumer acceptability, farmed salmon are fed diets containing carotenoid pigments such as astaxanthin and canthaxanthin to give their flesh the natural "salmon pink" color that consumers expect (Stead & Laird 2002). Without the addition of such colorants to their diet, the flesh has an unappealing grayish color. Many people find this addition of chemical dyes to the flesh an undesirable process (Fig. 26.9).

The salmon farming industry is aware of the controversies and is actively engaged in minimizing or correcting identified and potential problems (e.g., www.salmonfarmers.org, www.salmonoftheamericas.com). However, taken together, the economic, ecological, and aesthetic liabilities of farmed salmon appear to outweigh any benefits: "Fish are not for farming; eat wild salmon" (R. Troll, www.trollart.com).

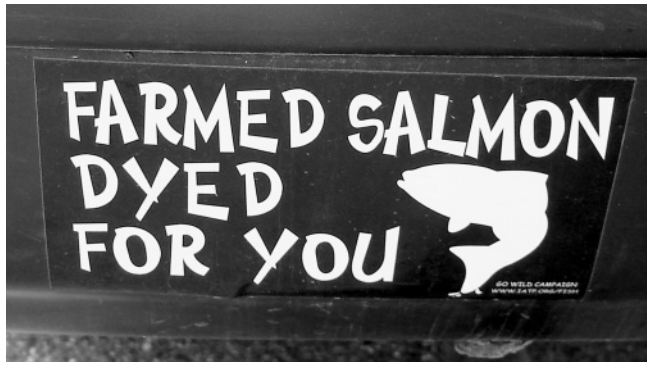


Fig. 26.9
Sentiment expressed on a bumper sticker, Burlington, Washington. Photo by G. Helfman.

Proterorhinus marmoratus, both native to the Black and Caspian seas, arrived in the Laurentian Great Lakes around 1990 via ballast water and quickly spread through all five lakes. Round Gobies reach densities of up to 133/m^2 and are egg predators. At high densities, they could compete with native sculpin and affect benthic spawners such as Lake Sturgeon, *Acipenser fulvescens*, and Lake Trout, *Salvelinus namaycush*, thus compromising expensive rehabilitation efforts (e.g., Moyle 1991; Dubs & Corkum 1996; Chotkowski & Marsden 1999; K. M. Jones, pers. comm.).

Assessing the potential impacts of introductions

Many species introductions, including those precipitating some of the worst-case ecological scenarios, occur in developing nations where the focus is on human economic and nutritional problems. In addition to the negative ecological consequences of many introductions, traditional fishing methods are frequently displaced by introduced species, requiring new harvesting technologies or replacing local **artisanal** fishers with commercial or sports fishers. Although many developing nations are in desperate need of capital

and of animal protein sources, simple planning measures and attention to natural distributions and local fishing techniques could often minimize results that are destructive to both the local biota and culture (e.g., CRC 2006). Whenever an introduction is being considered, be it transplantation or exotic, a protocol such as that outlined by Kohler and Courtenay (1986a, 1986b) should be followed to assess the potential biological and sociological costs and benefits of the introduction.

Pollution

Pollution enters aquatic systems as sediments or in the form of dissolved or suspended substances in runoff or precipitation, while attached to sediments, or while airborne. Human-produced toxic substances number in the thousands, ranging from elemental contaminants such as chlorine and heavy metals to chemical complexes such as persistent pesticides, detergents, **endocrine disrupting compounds** (**EDCs**), and petroleum products (NRC 1999a). Harmful effects on fishes occur as a result of direct toxicity, by interfering with developmental pathways in the case of EDCs, or through food chain effects (e.g., eutrophication, bioaccumulation), ultimately affecting individual survival and reproduction. Food chain effects also link contaminated fishes to other endangered species such as marine and terrestrial mammals and birds of prey (Lloyd 1992; Ewald et al. 1998).

Pollution-related reductions in fish biodiversity occur worldwide. Some of the best documented examples have occurred in North America and Europe due to acid rain and agricultural chemicals. **Acid rain** has a pH of less than 5.6. It results when oxides of nitrogen and sulfur (NO_x, SO_4) from internal combustion engines and coal-burning operations are further oxidized in the atmosphere to form nitric and sulfuric acid. Acid rain becomes a particularly serious problem in watersheds composed of rock types that are incapable of buffering the acids, such as the metamorphic rocks of northern North America and Europe. Most acid rain-contaminated systems suffer prolonged periods of low pH, but episodic inputs during snowmelt or storms can exacerbate already stressful conditions, including increased acute toxicity from aluminum and mercury (see Gensemer & Playle 1999). Mercury mobilization occurs because bacteria convert mercury to methylmercury more rapidly at lower pH. Spring rainstorms and snowmelt are especially injurious: acidic compounds accumulate in winter snowpack, flushing occurs when eggs and larvae are most abundant, and early life stages are particularly vulnerable to low pH (e.g., Sullivan 2000).

Acid rain has caused dramatic chemical changes in more than 100,000 lakes in Ontario and Quebec, wiping out all wild stocks of the endangered Aurora Trout (*Salvelinus fontinalis timagiensis*), and has reduced the range of the endangered Acadian Whitefish (*Coregonus huntsmani*) by 50% (Williams et al. 1989). Similar acidification and salmonid declines have occurred in the Adirondack Mountains of New York and in many Scandinavian lakes. Acid deposition is considered a prime contributor to the decline of Atlantic Salmon stocks in eastern Canada and will probably prevent their recovery (e.g., Watt et al. 2000). Fish kills in Norway following episodic acidification affected both Atlantic Salmon and Brown Trout (Baker & Christensen 1991). Norway lost 18 stocks of Atlantic Salmon, with eight more considered threatened, and Brown Trout have disappeared from 39% of Norway's lakes, with significant declines in another 17% (Sandøy & Langåker 2001). Brook Trout, which are relatively acid tolerant, have disappeared from approximately 11% of the lakes in the Adirondack Mountains of New York due to acidification (Baker et al. 1993). Minnows are even more acid sensitive and have disappeared from 19% of surveyed lakes.

Agricultural chemicals – pesticides, herbicides, and fertilizers – have been responsible for the extermination of many fishes in the American southwest, particularly those in isolated habitats. The toxic chemicals work directly on the fishes or are ingested with food, whereas fertilizers lead to eutrophication, which changes the balance of algae from edible species to inedible blue-greens, raises lake temperature, and lowers oxygen content. The Clear Lake Splittail, *Pogonichthys ciscoides*, a cyprinid endemic to Clear Lake in northern California, was extremely abundant through the 1940s. Agricultural development of the lake basin transformed the lake from a clear, cool habitat dominated by native fishes to a warm, turbid lake dominated by introduced species. The last Splittail was taken from the lake in 1970. Eutrophication or toxic chemicals have been similarly implicated in the demise of such unusual fishes as the Lake Ontario Kiyi, Phantom Shiner, Stumptooth Minnow, Blue Pike, and Utah Lake Sculpin. Overall, pollution has contributed to the demise of 15 of the 40 species and subspecies of fishes that have gone extinct in North America during the past century (Williams et al. 1989).

Endocrine disrupters are an insidious form of pollution because they interfere with growth and development at extremely low chemical concentrations, with consequences that we are only now coming to appreciate (Colborn et al. 1996; Arcand-Hoy & Benson 1998; NRC 1999a). In fishes, EDCs affect sexual differentiation and reproductive performance, acting early in sex determination as well as later when gonads produce sex products (Devlin & Nagahama 2002). Documented impacts on wild populations are reported increasingly and include abnormal gonad morphology, reduced rates of sperm and egg production and release, and reduced quality of gametes (Arukwe 2001) (Table 26.3). Other effects are altered reproductive behavior and unnatural sex reversal or failure to mature, with reproductive failure an ultimate result (e.g., Jones & Reynolds 1997) (see Box 7.1).

EDCs contribute to and exacerbate declines among imperiled fishes. The Columbia River of Oregon and

Table 26.3

Examples from field studies demonstrating reproductive and developmental impairment after exposure to endocrine disrupting compounds and other chemical pollutants. From Helfman (2007), expanded from Arukwe and Goksoyr (1998); see that review for references.

Xenobiotic/source	Effect	Species
BKME	Masculinization of females	Mosquitofish, eel-pout, Fathead Minnow
Columbia River pollutants, DDT	Phenotypic sex reversal	Chinook Salmon, Ricefish
Sewage estrogenic compounds	Intersexuality	Roach
PCBs, DDT/sewage effluent, oil spill	Increased egg mortality	Sand Goby, Arctic Char
Oil spill	Premature hatch, deformities	Pacific Herring
North Sea pollutants, DDE	Embryonic deformities	Flatfishes, cod
PCBs, DDT/various discharges	Chromosomal aberrations	Whiting
PCBs, PAHs/urban discharge, landfill leachate	Precocious maturation, decreased gonad development	English Sole, Eurasian Perch, Brook Trout
Crude oil, BKME/oil spill	Altered ovarian development	Plaice, White Sucker
Alkylphenols/sewage effluent	Altered vitellogenesis	Rainbow Trout, etc.
Pulp mill effluent, oil spill	Reduced plasma steroids, sperm motility	White Sucker, Atlantic Salmon, flounder
Textile mill, vegetable oil effluent	Retarded/reversed ovarian recrudescence	Airsac catfish, snakehead
EE2/sewage effluent	Reduced territory acquisition	Fathead Minnow

BKME, bleached kraft mill effluent; DDE, metabolic byproduct of DDT; DDT, dichlorodiphenyltrichloroethane; EE2, ethynylestradiol; PAH, polycyclic aromatic hydrocarbons; PCB, polychlorinated biphenyl.

Washington, previously the most productive salmon river in America, suffers from damming, overfishing, introductions from fish hatcheries, and agricultural and industrial pollution. Columbia River water now contains at least 92 chemical contaminants found in fish samples, including 14 metals, DDT, chlordane, polychlorinated biphenyls (PCBs), and chlorinated dioxin and furans (USEPA 2002); some of these chemicals are known endocrine disrupters. Approximately 85% of female-appearing Chinook Salmon sampled from the Columbia River possessed a genetic marker for the Y chromosome, indicating that they were in fact sex-reversed males (Nagler et al. 2001). When XY females mate with normal XY males, 25% of the F1 generation can be expected to exist as YY males, skewing the population sex ratio from a normal 1 : 1 to a male dominated 3 : 1. Subsequent matings could increase the proportion of males as YY males mated with normal XX females, which would be potentially disastrous for already stressed populations.

Fishes as indicators of environmental health

"The quality of fishing reflects the quality of living." This motto of the American Sportfishing Association, although focusing on exploitable species, summarizes the host of problems facing aquatic ecosystems worldwide. Lakes, rivers, and oceans with abundant, diverse fishes are reliable indicators of a healthy environment for all life forms. Quantifying the condition of aquatic habitats therefore becomes a crucial exercise in understanding and predicting potential hazards to human welfare.

Fishes can serve as **indicators** of the health of aquatic systems, in advance of effects on human health. At one extreme, massive fish kills indicate high levels of lethal contaminants, or low levels of oxygen. Ideally, less acute warnings are preferable. To this end, several measures have been developed that use quantifiable aspects of fish assemblage structure, health, and behavior as a means of monitoring conditions in aquatic systems. One approach used widely is the **index of biotic integrity** or **IBI** (Karr 1981, 1991; Miller et al. 1988a; Karr & Chu 1999), which combines measurements of species composition, abundance, and trophic relationships for different habitats. An IBI provides a quantitative comparison between the habitat in question and "unimpaired" reference systems to assess relative degrees of disturbance. The IBI bases its comparisons on a number of traits that generally characterize disturbed systems, such as an increase in number of introduced species, replacement of specialist species with generalist species, decline in the number of sensitive species, impair-

ment of reproduction, change in age structure of populations away from older age classes, and an increase in disease and anatomical anomalies. The IBI was originally developed for midwestern US streams, but has been applied successfully in a variety of systems (Hughes & Noss 1992; Simon & Lyons 1995).

Environmental contamination is more conventionally investigated by assaying water and sediments for known toxins, correlating growth abnormalities with sediment contaminants, or by observing the responses of fishes exposed to suspect water (Heath 1987; Gassman et al. 1994). Traditionally, the concentration at which 50% of the animals die (LD_{50}) is considered a critical threshold. Lower levels of contamination can be indicated by behavioral measures, such as elevated breathing rates, coughing, chafing against the bottom, impaired locomotion and schooling, and suppressed activity or hyperactivity. Although relatively rapid, such bioassays primarily measure immediate conditions. The measurement of "body burdens" of bioaccumulated contaminants in fish tissues gives a broader picture, but can vary with season, feeding habits, or metabolic activity.

A more integrated, long-term picture can be obtained by measuring alterations in energetics, metabolism, growth, reproduction, and behavior (the **biomarker** approach of Hellawell (1983) and McCarthy and Shugart (1990)). At a biochemical and energetic level, stress is indicated by changes in such attributes as liver enzyme function, occurrence of DNA damage, unusual ratios of intermediate metabolites (ADP : ATP), amounts of or ability to store lipids, and growth and developmental anomalies. Histological markers include parasite loads and damage, tissue necrosis or abnormal growth (particularly pathologies of the gills and liver), and both elevation and suppression of immune responses. At the population level, reproductive output can be monitored, whereas species richness, presence/absence of sensitive species, and indices such as the IBI indicate assemblage and community-level effects. These measures are useful for monitoring water quality as it directly affects fishes, but also because fishes are effective sentinels against human health problems (Adams 1990; McCarthy & Shugart 1990). Many of the responses listed in Table 26.3 can be considered biomarkers.

Commercial exploitation

Direct exploitation of fishes by humans is an obvious cause of fish population declines. However, humans are just one of many predators on most smaller fishes, and species or populations subject to predation generally possess compensatory mechanisms for sustaining predation losses (see Chapter 24, Population dynamics and regulation).

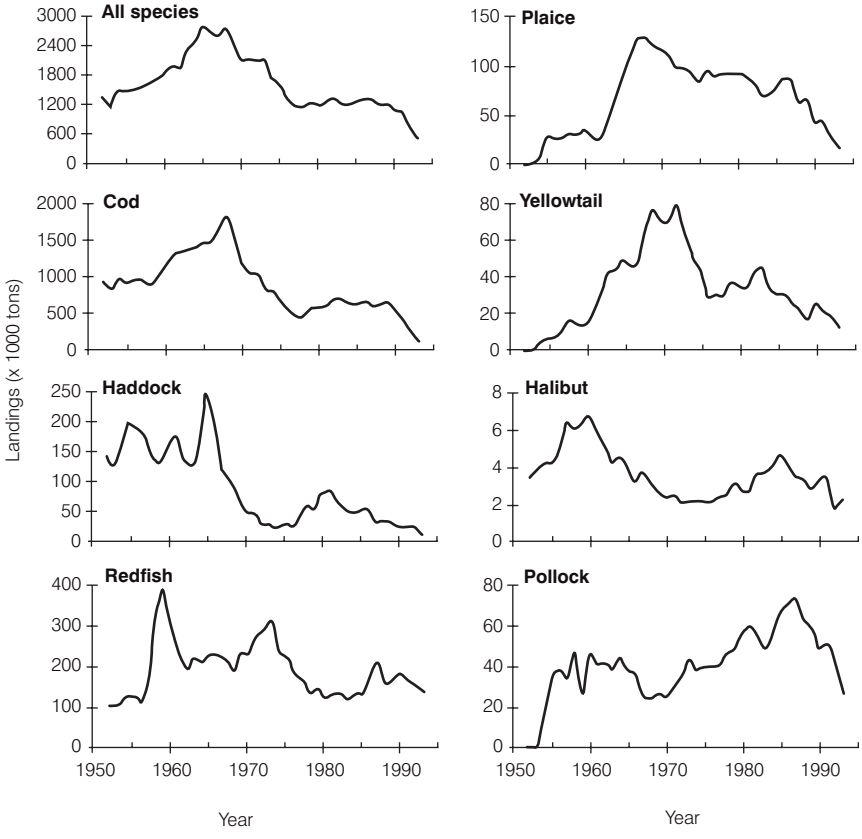


Figure 26.10
Trends of landings among North Atlantic groundfishes. Most major groundfish fisheries experienced rapid or continual population declines after an upsurge in fishing in the 1960s to 1970s. Species entered the 21st century at or close to all-time low levels. From Sinclair and Murawski (1999), used with permission.

Predation by humans, however, has extraordinary characteristics. Most "natural" predators focus their activities on young individuals, which tend to be the most abundant cohorts within a population, or on sick individuals with little reproductive potential, or on old individuals that have already reproduced. Human fisheries are at best indiscriminate (e.g., trawl and purse seine fisheries); at worst they target larger individuals that have not spawned (e.g., ocean-going salmonids).

As a result, many species of fresh- and saltwater fishes are in severe decline as a direct result of fishing pressure (e.g., Bluefin Tuna, many sharks and billfishes, Atlantic Cod and other groundfishes, Atlantic Salmon, Orange Roughy, Patagonian Toothfish, Pacific rockfishes, seabasses). The United States National Marine Fisheries Service (NMFS) estimated that 40% of the marine species important to commercial and recreational fisheries in the USA were exploited at unsustainable rates (NMFS 1997, 1999; NRC 1999b) (Fig. 26.10); similar numbers apply globally, especially to larger commercial species (see FAO 2007) (Fig. 26.11). In the 1990s, the actual worldwide annual marine fish catch hovered around 80–85 mmt; the sustainable catch is theoretically somewhere between 69 and 96 mmt (FAO 1995, 2000a; NRC 1999b), again suggesting we are at or beyond what is sustainable. Extrapolations from current population levels and fishing effort indicate that most global stocks of important commercial fishes will be exhausted by the middle of the 21st century (e.g., Worm et al. 2006). Also, many freshwater fisheries worldwide have experienced extreme degradation and decline as a result of a variety of human-induced insults, with the strongest impacts felt again among larger species (Allan et al. 2005) (Table 26.4).

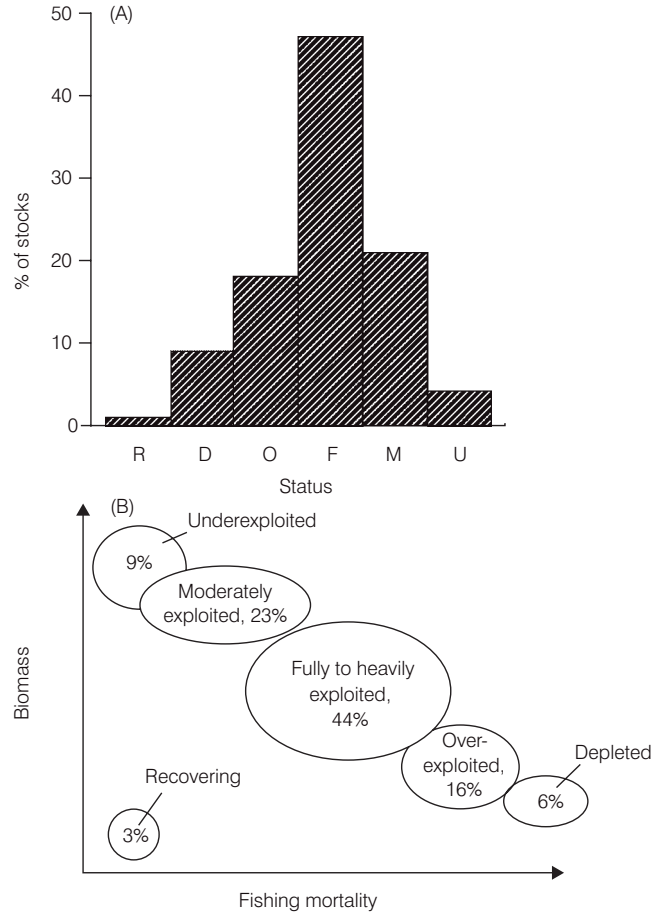


Figure 26.11

Status of the world's fisheries stocks. (A) Most stocks are fully or overexploited, leaving little room for more fishing. Most underexploited stocks occur in the Indian Ocean. Recovering (R), depleted (D), overexploited (O), fully exploited (F), moderately exploited (M), and underexploited (U). (B) Status relative to the relationship between stock biomass and fishing mortality for different exploitation levels. Stocks fished most heavily have been driven to the lowest levels of biomass, which reduces their ability to recover. (A) from Helfman (2007), data from FAO (2000a); (B) from Helfman (2007), redrawn from Botsford et al. (1997).

Overfishing

In some well-documented examples, overfishing, often in combination with climatic change (Horn & Stephens 2006), has produced dramatic crashes in seemingly inexhaustible stocks. The clupeoid fisheries of California and South America offer an interesting, interwoven example. The history of the California sardine fishery "is a classic case of the rise and fall of a fishery dependent on a pelagic species, of overcapitalization of an industry, and of too many fishing boats using new technologies to harvest a fragile, if not dwindling, resource" (Ueber & MacCall 1990, p.17).

The Pacific Sardine (*Sardinops sagax caeruleus*) is a 10–15 cm long, schooling, epipelagic clupeid that occurs from northern Mexico to the Bering Sea. The fish were typically captured by purse seiners and canned for human consumption. The fishery off California dates to the late 1800s. By 1925, it was the largest fishery in California, with landings of about 175,000 tons. Waste from the canning process was "reduced" into poultry food and fertilizer. The value of reduced sardines soon surpassed that of the canned product and whole fish were then reduced. Floating reduction plants, anchored outside the 3-mile limit to bypass regulative legislation, became common. Catches climbed steadily to a maximum of 790,000 tons in 1937. For the next 10 years, catches averaged 600,000 tons per year, despite fishery calculations that the stock could only sustain a harvest of 250,000 tons annually. Catches began a steady decline, averaging 230,000 tons from 1946 to 1952, then 55,000 tons from 1953 to 1962, and finally only 24,000 tons from 1963 to 1968. Commercial fishing for Pacific Sardine ended in 1968.

The collapse of the California sardine fishery was in part responsible for the later development, overexploitation, and eventual collapse of similar fisheries in South America

Table 26.4

Conservation status of some of the world's largest freshwater fish species. Conservation status taken from the IUCN Red List (www.redlist.org). After Allan et al. 2005.

Species	Maximum size	Distribution[a]	IUCN Red List Rank[b]	Threatened by
Pristis microdon, Largetooth Sawfish	650 cm, 600 kg	SE Asia rivers	EN	Harvest, habitat loss
Himantura chaophraya, Freshwater Whipray	500 cm, 600 kg	Mekong R.	VU	Harvest, habitat loss
Psephurus gladius, Chinese Paddlefish	300 cm, 300 kg	Yangtze R.	CR	Harvest, habitat loss
Atractosteus spatula, Alligator Gar	305 cm, 137 kg	Mississippi R.	NE	
Arapaima gigas, Pirarucu	450 cm, 200 kg	Amazon R.	DD	Harvest
Barbus esocinus, Tigris River "salmon"	230 cm, 136 kg	Tigris R.	NE	
Catlocarpio siamensis, Giant Barb	300 cm, 300 kg	Mekong R.	NE	
Probarbus jullieni, Julien's Golden Carp[c]	180 cm, 100 kg	Mekong R.	EN	Harvest
Ptychocheilus lucius, Colorado Pikeminnow	200 cm, 50 kg?	Colorado R.	VU	Habitat loss
Silurus glanis, Wels Catfish	500 cm, 306 kg	Europe, Asia	NE	
Brachyplatysoma filamentosum, Piraíba Catfish	360 cm, 200 kg	Amazon R.	NE	
Pangasianodon gigas, Mekong Giant Catfish[c]	300 cm, 300 kg	Mekong R.	CR	Harvest, habitat loss
Pangasius sanitwongsei, Giant Pangasius	300 cm, 300 kg	Mekong R.	DD	Harvest
Hucho hucho, Huchen Salmon	150 cm, 52 kg	Danube R.	EN	Harvest, habitat loss
Hucho taimen, Taimen Salmon	200 cm, 100 kg	Selenge R., FSU	NE	
Maccullochella peelii, Murray Cod	200 cm, 113 kg	Murray R.	CR	Harvest, habitat loss

FSU, former Soviet Union.
[a] River names include mainstem and tributaries in the river basin.
[b] CR, Critically endangered; DD, data deficient; EN, Endangered; NE, status not evaluated; VU, Vulnerable.
[c] CITES Appendix I species.

and Africa, as well as of king crabs in Alaska. Boats, gear, and processing equipment were sold at below cost, or costs were subsidized by international agencies. With the influx of former sardine boats and personnel, Alaska king crab landings rose from 11.3 tons in 1960 to 81.7 tons in 1980, only to crash to 15.8 tons 2 years later, despite continued activity of the imported boats (Wooster 1990). The exact causes of the decline are debated, but a likely explanation is that overexploited breeding stocks and unfavorable climatic conditions combined to result in poor recruitment of young crabs, demise of the fishery, and lost jobs for most persons associated with the industry.

A similar scenario is offered for the Peruvian fishery for Anchoveta (*Engraulis ringens*). The fishery became established in the 1950s, when fish were primarily used for human consumption. After 1953, reduction plants were built and boats were added to the fleet, many from the former California sardine fishery. By 1969, Peru caught more tonnage of fish than any other nation, with Anchoveta accounting for up to 98% of the catch. The exploitation of Anchoveta was uncontrolled: in 1970, 12.4 mmt were harvested, about 5 mmt above the calculated maximum sustainable yield. The fishery collapsed soon after, falling below 1 mmt in the mid-1970s. The collapse was again probably caused by a combination of overfished stocks and unfavorable climatic factors, including depressed upwellings associated with the El Niño–Southern Oscillation events of 1972–73 (Caviedes & Fik 1990).

Neither the Pacific Sardine nor the Peruvian Anchovetta have been driven close to extinction, although the term **commercial extinction** is applied to once-abundant fishes that no longer support significant fisheries. Uncontrolled

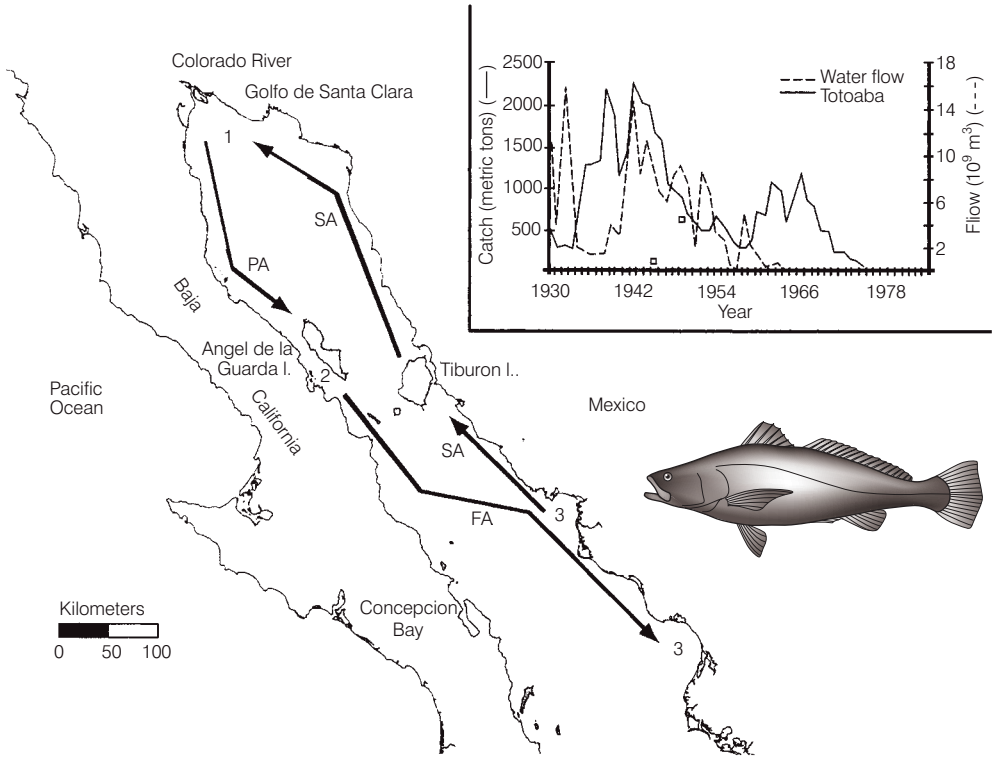


Figure 26.12

(A) The Gulf of California and a reconstruction of the presumed seasonal migration route of the endangered Totoaba, the world's largest sciaenid: SA, pre-spawning adults; PA, post-spawning adults; FA, adults during fall migration. Numbers indicate life history zones: 1, spring spawning zone and nursery ground of juveniles; 2, summer feeding zone; 3, fall feeding zone. Zone 1 is now largely a biosphere reserve. (B) The relationship between water delivery from the Colorado River and Totoaba population size as calculated from commercial catches. From Cisneros-Mata et al. (1995), used with permission of Blackwell Science; inset Totoaba drawing from Universidad Autonoma de Baja California, www.ens.uabc.mx/Reportaies/Totoaba

exploitation of marine species, particularly those dependent on stressed estuarine systems, can lead to even more serious declines in a species' abundance. The Giant Totoaba, *Totoaba macdonaldi* (Sciaenidae) is endemic to the upper Gulf of California and is the largest member of its widespread family, reaching 2 m in length and weighing over 100 kg. Its numbers have been drastically reduced as a result of overfishing on the spawning grounds, dewatering of the Colorado River estuary where it spawns, and bycatch of juveniles by shrimp boats (Fig. 26.12). At one time, it ranked as the most important commercial fish species in the Gulf of California, sought chiefly for its large gas bladder, which was dried and made into soup (the remainder of the body was often discarded). Spawning fish were so abundant that they were speared from small boats. The fishery peaked in 1942 and has declined steadily since (Ono et al. 1983; Cisneros-Mata et al. 1995, 1997). The Totoaba was declared an Endangered US species in 1979, has Critically Endangered status with IUCN, and is one of only nine fish species listed in Appendix I of CITES. The clearest message from these and similar examples, including another very large sciaenid fished off China (Sadovy & Cheung 2003), is that maximizing short-term profits and ignoring biological parameters have long-term, dire ecological and socioeconomic consequences (Glantz & Feingold 1990).

Overfishing creates problems besides reduced opportunities for human exploitation. Genotypic and phenotypic alterations occur commonly among heavily exploited fishes. Overfishing can create **bottlenecks** in the breeding biology of a species when populations reach critically small numbers, thereby reducing the genetic diversity of the species. For example, the fishery for Orange Roughy (*Hoplostethus atlanticus*, Trachichthyidae) in New Zealand started up in the early 1980s. Within 6 years, biomass of the stocks was reduced by 70%. Electrophoretic studies indicated significant reductions in genetic diversity of the three monitored stocks (Smith et al. 1991). The danger of reduced genetic diversity is that remaining individuals produce offspring that possess only a limited subset of the original genetic diversity of the species. Genetic adaptation to local conditions does not guarantee tolerance of new or altered environments. Altered conditions are increasingly likely due to human-caused climatic or chemical changes, such as might occur from global warming or ozone depletion. Breeding bottlenecks are one step short of species extinction.

Given enough time, animals can and will adjust their life history characteristics in response to strong predation. Life history theory predicts that individuals in populations exposed to high levels of adult mortality will respond by reproducing at smaller average sizes and ages, will shift from multiple to single reproductive seasons (from iteroparity to semelparity), and will have shorter life spans. Just these kinds of changes have been observed in several exploited species, including Atlantic Cod (*Gadus morhua*), Haddock (*Melanogrammus aeglefinus*), other gadids, Gag Grouper (*Mycteroperca microlepis*), Vermilion Snapper (*Rhomboplites aurorubens*), Atlantic Mackerel (*Scomber*

scombrus), and Pacific Halibut (*Hippoglossus stenolepis*) (Upton 1992; O'Brien et al. 1993). Such shifts may reflect adjustments in the phenotype of remaining individuals or selection for genotypically determined differences in life history traits, or both. The alarming fact is that most of our marine fish stocks are overutilized and that the observed shifts in life history characteristics create fish populations that are less useful to humans. Increasing evidence indicates that fishes undergo actual evolutionary change as a result of overexploitation.

Fishing as an evolutionary force

It is well established that fish populations under exploitation shift their growth rates and ages and sizes of reproduction, growing rapidly and maturing at smaller sizes and younger ages than unexploited populations. The fisheries literature documents many examples of changes in weight at age, length at age, length at maturation, and age at maturation in exploited stocks, with most species showing reduced weights, lengths, and ages, as well as accelerated growth (Law 2000). The response is in part phenotypic. Reductions in abundance cause increased body growth in the remaining individuals (perhaps due to reduced intraspecific competition for food); the ensuing faster growth rates generally result in maturation at smaller sizes and younger ages (see Trippel 1995). The response is also in part statistical because of what we measure. Fisheries tend to target larger individuals in a population. We measure what remains, and what remains are smaller individuals. In either case – phenotypic response or statistical artifact – no evolution is necessary, beyond an evolved response that programs individuals to grow faster and reproduce at smaller sizes when food is more available or numbers of conspecifics are low (the latter condition, a behavioral response dependent on the abundance of conspecifics, is the oft-described **Allee effect**).

However, we are becoming increasingly aware of actual evolutionary impacts of exploitation on fish life histories. Initial support for the idea came from a few field studies or was inferred from laboratory manipulations using small, short generation, nonexploited species (Hutchings 2000b). Geneticists had little doubt that fishing could cause evolution. Allendorf et al. (1987, p. 141) unequivocally stated that "all populations of fish that are included in a sport or commercial fishery will inevitably be genetically changed by harvesting". But before the early 1980s, the idea that fish populations would experience **genetically based changes** as a result of fishing was discounted by most fishery biologists (Policansky 1993a; see also Miller 1957); evolution was not incorporated into management models and plans (Policansky 1993b). Plastic phenotypic responses were likely to occur more quickly and be more noticeable than evolved changes (Jennings & Kaiser 1998), and fisheries managers showed "a continuing reluctance . . . to take seriously the threat of genetic change brought about through fishing" (Law & Stokes 2005, p. 241).

However, fishing has considerable potential as an evolutionary force. Fishing is a tremendous source of mortality (think of the evolved responses of prey to predators discussed in Chapter 20), and most fisheries target prey nonrandomly and are size and locale selective. Such constant, strong, "directional" selection often leads to rapid, evolved counteradaptations. Many life history traits that influence fisheries yields – such as growth rate, fecundity, and age and size at maturation – are under genetic control with relatively **high heritability** (Policansky 1993a, 1993b; Law 2000; Palumbi 2001). Also, life history traits display sufficient variation to be changed by evolution (Trippel 1995). There has also been sufficient time for evolution to occur, in terms of number of generations needed for significant genetic change. Across a range of taxa, evolution has been shown in less than 10 generations, sometimes in as few as two or three (e.g., Falconer & Mackay 1996). Field studies of salmonids have shown detectable divergence among populations in eight to 13 generations (Hendry et al. 2000; Haugen & Vollestad 2001; Hendry 2001).

Given this set of criteria that are often used to determine whether traits can be expected to change in response to selection forces, it is not surprising to find many examples of evolved, adaptive change in exploited fishes, including findings from several decades ago. Pacific salmon species have been subjected to commercial and recreational trolling, gill netting, and seining. Population characteristics have changed over time in response to exploitation patterns, including an overall decline in average size in all species studied (Ricker 1981). Over a 60-year period, Chinook Salmon matured on average *2 years earlier and at half the original size*. In 1950, when fishers for Coho and Pink Salmon began to be paid according to size rather than number of fish caught, larger mesh gill nets were employed to catch larger fish, accelerating the shift in stocks to smaller, younger fish. Ricker (1981) attributed these shifts to cumulative genetic effects of removing fish of larger than average size.

A clearer example comes from a gill net fishery in Lesser Slave Lake, Alberta, for Lake Whitefish, *Coregonus clupeaformis* (Handford et al. 1977). Gill nets removed large, heavy, fast-growing fish, leading to declines in growth rate and condition factor and an increase in mean age, but little change in mean length at age. Declining growth rate and increasing mean age contrast with the usual, density-dependent, compensatory (phenotypic) response. Progressive changes in condition factor were particularly informative. **Condition factor** (see Chapter 10) is higher in fatter fish, but fat fish are more likely than thin fish to be trapped in gill nets. Condition factor declined dramatically with time in all age groups, to the extent that fish of a given age and length in the 1970s often weighed half what similar age or length fish weighed in the 1940s (Figure 26.13).

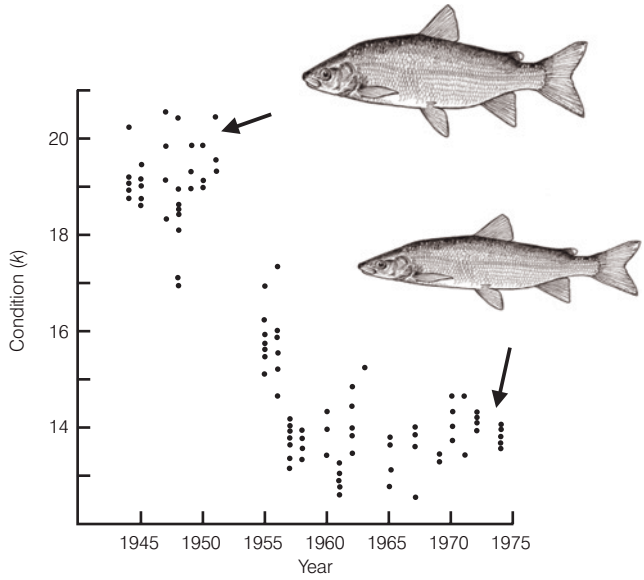


Figure 26.13

Evolution of body shape in exploited whitefish. Lake Whitefish in Lesser Slave Lake became skinnier over time as a result of gill netting; fat fish were more likely to be captured. Data plotted are condition factors, *k* ($k = 10^5$ weight/length^3), for male whitefish, 1940–75; females showed similar patterns but were not used because of weight changes caused by egg-bearing. From Helfman (2007), after Handford et al. (1977).

Similar results have been shown in gill net fisheries for Grayling, *Thymallus thymallus*, and Sockeye Salmon (Hamon et al. 2000; Haugen & Vollestad 2001).

Most convincing are laboratory tests imposing the kind of selection experienced by exploited fishes. Conover and Munch (2002) simulated size-selective fishing by rearing fast- and slow-growing Atlantic Silversides, *Menidia menidia*. After only four generations of directional selection for growth rate, groups from which fish with the fastest growth rates were removed (large-harvested fish) and groups from which slow-growing individuals were removed (small-harvested fish) reversed their growth rate characteristics. The previous fast growers (large-harvested fish) had mean weights nearly half those of the small-harvested lineage that previously possessed slow growth characteristics. The growth differences had a demonstrated genetic basis. Egg size and biomass yield also differed, indicating that continued harvest of the largest members of a stock reduced biomass and egg production. "Selection on adult size caused the evolution of a suite of traits likely to influence population growth rate and productivity" (Conover & Munch 2002, p. 95). The traits evolved are largely the opposite of what the fishing industry and society would prefer.

At least 40 generations of North Atlantic cod, herring, plaice, and sole have experienced intensive fishing, sufficient to alter genetic make-up (Policansky 1993a). Anything that causes mortality is a strong selection force, and fishing mortality often exceeds natural mortality by a factor of two or three in many if not most heavily exploited species (e.g., Stokes et al. 1993; Stokes & Law 2000). Annual, non-fishing, mortality rates in many post-larval and post-recruitment finfish species run at less than 10%, whereas mortality rates targeted to achieve maximum sustainable yields are around 50%, and actual fishing mortality is often between 70% and 90%. In the case of depleted Atlantic Cod, clear evidence of progressive, fisheries-induced evolution of maturation patterns existed and could have foretold imminent collapse (Olsen et al. 2004). Given the history and intensity of most commercial fisheries, fishing can be considered a long experiment with "more than enough time for selection to produce substantial genetic changes on almost every quantitative character that has been examined" (Policansky 1993a, p. 6).

Palumbi (2001) argued that humans have become the world's greatest evolutionary force, having exerted strong natural selection in such areas as disease-resistant viruses and bacteria, pesticide-resistant insects and plants, artificial selection via domestication (hatchery salmon), and altered characteristics in introduced species, many of which are detrimental to human welfare. To this list should be added the evolutionary impacts that intensive exploitation has had on the many fish species that provide essential goods and services to humanity.

A nonsolution: free enterprise

Reliance on market factors to protect declining stocks has proven illusory. A decrease in catch despite increased effort does not necessarily discourage exploitation, especially for so-called **market force-free species**, i.e., fish that are too valuable to not catch. For example, western Atlantic stocks of Bluefin Tuna decreased by 90% between 1972 and 1992, from 225,000 fish to 22,000 fish, and yet intensive fishing continued. In 2001, a 201 kg Bluefin Tuna caught off northern Japan was sold at the Tsukiji Central Fish Market in Tokyo for a record $173,600 ($863/kg or $391/lb) (AP 2001). This sort of profitability threatens other large and valuable fish species such as sturgeons, coelacanths, Swordfish, Whale Sharks, and some tropical reef species desirable for aquaria and the live fish restaurant trade (Sadovy & Vincent 2002; Helfman 2007).

Bycatch

A topic of increasing relevance to the conservation of marine fishes concerns bycatch in trawl and longline fisheries (Murray et al. 1992; Perra 1992; Safina 2001a, 2002). Few fisheries employ gear that can catch one species to the exclusion of all others. For example, dolphins, whales, turtles, and pinnipeds are frequently captured in gill nets or in purse seine nets set for tunas and billfishes, and seabirds and turtles are caught in longline sets. Because bycatch often goes unreported, it is difficult to accurately estimate its extent. Different assessments come to different conclu-

sions, but available data indicate that **discarded biomass** amounts to 25–30% of nominal catch, or about 30 mmt (Alverson et al. 1994; FAO 1995; Alverson 1997). By some estimates, bycatch has contributed to declines among 42–48% of marine and diadromous species that are considered imperiled by the USA and IUCN (Kappel 2005).

The bycatch problem is particularly acute when trawl nets with small mesh sizes are dragged along the bottom of the ocean in pursuit of groundfish or shrimp. Frequently, the **incidental** or **bycatch** (or **by-kill**) of fishes exceeds the catch of the targeted species. Although varying on a seasonal and regional basis, average fish : shrimp weight ratios of 1 : 1 to 3 : 1 have been reported for southeastern US shrimp fisheries. These numbers can run as high as 130 : 1 (= 130 kg of "scrap" fish for each kilogram of shrimp). Overall, 105 species of finfishes are captured by shrimp trawlers in the southeastern USA. On a species basis, 5 billion Atlantic Croaker (*Micropogonias undulatus*, Sciaenidae), 19 million Red Snapper (*Lutjanus campechanus*, Lutjanidae), and 3 million Spanish Mackerel (*Scomberomorus maculatus*, Scombridae) were among nearly 10 billion individuals and 180 million kg of incidental fishes killed by shrimp trawlers in the Gulf of Mexico in 1989 (Nichols et al. 1990).

Because of the small mesh size of the shrimp trawl nets, most of the fishes captured are (i) juveniles, (ii) smaller than legal size limits, or (iii) undesirable small species. Even larger mesh sizes do not prevent bycatch because once the net begins to fill with fish or shrimp, small individuals caught subsequently are trapped without ever encountering the mesh. In any case, these incidental captures are unmarketable and are usually shoveled back over the side of the vessel dead or dying.

The bycatch problem is complicated economically, ecologically, and sociologically. Bycatch is a liability to shrimp fishers, clogging the nets and increasing fuel costs because of increased drag on the vessel. Sorting the catch requires time, leading to spoilage of harvested shrimp and reduced time for fishing. Ecologically, high mortality rates among juvenile fishes could contribute to population declines of recreational and commercial species. Evidence to this effect exists for Gulf of Mexico Red Snapper and Atlantic Coast Weakfish (*Cynoscion regalis*, Sciaenidae). Because the nearshore areas where shrimp concentrate are also important nursery grounds for many fish species, shrimp trawling could have a profound impact on stock size (e.g., Miller et al. 1990).

Alternatively, bycatch is returned to the ecosystem and consumed by predators, detritivores, and decomposers, which could have a positive effect on sportfish, seabird, crab, and even shrimp populations. Available evidence indicates that 40–60% of the 30 mmt of catch discarded annually by commercial fishing vessels, and even more of **noncatch waste** (organisms killed but never brought to the surface), does not lie unused on the bottom of the sea. It becomes available to midwater and benthic scavengers, transferring material into the benthic food web and making energy available to foragers that is normally tied up in benthic, suprabenthic, midwater, and pelagic species (Britton & Morton 1994; Groenewold & Fonds 2000).

Overfishing and overdiscarding may thus contribute to a syndrome known as **fishing down of food webs** (Fig. 26.14), whereby we eliminate apex predators and large species while transforming the ocean into a simplified system increasingly dominated by microbes, jellyfish, benthic invertebrates, plankton, and planktivores (e.g., Pauly et al. 1998; Jackson et al. 2001). The strongest evidence for the fishing down phenomenon exists in global catch statistics that show alarming shifts in species composition from high value demersal species to lower value pelagic species: "the world fish supply is increasingly relying on variable, small pelagic and other-low value species, thereby concealing the slow but steady degradation of the demersal, high-value resources" (Garcia & Newton 1997, p. 23). In the last three decades of the 20th century, the global fishing fleet doubled in size and technology advanced immeasurably. Despite increased effort and technology, total catch stabilized, but landing rates of the most valuable species fell by 25%.

Conservation organizations have decried the obvious and wanton waste associated with bycatch. Public concern

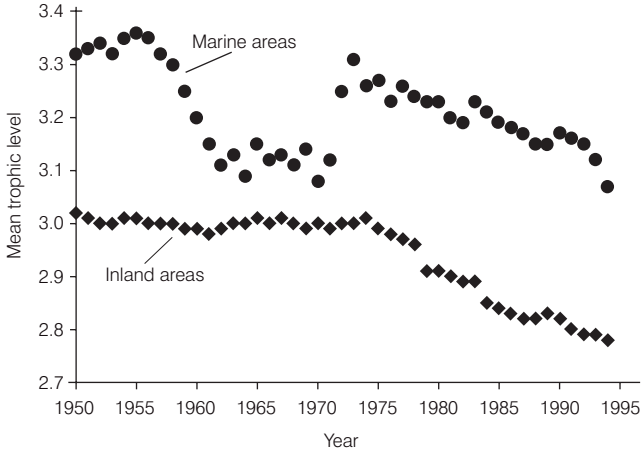


Figure 26.14

Fishing down food webs. Over the past half century, most of the world's marine and freshwater fisheries have been taking species progressively lower in food webs. The mean annual trophic levels of marine fisheries landings are calculated as total landings times the fractional trophic level of species groups (primary producers and detritus = 1, top predators = 4; species that feed at more than one level are assigned fractional values). The decline in trophic levels in the 1960s represents extremely large catches of planktivorous Peruvian Anchoveta, a fishery that collapsed in the early 1970s. A parallel trend exists in freshwater fisheries; the plateau region between 1950 and 1975 probably reflects incomplete information. From Helfman (2007), redrawn from Pauly et al. (1998).

over high mortality rates of endangered marine turtles captured in shrimp trawls led to the development of **turtle exclusion devices (TEDs)** in the 1980s. TEDs were incorporated into the shrimp net design with the purpose of directing turtles out of nets without unacceptably reducing shrimp catches (Broadhurst 2000). Marine engineers and fishers also developed shrimp net designs that incorporate **bycatch reduction devices (BRDs)**, taking advantage of behavioral differences between shrimp and fish or between different fishes to separate species (Engas et al. 1998). Other suggested solutions include prohibiting shrimping during seasons when bycatch is relatively high or where vulnerable life history stages of nontargeted species are concentrated.

Aquarium fishes

> Data on numbers of fishes involved [in the aquarium trade] are scattered, incomplete, often contradictory, seldom documented, plagued by misidentifications, and generally out-of-date.
>
> Helfman (2007, p. 375)

The export value of all marine and freshwater fishes and invertebrates used in the aquarium trade in the late 1990s was estimated at around US$200 million (FAO 1999, 2000b). Import values were roughly twice that number, and the retail values doubled the price again (Wood 2001), making the global retail trade worth roughly $800 million. That number undoubtedly underestimates the real value, given other calculations. Total expenditures for aquarium keeping include the value of tanks, pumps, filtration, lighting, chemicals, plants, foods, transportation, and packaging. A 1970s estimate put the total retail value at $4 billion (Pyle 1993), which climbed to $15 or even $30 billion by the mid-1990s (Tomey 1996; Bartley 2000). Freshwater fishes dominate the trade, accounting for 80–90% of the estimated 350 million fishes traded annually (Andrews 1990; Young 1997). Annual imports of marine tropical fishes involved 10–40 million fish (Wood 2001), or about 10% of the total trade (90% freshwater species, 9% marine, and 1% estuarine; 98% tropical and 2% cold water; Young 1997). Although 60% of income from the sale of fishes goes to developing, tropical countries, non-fish components are produced more widely and much of these profits goes to developed nations.

Geographic origins and ecological impacts also differ greatly between marine and fresh water. Twenty percent of the freshwater fishes are wild caught, with most fishes cultured in ponds, often far from their native habitats (Chapman et al. 1997). Centers of production of farm-raised freshwater species in the Far East are Thailand, Singapore, Indonesia, Hong Kong, and Malaysia; in the US, Florida in particular, and Texas, California, and Hawaii rear and distribute species native to a variety of countries. Freshwater ornamental species are biogeographically tied to Southeast Asia, South America, and Africa, although wild-caught species most recently are taken from the Amazon and the major river systems of Southeast Asia (Watson & Shireman 1996).

In contrast, 99% of the marine fishes come directly from the sea. Only a small number, no more than 25 or 30 species of the more than 1000 species traded, are captive-reared with commercial success (Moe 1999; Tlusty 2002). Commonly cultured species include anemonefishes (*Amphiprion* and *Premnas*), gobies (*Gobiosoma*, *Gobiodon*, *Amblygobius*), pseudochromid dottybacks (*Pseudochromis*), jawfish (*Opisthognathus*), basslets (*Gramma*), and Banggai Cardinalfish (*Pterapogon quaderni*). Marine collecting is particularly destructive because of the widespread use of poisons, such as sodium cyanide, rotenone, bleach, and quinaldine, to "anesthetize" the fishes prior to capture. In the 1980s, 80–90% of fish caught in the Philippines may have been collected using cyanide (Rubec 1986, 1988); similar numbers likely characterized other countries (Barber & Pratt 1997; Sadovy & Vincent 2002). These toxins kill targeted fishes as well as other reef organisms. On the positive side, efforts at reducing cyanide use via training collectors in nondestructive methods have shown results. Fish with detectable cyanide residues in the Philippines fell from over 80% in 1993 to 47% in 1996, and 20% in 1998 (Rubec et al. 2000).

Destruction of fishes by the aquarium trade is a sordid and underpublicized fact. **Mortality rates** of wild-captured fishes, ignoring fishes that die during or incidental to capture, are difficult to establish and vary by locale and collecting method (one estimate is that only 10% of the fishes affected by cyanide were actually targeted; Rubec 1988). Mortality rates of 80% for cyanide-captured fishes are not unusual. For noncyanide-caught reef fishes, estimates from a variety of locales indicate 10–40% mortality during holding prior to export, 5–10% during initial transport, and 5–60% during holding after import. Summed mortalities therefore range between 20% and 80% after capture and before retail sales (Wood 1985; Sadovy 1992; Pyle 1993; Vallejo 1997; Rubec et al. 2000). For wild-caught South American and African freshwater fishes, pre-export mortality has been placed at 50–70%, with as much as 80% additional loss for cardinal and neon tetras shipped from South America to the USA (Waichman et al. 2001). African cichlids are treated more kindly and have lower mortalities, perhaps less than 5% (www.lakemalawi.com).

Data on **aquarium longevity** are largely anecdotal and subject to unknown biases, but are far from encouraging. Wood (1985), surveying UK hobbyists, reported that 50% of marine fish died within 6 months of purchase, and nearly 70% died within a year. In home aquaria, cyanide-caught fishes may die when fed due to irreversible, progressive liver damage caused by the cyanide. Such **delayed mortality** may occur several weeks after capture and sale. Many tropical marine species are ill-suited for aquaria because of envi-

ronmental intolerance or specialized feeding habits. They are "impossible or difficult to keep, even when maintained under ideal conditions by experienced aquarists" (Wood 2001, p. 31). Sadovy and Vincent (2002) estimated that perhaps 40% of frequently traded ornamental marine species were unsuitable for the average aquarist. Hard to keep species include those dependent on live coral and other live organisms for food, such as some butterflyfishes and angelfishes. These are often colorful species and hence desirable, but their capture and sale are unjustifiable.

A number of other ecological and sociological issues plague the aquarium trade (see Helfman 2007 for details). These includes the unsustainable harvesting of live coral and "live rock"; coral death from cyanide and other destructive collecting methods; compromised health of collectors due to cyanide toxicity and unsafe diving practices; destruction of food fishes important to local economies; alien introductions due to escapes from holding facilities and release of unwanted pets, which also transmit pathogens (see Fuller et al. 1999; Whitfield et al. 2002; Semmens et al. 2004); and population depletions and biodiversity loss. The latter problem was suspected but only recently confirmed with good data. Tissot and Hallacher (2003) compared population sizes of popular aquarium fishes at locales on the island of Hawaii where collecting occurred or was restricted. They found that seven of the 10 targeted, relatively common species were significantly depleted at collection sites, whereas only two of nine ecologically similar but nontargeted species showed reduced numbers at collection sites (Fig. 26.15). Declines among aquarium species ranged from 38% to 75%. In all likelihood, moderate levels of collecting have minimal impact, especially for abundant species. But the available data shift the burden of proof onto those who maintain that collecting has minimal impact. We now know otherwise.

Public aquaria promote important conservation and public education goals. Home aquaria are of unquestionable educational and aesthetic value. Most ichthyologists have at least one in their own home. However, these values do not justify the ecological problems created by an unregulated industry, including the detrimental effects of introduced species and diseases on native fishes, invertebrates, and plants, and the defaunation of tropical reefs and rivers. Keeping reef fishes in aquaria cannot be rationalized on the grounds of species preservation. Few reef species have been successfully bred and raised in captivity, largely because of their complex life histories and age-specific habitat and feeding requirements (see Chapter 9, Larval feeding and survival). Nondestructive capture methods, bag limits, restricted areas and seasons, and most importantly, licensed captive breeding, can provide a diversity of interesting fishes to meet the home aquarist's needs while protecting natural environments.

A number of agencies and organizations have emerged in recent years to improve conditions in all steps of the supply chain, to lessen ecological impacts, and to better the lives of the people involved in the trade, especially the collectors. The **American Marinelife Dealers' Association** has produced an "Ecolist" that classifies aquarium fishes according to their likelihood of surviving in captivity (www.amdareef.com). **Project Seahorse** (http://seahorse.fisheries.ubc.ca) has specifically addressed socioeconomic and ecological issues associated with the seahorse trade. The **Marine Aquarium Council** (www.aquariumcouncil.org) has mounted a campaign to develop an ecologically responsible chain of supply, including certification of fishes caught and kept in a sustainable, responsible manner. **Project Piaba**, a community-based organization centered in Amazonas, pro-

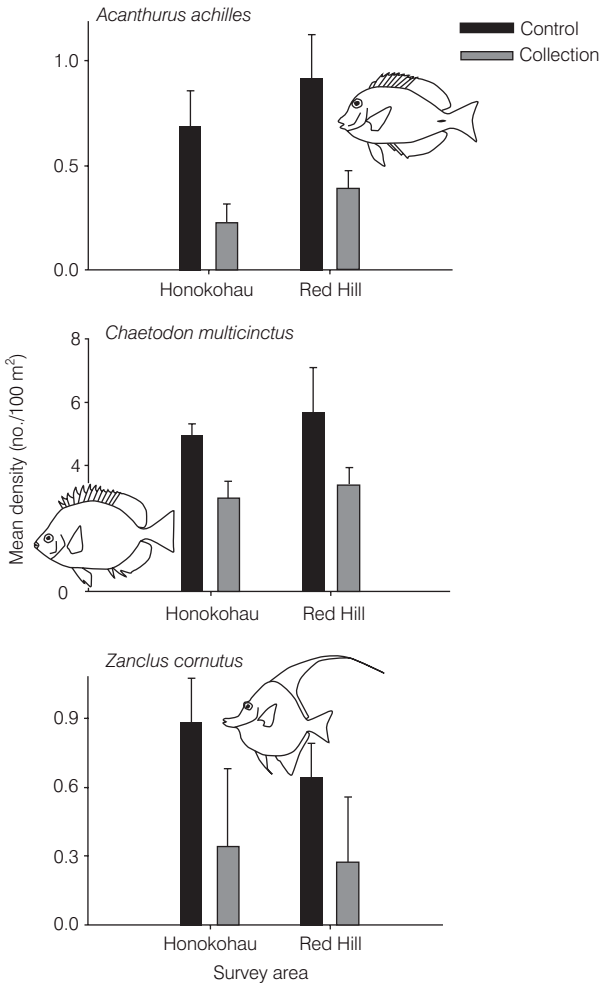


Figure 26.15

Impacts of aquarium collecting on reef fishes, Kona Coast, Hawaii. Underwater surveys at two areas showed significant declines among targeted species at collection locales compared to control sites protected from collecting. Data are given for three aquarium species: Achilles Tang (Pakuikui, *Acanthurus achilles*), Multiband Butterflyfish (Kikakapu, *Chaetodon multicinctus*), and Moorish Idol (Kihikihi, *Zanclus cornutus*). From Tissot and Hallacher (2003), used with permission; line drawings by Helen Randall and Loreen Bauman, from Randall (1981), used with permission.

motes a sustainable fishery and emphasizes diversification of the fishery, rotation among collecting areas, and ecosystem protection, with a goal of developing a "green certification" process that would identify sustainably caught fish (Chao et al. 2001; Chao & Prang 2002; see http://opefe.com/piaba.html). Project Piaba points out that by providing stable incomes, collecting in Amazonia diverts people from more dangerous, ecologically destructive, extractive activities such as gold mining (which causes sedimentation and mercury pollution problems), cattle raising (requiring large-scale deforestation), uncontrolled lumbering, and exploitation of endangered manatees and turtles (Prang 1996; Norris & Chao 2002). Ornamental fishes are "a sustainable by-product of an intact forest . . . Buy a fish and save a tree" (Norris & Chao 2002).

Global climate change

> Global warming . . . must be regarded as the major environmental problem for the future.
>
> Horn and Stephens (2006, p. 633)

Since the industrial revolution of the late 1800s, atmospheric concentrations of "**greenhouse gases**" – mostly carbon dioxide, methane, chloroflourocarbons, and nitrous oxide – have increased substantially as a direct result of human activity. Sunlight passes through the atmosphere, heats the planet, and this heat is radiated back to space as infrared energy. The greenhouse gases act as a blanket, trapping the infrared radiation, heating the earth even further. No one questions the process; without greenhouse gases, the average temperature on earth would be about –18°C, or about 33° colder than at present. Nor is there disagreement over the fact that greenhouse gases are increasing in the atmosphere at a rate of about 1–10% annually due to fossil fuel and wood burning, deforestation, cattle grazing, rice growing, and industrial pollution. What remains unknown is what effect this continued increase will have on regional and global climate. Average temperatures have increased about 0.5°C over the past century. If current trends of greenhouse gas production continue, most climate modelers predict that average temperatures will rise another 3°C over the next century, which is 10 times the rate at which the earth warmed after the last glacial advance (Ramanathan 1988; Smith 1990).

Of major concern are the likely climatic effects of this temperature increase and how they will be distributed (IPCC 2007a, 2007b, 2007c, 2007d). Altered wind direction and intensity and changes in the freeze–thaw cycle have been predicted. Vagaries of ocean currents and cloud behavior will undoubtedly lead to greater warming in some regions and even cooling in others. Similarly, rainfall patterns will shift, making some regions wetter, others drier. One likely result of temperature increase will be an increase in **sea level** of about 0.3–0.7 m due to thermal expansion of oceanic water and melting of polar ice caps. The postulated consequences for fishes of such a change are potentially dramatic.

Temperature and fishes

Temperature increases are likely to affect many aspects of fish biology. Metabolic processes are evolved responses to long-term thermal regimes characteristic of different climatic regions (Portner & Knust 2007; see Chapter 7, Temperature relationships). Alterations in thermal regime can affect the kinetics of such processes. Increased temperatures are a threat because fishes often live close to their **critical thermal maxima** (e.g., Magnuson & DeStasio 1997), because oxygen solubility is reduced at higher temperatures at the same time that metabolic requirements increase, and because many pollutants are more toxic at higher temperatures (Roessig et al. 2004).

Fishes respond to temperature changes by altering metabolic processes, reproduction, behavior, and distribution. Sex determination in fishes can be sensitive to thermal alteration, with different species producing unequal numbers of males or females in response to elevated temperatures (Devlin & Nagahama 2002; see Chapter 10, Determination, differentiation, and maturation). Gonadal development and germ cell viability are also temperature sensitive (Strüssmann et al. 1998). Timing of reproduction is highly sensitive to seasonal temperature cycles, via effects on precipitation and freeze–thaw cycles. In the northern hemisphere, lake freezing has occurred about 10 days later than 150 years ago (Magnuson et al. 2000), and in parts of Europe, snows melt 1–2 months earlier than 50 years ago, reducing spring floods and disrupting fish migrations and spawning. In Estonia, spawning migrations and timing of several freshwater fishes (Pike, Ruff, Bream, Smelt) have advanced on average 12–28 days from historical values (Ahas 1999; Ahas & Aasa 2006).

The latitudinal and altitudinal distribution of many fish species is determined by water temperature (see Chapters 16, 18). Ultimately, species ranges can be altered via extensive dispersal, or population collapse can occur where suboptimal conditions cannot be avoided. Shifts in distribution of commercial and non-commercial marine species have been observed in the North Atlantic, where bottom temperatures increased 1°C between 1977 and 2001 (Perry et al. 2005). Among 36 species assessed, two-thirds moved northward or deeper toward cooler waters over that period. Such large-scale changes can have multiple, serious impacts on community structure, ecosystem function, and recovery of depleted fisheries (Murawski 1993). Elevated temperatures often prevent cold water species from occurring at lower latitudes and elevations. The temperature dependence of some species squeezes them into seasonally reduced habitat space, such as Striped Bass in the southern portions of their range (see Chapter 7, Thermal preference).

Continued elevated temperatures would be potentially lethal (Coutant 1990; Power et al. 1999).

Many other impacts of elevated global temperatures can be anticipated (see McGinn 2002). Sea level rise will flood coastal marshes. Coastal wetlands, mangroves, and saltmarshes are major nursery grounds for numerous fish species. Vegetation loss due to flooding has several ecological consequences. The food webs of coastal marshes depend on vegetation as both a source of and a physical trap for detritus, and vegetation also provides spawning substrates, physical refugia for juvenile fishes, and substrates for prey. Marshes and their defining flora and fauna could disappear from many coastal areas (Kennedy 1990; Meier 1990).

Low latitudes

Most global climate models predict less pronounced climatic changes at low latitudes. However, tropical animals tend to have relatively narrow climatic tolerances compared to high-latitude species and may therefore be more vulnerable to slight deviations from normal conditions (Stevens 1989). Coral reefs, already stressed by periods of slight temperature elevation, will be devastated by higher temperatures and accompanying stresses such as **acidification** (Hoegh-Guldberg 1999; Hoegh-Guldberg et al. 2007). Coral reefs globally are declining due to a number of local impacts, but global climate change, especially global warming, has already affected reefs throughout the tropics. Reef-building (hermatypic) corals generally exist in water close to their upper thermal limits. Increases of only a few degrees cause **coral bleaching** (loss of symbiotic algae) and death. Strong El Niño–Southern Oscillation (ENSO) events in 1982–83 and 1998 killed 50–100% of the corals in many areas, often as a result of average temperature rises of no more than a degree (Goreau et al. 2000; Glynn et al. 2001; Guzman & Cortes 2007). As the corals died, algae spread and covered all surfaces, followed by erosion and physical collapse of the limestone.

These alterations to the basic, underlying biological and physical structure of the reef have had far-reaching impacts on the fish assemblages. Where coral death exceeded 10%, more than 60% of fish species declined in abundance, with losses strongest among species that relied on live coral for food and shelter. Abundances among herbivorous and detritivorous species increased initially, but even these groups declined as reef erosion progressed. Overall fish diversity declined in direct response to the amount of coral lost, and prospects for long-term recovery are poor given projected trends in climate (Garpe et al. 2006; Wilson et al. 2006a; Feary et al. 2007). El Niños are expected to intensify as the climate warms, portending further, widespread reef degradation (Timmermann et al. 1999; Lesser 2007). The implications for reef fish diversity, reef fisheries, marine protected area design, and the economics of small tropical nations are immense (Soto 2001; Bellwood et al. 2004). Of related importance to human welfare, bleached corals appear to provide an enhanced surface for the growth of dinoflagellates, including the ones responsible for ciguatera poisoning among humans that eat coral reef fishes (Kohler & Kohler 1992; see Chapter 25, The effects of fishes on plants).

Impacts on seasonal phenomena

Phenological (seasonal) cycles are likely to be disrupted, especially spawning periods that are timed to deliver larvae into regions of high productivity. Such productivity, which is driven by ocean currents and upwellings, has already been disrupted (Gregg et al. 2003; Schmittner 2005). Some global climate models indicate major shifts in ocean currents and upwelling patterns as a result of global warming. Such changes may alter or intensify the ENSO phenomenon, which has a substantial influence on major oceanic and coastal food webs (see Chapter 18, **The open sea**). Some models predict weakening of major low-latitude currents such as the Gulf Stream and Kuroshio currents, reduction in nutrient-transporting eddies of these currents, and reduced upwelling off the western coasts of South America and Africa. Climate determines the vertical and horizontal distribution of ocean currents, and altered currents could affect the distribution and production of pelagic species that make up 70% of the world's fisheries (Bakun 1990; Francis 1990; Gucinski et al. 1990). Timing of reproduction, particularly in migratory fish, would undoubtedly be disrupted. Migrations of anadromous salmonids are timed to take advantage of increased flows and cold water temperatures associated with snowmelt. Genetically determined migration times would be decoupled from altered melt cycles. Decoupling of phenological relationships will affect trophic interactions, alter food web structure, and produce ecosystem-level changes (Harley et al. 2006). Temperate marine environments may be particularly vulnerable because the recruitment success of fishes depends on synchronization with pulsed planktonic production (Edwards & Richardson 2004).

Weather patterns

Variations in the frequency and severity of climatic extremes of drought, flood, and cyclonic force storms are also predicted. Storms and attendant floods wash young fish out of appropriate habitats, and can dilute high salinity, nearshore regions with fresh water, lessening their value as nursery grounds for larvae and juveniles. Altered rainfall patterns are expected to intensify droughts. Droughts would also affect water-stressed areas such as deserts and their already imperiled fish species, aridify areas that now have intermittent rainfall, and lead to contraction of the habitat space available for many species. Droughts also cause shifts in the distribution of estuarine habitats, because sea water typically intrudes farther up river basins during periods of low

rainfall. Drought conditions would also exacerbate human impacts on fish habitat by reducing stream flow, elevating temperatures, and increasing pollutant concentrations.

Increased evaporation or decreased rainfall would decrease river flows and lake levels, causing wetlands to disappear and water tables to decline. The volume of cool water in many lakes would shrink, especially in summer. Cool water species whose ranges extend into warmer regions, such as Brook Trout, would be excluded from lower portions of streams during the summer. A few degrees of warming could be catastrophic for fishes that live near their critical thermal maxima because groundwater temperature is strongly dependent on air temperature (Power et al. 1999). Many stream fishes in the southwestern USA find temperatures above 38–40°C lethal. When temperatures in southern rivers exceed these limits, heat-related deaths occur, as they do with salmonids on the West coast at even lower temperatures (NRC 2004a). A 3°C temperature rise would potentially exterminate 20 species of fishes endemic to the southwest (Matthews & Zimmerman 1990). Warming would contract the geographic ranges of Arctic species, pushing the southern edge of their ranges northward (e.g., IPCC 2001).

Benefits of climate change?

Global warming also means that some warm water species would benefit from an increase in available habitat space at northerly latitudes, and some cool water species would gain access to higher altitudes and latitudes that are currently too cold to inhabit (Magnuson et al. 1990; Magnuson 2002). However, these shifts would dramatically alter assemblage relationships, with unknown consequences (Mandrak 1989). Cold water species will probably be both replaced and displaced by warm water species, especially invasive generalists, accelerating the process of faunal homogenization. Any "gains" would be offset by an overall loss of genetic and species diversity, especially because climate appears to be changing too quickly for genetic change to keep pace. New species will not have time to evolve to take the place of those that cannot adapt (IPCC 2001). A likely reduction in biodiversity is a serious, potential, negative impact of climate warming.

What can be done?

Biodiversity loss is a symptom of environmental deterioration on a global scale. A growing number of scientists, traditionally occupied with the descriptive and experimental pursuit of knowledge, have turned their efforts to environmental issues in an effort to reverse these declines. Even regional fish books that had previously focused on occurrence and distribution now include lengthy discussions of the conservation status of their fishes (e.g., Moyle 2002; Boschung & Mayden 2004). From these and other contributions, a large number of practical solutions to the various problems discussed here have emerged. Many have been tried, many more remain to be applied. A few are discussed below, but the concerned reader should refer to the diversity of synthetic discussions for details, such as FAO (1995, 1997), Leidy and Moyle (1997), Winter and Hughes (1997), Mace and Hudson (1999), NRC (1999b, among others), Hilborn (2005), and Helfman (2007). The most frequently offered solutions (in addition to the crucial need for surveying, documenting, and monitoring problem areas) include:

- Pass national and international legislation that promotes sustainable resource use, and enforce that legislation.
- Create reserves, as large as possible.
- Promote ecosystem-based management and evolutionarily compatible, prudent predation.
- Be precautionary: act despite uncertainty, without waiting for scientific consensus.
- Monitor results and manage adaptively, modifying management plans in response to changing conditions.
- Promote ecocertification efforts and other programs that reward sustainable fishing practices.
- Avoid technoarrogance, e.g., technological fixes that treat symptoms rather than causes.
- Restore degraded habitat to promote the recovery of imperiled species, and engage in captive breeding of endangered species as a last resort and only in conjunction with habitat restoration.
- Educate resource users and the public about biodiversity loss and sustainable use.
- Include all stakeholders at all stages in management decisions, and encourage local/community control wherever possible.
- Reduce fishing effort and eliminate subsidies that encourage overfishing.

Conservation efforts are of necessity **multidisciplinary**, requiring knowledge and integration from the biological and physical sciences, as well as from sociology, anthropology, and economics. Regardless, it is apparent to all concerned that the major task of conservation efforts is to reverse previous and minimize future human impacts on natural systems.

The level at which efforts must be addressed

Little doubt exists as to the declining state of global fish stocks. At the four levels of biodiversity – genetic, species, communities, and landscapes – we are witnessing alarming reductions. Historically, attention and concern have been focused on threats to individual species or populations. The

US Endangered Species Act of 1973 (ESA) focused on identifying and protecting species at risk; similar legislation exists in most developed and many developing nations (Leidy & Moyle 1997; Helfman 2007). Although the ESA was innovative and far-reaching, it is generally agreed among biologists that emphasizing species rather than habitats is at best a partial solution to biodiversity loss. Endangered species problems are really **endangered habitat** problems; captive breeding programs are futile if insufficient natural habitat exists into which a species can be reintroduced. The majority of extinctions result from habitat destruction, including the facilitated establishment of alien species in altered habitats (see above). Often more than one rare species is affected by the loss of a particular habitat, and organisms live in co-evolved, interacting communities, the elements of which are necessary for the welfare of most of the species in question.

Increasing emphasis is now being given to ecosystem and landscape conservation, which is logistically, economically, and politically more difficult to attain than species protection. In fact, and as recognition of the intricate interdependence of organisms and their habitats, conservation in the 21st century increasingly focuses on **ecosystem-based management** (Leidy & Moyle 1997; Winter & Hughes 1997; Mace & Hudson 1999; NRC 1999b; Agardy 2000; www.maweb.org). Our actions toward species or habitat components invariably ripple through and feed back upon other elements in the ecosystem, rendering efforts focused on a particular species shortsighted and ineffectual. In this context, humans are best regarded as a predator or competitor embedded in the evolved interactions of species. To minimize our impacts and to sustain resources for our use and the use of other ecosystem components in the future, *we should act like natural predators*. This means we should limit our exploitation within the bounds of other predators and competitors by harvesting in accord with the average take of other predators, and by focusing our predation on species and population segments that naturally experience high mortality rates (i.e., abundant, pelagic species low in the food web rather than top predators; young, prereproductive age groups rather than older, reproductively active and valuable age groups) (Kitchell et al. 1997; Fowler 1999; Hutchings 2000b; Stergiou 2002).

Biological preserves

One direct application of an ecosystem-level approach is through the creation of biological preserves (Moyle & Leidy 1992; NRC 2001). Few biological preserves exist today that are targeted directly at freshwater organisms (Saunders et al. 2002) (pupfishes in the Great Basin/Death Valley area of the southwestern USA are an exception; see Miller & Pister 1971). Most preserves are created as terrestrial parks that include lakes and portions of streams and rivers. Unfortunately, human activities upstream of such parks can threaten the aquatic biota in the park, and seasonal migrations by many fishes carry them beyond the protection of park and even international boundaries.

Marine parks (**marine protected areas** or **MPAs**) are much more common and generally considered to be successful, although enforcement has often proved problematic (Russ 2002; Halpern 2003). MPAs are established to both **preserve biodiversity** and **promote biomass**; the two goals are not mutually exclusive. Improved conditions result from relaxation of both exploitation (lowered mortality due to fishing) and habitat disturbance, which lead to changes in ecological and life history traits of resident fishes. Fishes within a protected area may increase in diversity, density, average size and age, and overall biomass. On average, density has been found to increase two-fold, biomass three-fold, and fish size and number of species to increase 20–30% (Halpern 2003). As a result, fishes disperse from the densely populated, protected area to surrounding areas (the **spillover effect**) (Fig. 26.16). When effective, spillover more than compensates for lost fishing opportunities within the reserve, although that can be slow to occur (e.g., McClanahan & Mangi 2000). At a more regional scale, many large fishes in reserves lead to increased reproductive output in the protected area, which should result in increased export of larvae that potentially settle in downstream, often distant areas (the **recruitment effect**), although demonstrations of the recruitment effect remain rare.

The most effective MPAs are those that are "**no-take**", that restrict all extractive activities. Recreational diving with no contact of the bottom is minimally intrusive (some parks restrict the use of gloves, which minimizes bottom contact). Multiple-use objectives often compromise the refuge quality of marine preserves. Protection is often limited, e.g., spearfishing and nets may be prohibited, but not hook-and-line fishing. Again, many species move out of reserve waters as a normal part of their life histories, which then subjects them to commercial and recreational exploitation. Dependence on dispersed larvae for recruitment means that "upstream" habitats must also be protected or populations in an area may decline. Larger parks, such as much of the Great Barrier Reef in Australia and the Florida Keys National Marine Sanctuary in Florida, encompass more species and life history stages but are more difficult to police. Where such preserves are established, marine life and particularly fish populations rebound dramatically (e.g., Hanauma Bay in Hawaii, Dry Tortugas in Florida). In all cases, whether the area is fresh water, estuarine, or marine, the costs of acquisition are high, and opposition to "loss" of the area to exploitation is often strong.

Rehabilitation and restoration

Costs are a major factor in **restoring degraded habitat** to something approximating original (or at least better)

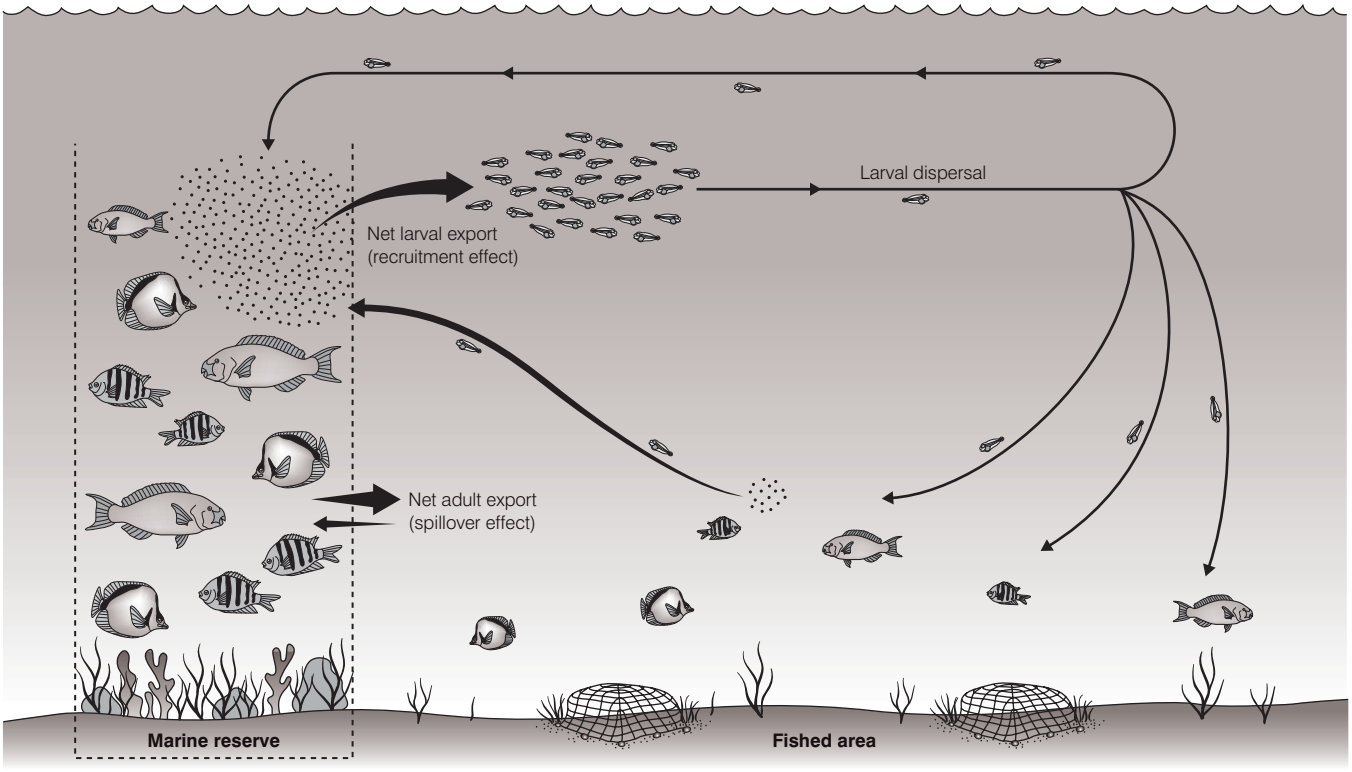


Figure 26.16

Functions of marine protected areas from a fisheries management perspective. Inside the reserve, the numbers, size, and age of residents increase in response to reduced fishing pressure. This leads to increased reproduction and net export of both adults and larvae into adjacent regions. Diversity can also increase. After Russ (2002).

conditions. Dramatic results can be achieved if restoration becomes a high priority, although many restoration efforts in flowing water systems have focused on recreating instream habitat rather than arresting practices in surrounding watersheds that actually cause habitat loss (e.g., Frissel & Nawa 1992; Bernhardt et al. 2005). Also missing from many such restoration projects, and many conservation efforts in general, is **post-project monitoring** that accurately assesses the outcome, rather than assuming success when restoration efforts cease (e.g., Kondolf 1995; Bash & Ryan 2002).

Reversals and partial restorations of badly polluted and degraded systems have been achieved in Puget Sound in Washington State, Kaneohe Bay in Hawaii, the upper Illinois River in Illinois, the Willamette River in Oregon, the Mattole River in northern California, and the Merrimack River in New Hampshire and Massachusetts (NRC 1992). Success in restoring depleted fish populations can result from such actions, as is apparently the case for Lake Trout, *Salvelinus namaycush*, in the Laurentian Great Lakes and Striped Bass, *Morone saxatilis*, in the Chesapeake Bay. However, few if any ecosystems are ever restored to their original conditions; improvement from a state of extreme degradation is often the most that can be achieved. The complexity of natural, evolved systems works against human-induced solutions, which often strive for simplicity. In truth, restoration efforts have often demonstrated that "corrective measures to restore ecosystem function [are] obtained only at very high costs, that some attributes can be maintained only with continuous management, and that certain losses in the ecosystem [are] irreversible" (Schelske & Carpenter 1992, p. 383).

Captive breeding

Captive propagation of endangered species, with eventual release into the wild, is an oft-cited solution to the extinction problem (e.g., Ribbink 1987; Johnson & Jensen 1991). Government agencies, private organizations, native peoples, and private individuals culture and reintroduce imperiled fishes, into either restored native habitat or acceptable, alternative habitat (e.g., Wikramanayake 1990; Minckley 1995). Such efforts can be costly and time-consuming, small numbers of breeding individuals lead to genetic bottlenecks and loss of diversity, and the breeding and rearing requirements of most species are poorly known or difficult to replicate outside of the natural habitat (e.g., Anders 1998; Rakes et al. 1999). **Conservation genetics** is a rela-

tively new discipline that focuses on the myriad problems associated with trying to resurrect endangered species from small numbers of breeding individuals (e.g., Meffe 1986; see Chapter 17). In some instances, captive propagation may be the only hope for a species.

Education and population control

The protection of species and preservation of the habitats in which they live requires an **educated public** that recognizes the enormity of our impacts, appreciates the value of biodiversity, and understands the degree to which humans depend on aquatic ecosystems. Major changes in attitudes – of citizens, scientists, politicians, and managers – toward how we value fishes, aquatic environments, and natural resources will have to take place (Callicott 1991; Pister 1992). Evidence of changing attitudes exists in the popularity and success of **ecocertification** programs that encourage sustainable use of fishery resources. Dophin-Safe Tuna, Give Swordfish a Break, Take a Pass on Patagonian Toothfish, FAO Code of Conduct for Responsible Fisheries, and the more general Seafood Watch/Sustainable Seafood guides facilitate sustainable use and allow consumers to encourage exploitation activities that involve sustainable practices (e.g., Pacific Halibut and Alaskan wild-caught salmon) and discourage fisheries that are pursued in a nonsustainable manner (see Peterman 2002; www.mbayaq.org; www.msc.org).

Ultimately, however, the future of aquatic and terrestrial life on earth will be determined by whether the human species continues to multiply and consume at current rates. Realistically, conservation efforts are doomed if **human population growth** and **resource consumption** cannot be checked. The impact that humans have on the earth's resources are the combined effects of large numbers of people consuming at unsustainable rates. In developed nations, achieving sustainable consumption rates will require an educated and concerned public that is willing to adjust its standard of living in order to maintain a high quality of life (Pister 1992). National and international programs to control human population growth are crucial to reversing global and local environmental deterioration (Becker 1992; Meffe et al. 1993). Any refusal to take remedial action in the form of human population control only forestalls an inevitable Malthusian scenario. Predator populations cycle in step with their prey. Humans, with alternative prey resources, have managed to increase the time lag separating the cycles. But the laws and principles of natural selection and of population dynamics will eventually be upheld, and order restored.

Summary

SUMMARY

1. Extinction rates have increased dramatically in the past 50 years due to human activities; present rates are 1000 times greater than average and 10–100 times greater than during past periods of mass extinction. About 20% of the world's 9000 species of freshwater fishes are either extinct or nearly so; 40 fishes have gone extinct in North America in the past century and the rate is accelerating. Marine fishes are less threatened because of their wider distributions, although many commercially important species are showing serious declines.
2. Major causes of biodiversity loss are habitat loss and modification, species introductions, pollution, commercial exploitation, and global climate change. Habitat loss occurs through modification of bottom type, as happens during dredging, log removal, coral or gravel mining, trawling, and from silt deposition due to deforestation of the surrounding watershed. Other causes of habitat loss include channelization of streams and rivers, dam building, and water withdrawal.
3. Introduced species affect native species because introduced fishes are often freed from their evolved population controls, and natives are evolutionarily unprepared for the introductions. Predation by and competition and hybridization with introduced species are common results, as is the introduction of new pathogens. The introduction of Nile Perch into Lake Victoria has led to the possible extinction of hundreds of species of endemic cichlids that previously supported an important local fishery.
4. Chemical, nutrient, and sediment pollution all have adverse effects on fishes; predation on fishes by birds and mammals links aquatic and terrestrial ecosystems via such pollution. Fishes can therefore serve as valuable indicators of environmental health.
5. Approximately 40% of the commercial marine fish species important to the USA are exploited at unsustainable rates. The Pacific Sardine, Peruvian Anchoveta, and Giant Totoaba were all very abundant commercial species that have essentially disappeared due largely to overfishing. Some species reductions

are the indirect result of other fisheries. Bycatch in the shrimp fisheries of the Gulf of Mexico greatly reduces the available stocks of Red Snapper and Spanish Mackerel, among other species. Coral reef fishes are commercially exploited for the home aquarium trade, which has led to reef destruction and species depletion in many places. Few such fishes live more than a few months in captivity.

6 Greenhouse gases have been pumped into the atmosphere at increasing rates during the past century, raising the prospect of global warming, sea level rises, ocean current shifts, and major climatic changes such as drought, floods, and cyclonic storms. Global warming has and will alter the distribution, abundance, reproductive timing, trophic relationships, and migration patterns of fishes through its impacts on water temperature, rainfall patterns, freeze–thaw cycles, oxygen availability, heat budgets, oceanic currents, primary productivity, ocean acidification, and metabolic processes. Coral reef ecosystems have been especially degraded due to slightly elevated temperatures, and prospects for the future are not promising. Major shifts in freshwater fish distribution and diversity would also occur.

7 Biodiversity loss is a symptom of environmental deterioration on a global scale. Solutions to environmental problems include ecosystem and landscape preservation, development of reserves, habitat restoration, and captive breeding of endangered species. None of these efforts will be successful if human population growth and overconsumption are not curtailed.

Supplementary reading

SUPPLEMENTARY READING

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Species accounts of many of the world's imperiled fishes have appeared in the series "Threatened fishes of the world" in the journal *Environmental Biology of Fishes*.

Websites

Committee on Recently Extinct Organisms, CREO, creo.amnh.org.

Convention on International Trade in Endangered Species, CITES, www.cites.org.

Global lists and descriptions of MPAs are at http://sea.unep-wcmc.org/wdbpa.

Information on marine protected areas in the USA is available at www.mpa.gov.

Intergovernmental Panel on Climate Change, www.ipcc.ch.

International Union for the Conservation of Nature, IUCN, www.redlist.org.

UN Food and Agricultural Organization, FAO biennial report on world fisheries, www.fao.org/sof/sofia.

US Fish and Wildlife Service, endangered species database, http://ecos.fws.gov/tess_public.

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