# Aquaculture and Behavior

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# Preface

There are many problems to be overcome in aquaculture, irrespective of whether the fish are being farmed for food, cultivated for release into the wild or are being reared as pets or ornamentals or for scientific research. A number of disciplines, including engineering, veterinary science, nutrition, genetics, animal breeding and reproductive biology, have contributed to finding solutions to problems related to holding fish in captivity. This book has been written in the belief that, among these, the study of animal behaviour can make important contributions to effective, sustainable aquaculture. Many of the problems encountered when holding and rearing fish stem from the natural behaviour of the fish concerned and solutions to these could emerge from an understanding of why animals behave as they do. Consequently, there is a growing interest in the application of behavioural concepts to aquaculture. The overall aims of this book are to give an account of the behavioural biology of fish, to explore its implications for fish culture and to show how knowledge of fish behaviour can be used to solve problems and promote sustainable aquaculture.

The book has seven chapters that deal with specific behaviours relating to orientation and movement, foraging and feeding, antipredator behaviour, aggression and reproductive behaviour. For ease of comparison, the structure of these chapters has been standardised. Each chapter starts with an account of the behaviour as seen in fish in natural habitats, looking at the mechanisms that generate the behaviour, how the behaviour develops and how performing the behaviour relates to Darwinian fitness. The various ways in which these behaviours cause problems for production, for fish welfare and for the surrounding environment are then discussed and potential solutions to such problems are suggested based on a consideration of the biology of the behaviours concerned. To put these seven chapters in context, the book begins by giving a general introduction to aquaculture and behaviour. We look at the finfish species that are cultured, the systems used to culture them and criteria for successful captive rearing. We also define behaviour and describe how biologists study it and try to explain it. Fish are very different from other farmed animals so we devote the second chapter to an overview of fish biology, concentrating on those aspects that are of particular relevance to behaviour and to performance in culture. Because the behaviour of fish is particularly difficult to study in intensive culture systems, the third chapter gives a review of the methods available for studying the behaviour of farmed fish. In the final chapter, we identify some common principles for using our understanding of fish behaviour in aquaculture, both as it is practised today and in the light of likely future developments.

This book is aimed both at undergraduate and postgraduate students interested in fish biology, animal behaviour and aquaculture and at established researchers and technical and research managers in the aquaculture industry. Our goal is to achieve an authoritative, up to date scientific content, with an accessible jargon-free style. Rather than aiming at an exhaustive academic review of all that is known about a particular aspect of behaviour, we give a broad overview illustrated by selected examples and have supplemented this by referring the reader to up to date review articles and to the primary literature.

To cover all the topics with the desired authority and clarity has required an interdisciplinary approach, and our authors bring to the book complementary expertise in many areas of fish biology and aquaculture science. They have worked in teams, coming together in different combinations to write the various chapters. This has required a considerable amount of co-ordination and collaborative exchange among



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authors that, we hope, has produced a coherent end result. We would like to thank all the authors for taking part in this complicated project and the publishers for their patience in waiting for the end result. We would also like to thank Susan Linklater for setting up our electronic communication system, Lorna Kennedy for all kinds of help, including handling the copyright queries, Kirstin Harper for reviewing sections of the literature for us and Fraser Howarth for double checking some of the chapters and, with Fabio Borcato, for compiling references lists.

Felicity Huntingford, Malcolm Jobling and Sunil Kadri

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# Foreword

In my role as a scientist for one of the large salmon feed companies, I have worked directly with two of the editors of this book, namely Felicity Huntingford and Sunil Kadri. During the time we worked together I learnt first hand about the dedication, breath of knowledge and unbounded enthusiasm of the authors for the subject of fish behaviour. In particular, their belief that an understanding of fish behaviour can be applied to commercial fish farming practice to improve both the welfare of fish and the efficient and sustainable aquaculture production. This book is born from those qualities and beliefs.

In our work together co-supervising the work of some PhD students we came across some puzzling fish behaviour including that there were instances when, despite being offered sufficient amounts of feed, some fish chose to ignore the feed and consume almost no feed for many months; a behaviour that I found difficult to understand particularly since the feed was of such high quality.

The book is written with a clear audience in mind; anyone involved in aquaculture who would like to improve sustainable fish production. This is particularly clear from the 'Implications for Aquaculture' sections that round off each of the seven main chapters in the book. Its scope is very wide since it encompasses herbivorous to carnivorous species, extensive to intensive production, different production systems and the different purposes that aquaculture serves. They recognise that aquaculture is not just for food production but also production to supplement fish for conservation reasons and the production of ornamental species. Apart from appealing to those who aim to increase efficient and sustainable fish production, it will also interest students and teachers of aquaculture and fish behaviour. Its style is clear and easily accessible, the authors avoiding obscure terminology and excessive citing of published work and yet it is clearly authoritative and comprehensive. The text is liberally sprinkled with interesting illustrations of behaviour such as the cooperative hunting sorties between groupers and moray eels. It shows that careful observation of fish can give clear information about welfare; for example the colour of the ring around the eye darkens in salmonids in response to various stressors and this acts as a social signal.

For the practising fish farmer there are helpful ways in which an understanding of fish behaviour can be used to improve production and welfare. A few examples that caught my attention are given here. In Chapter 4 the authors explain that growth and feed efficiency can be improved by optimising the swimming speed and since this is often a function of body length it pays to site farms for smaller fish in slower moving waters compared to larger fish. Similarly, the carefully considered placement of underwater lights will allow reduced stress. Fish have a clear pattern of behaviour such as preferred swimming depth and trajectories and these vary with, for instance, time of day and hunger level. Hence, lights should be placed at depths that allow them to express this natural preference but also to avoid creating excessively high densities. The provision of cover allows the reduction in cannibalism in a variety of species and similarly the provision of cover for wrasse and spatial information or landmarks allow salmon to seek the attention of these cleaner fish when they are co-habited to control lice numbers. The need to give fish sufficient opportunity to consume feed during a meal is well known but from chapter nine it is clear that even where increasing feeding opportunity further gives no increase in growth or efficiency, there can still be a benefit in reduced aggression and thus less damage and a resultant improvement in health and value.

As for those odd-behaving salmon that did not consume any of my high quality feed for so many months, the answer lies within the book, so whether you simply wish to gain a better understanding of fish behaviour or are a fish farmer aiming to increase sustainable production, this book is for you.

V.O. Crampton, EWOS Innovation



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# 1
# Introduction: Aquaculture and Behaviour

*Felicity Huntingford, Sunil Kadri and Malcolm Jobling*

**Abstract:** This chapter starts by providing a review of what aquaculture is, which finfish are farmed, for what purposes and in what kinds of culture systems. It then considers what behaviour is, why biologists are interested in behaviour and how they study and explain it. The question of the complexity of fish behaviour is addressed, leading into a discussion of fish welfare and how it can be defined, identified and measured. The issues of domestication, selective breeding and the extent to which fish are domesticated animals are then covered, as are the effects of captive rearing; in both cases, effects on behaviour are given special consideration. The criteria for effective, sustainable fish culture are then spelled out; these include efficient production, environmental protection (with respect to land, water and feed resources and to impacts on wild fish populations) and fish welfare. Possible strategies for improving the welfare of farmed fish are discussed and consideration given to what is required of the behaviour of fish cultured for food, for science and the ornamental trade and for release. Finally, an outline is given of the structure and content of the remaining 10 chapters of this book.

**Keywords:** behavioural biology; **c**aptive rearing; consciousness; conservation; culture systems; domestication; **e**nvironmental protection; fish in research; food fish; ornamental fish; production; selective breeding; supplementation; sustainability; welfare.

## 1.1 WHY BEHAVIOUR AND AQUACULTURE?

There are many problems to be overcome in the culture of fish, in terms of producing sufficient numbers of larvae and juveniles, in rearing these to the desired age and size and in ensuring that the fish have the characteristics appropriate to the purpose for which they were farmed. For long-established aquaculture species, the most immediate problems of cultivation have been solved; farmers can obtain a sufficient supply of fish and know about the environmental and food requirements for survival and growth. Even so new problems can arise, such as emerging diseases and concern about the environmental impact of farming operations. For both established and new species, scientists representing many disciplines have contributed to finding solutions to the problems encountered in culturing fish; engineering, veterinary science, nutrition, genetics, animal breeding and reproductive biology represent a few of these.

This book has been written in the belief that the biological discipline of animal behaviour can also make important contributions to promoting aquaculture. Many of the problems encountered in fish culture might stem from the

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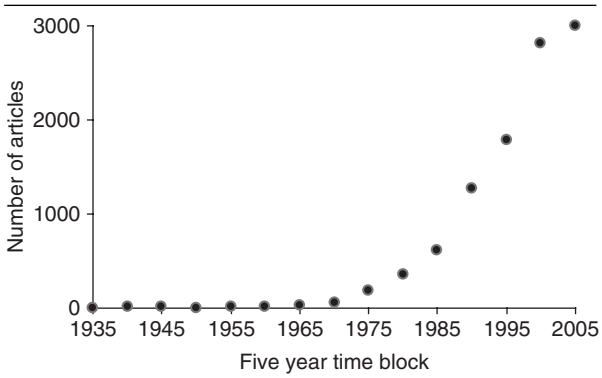


**Figure 1.1.** The number of papers on behaviour and aquaculture published in each 5 year period since 1935. Based on a Web of Science search using the key words behaviour (British and American spelling) and aquaculture.

natural behaviour of the fish concerned and solutions to these could emerge from an understanding of why animals behave as they do. Consequently, there is a growing interest in the application of behavioural concepts to aquaculture. This is reflected in the increasing number of published scientific articles on this topic (Figure 1.1). The overall aim of this book is to cover different aspects of behaviour that are relevant to fish culture, summarizing and illustrating the relevant fundamental behavioural biology and exploring its implications for aquaculture. The purpose of this introductory chapter is to provide the background information needed put this into context, starting with an overview of which finfish are cultured, for what reasons and how this is done. This includes an introduction to a group of species of fish cultured for various purposes that are used as 'spotlight species' to illustrate specific points throughout the book. There follows a brief review about what behaviour is and how biologists study and explain it, as well as a commentary on the degree to which fish are capable of the complex behaviour shown by other vertebrate groups that are farmed. This leads on to the tricky issue of the extent to which fish welfare is a meaningful concept about which it is legitimate to be concerned. The question of the effects of domestication and captive rearing on fish is addressed, both in general terms and in the context of potential effects on fish behaviour. Finally, criteria for effective and sustainable fish culture are considered, spelling out what it is that fish farmers aim to achieve; these include welfare-friendly, cost-effective production that is sustainable in terms of impact on the environment.

## 1.2 ABOUT AQUACULTURE

### 1.2.1 What aquaculture is

Aquaculture is the farming of aquatic organisms. In addition to finfish, which are the topic of this book, these include plants (both small phytoplankton and large macrophytes, such as seaweeds), molluscs (mussels, clams, scallops, marine gastropods, squid and octopus), crustaceans (freshwater and marine shrimps and prawns, crayfish and crawfish, lobsters and crabs), amphibians (frogs) and reptiles (sea turtles, freshwater turtles and terrapins, crocodiles and alligators). The fact that aquaculture is a form of farming implies that the organisms being cultivated are owned by farmers and that there is human intervention during the rearing process. The level of human intervention varies widely depending upon the species being cultured and the type of farming practice employed. For example, in the extensive cultivation of seaweeds and bivalve molluscs such as clams and mussels, there may be only a minimal degree of human intervention. This could involve no more than seed collection, selection of on-growing sites, occasional thinning of the stock and harvesting. On the other hand, the intensive farming of finfish and crustaceans may involve multiple interventions throughout the rearing cycle, from broodstock management, gamete collection and egg incubation to larval rearing and on-growing of the stock to market size. The interventions will often include regular feeding and observation of fish, management of water quality, treatment to combat diseases and infestation with parasites and protection from predators. The degree to which farmers intervene during the culture cycle will clearly have an impact on many aspects of the biology of their stock, including their behaviour.

### 1.2.2 Why finfish are cultured

Although understanding behaviour is important for culture of many kinds of animals, this book concentrates on behaviour and finfish aquaculture, since this in itself is a huge topic. When one considers finfish aquaculture, the first reaction is usually to think of the production of fish as a source of food for human consumption. The farming of fish for food undoubtedly accounts for the greatest proportion of finfish aquaculture, but it is by no means the only reason for which fish are farmed. Some are farmed for the ornamental fish trade, for use in domestic and display aquaria, whereas others are reared in large numbers for release into the wild to supplement wild populations used in recreational and commercial fisheries. A few species are raised in captivity for biomedical research or for environmental impact studies, while others have been taken into captivity

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in an attempt to conserve and save threatened natural populations. Finally, some fish species are farmed for use as pest control agents; for example, mosquitofish (*Gambusia affinis*) and guppies (*Poecilia reticulata*) are used to control the malarial mosquito and the grass carp (*Ctenopharyngodon idella*) is used to control aquatic vegetation that threatens to clog ponds, lakes, shipping canals and other waterways (Lever 1996; Shelton & Rothbard 2006).

### 1.2.3 Which finfish are cultured

The farming of finfish is recorded in antiquity, but a great expansion has occurred since the 1960s. The expansion has involved marked increases in production volumes and increases in the number of farmed species worldwide (http://www.fao.org/), driven by a combination of diminishing natural fisheries and an increased consumer demand for fish products (Shelton & Rothbard 2006; Le Francois *et al*. 2010). There are about 28 500 living species of finfish, inhabiting ponds, lakes, streams, rivers, estuaries and oceans throughout the world. About 40% of these species live in fresh water, particularly in tropical and subtropical regions, with freshwater species being most numerous in the river drainages of South-east Asia and South America. Just under 60% of the total number of species inhabit marine environments, the vast majority being found in shallow tropical and subtropical coastal waters. However, the coastal and shelf waters of temperate and polar regions also provide habitats for about 2000 species. Over 100 fish species are diadromous, migrating between marine and freshwater habitats for the purposes of feeding and breeding. Amongst these, most are anadromous, spawning in fresh water but having feeding grounds in the sea; however, a few are catadromous, spawning in the oceans but spending much of their life in fresh water. A major taxonomic division among finfish is between cartilaginous fish, such as sharks and rays, and bony fish, which include the lobe-finned fishes, such as the lungfishes, and the ray-finned fishes, which comprise the largest group of finfish.

Thus, living finfish represent a very large and diverse group in terms of both their taxonomy and their ecology. Only a small proportion of finfish is suitable for culture; for example, of the 300 species that are farmed for human consumption, less than half are produced in large quantities and farmed fish production is dominated by species from a few families (Shelton & Rothbard 2006; Le Francois *et al*. 2010; http://www.fao.org/figis). The majority of farmed species belong to the teleosts, which is the largest and most advanced division of the ray-finned bony fishes, containing almost 27 000 extant species. Some representatives of other groups of ray-finned fish, perhaps most notably the sturgeons, are also farmed. All the 25 species of sturgeons (family Acipenseridae) occur in the northern hemisphere and all spawn in fresh water, although some species are diadromous, moving seasonally between fresh water and the sea. The life history characteristics of the sturgeons make them susceptible to overexploitation by humans; they are long-lived, late-maturing species and mature females may not spawn each year. All sturgeon species are endangered as a result of overfishing, damming and regulation of waterways and industrial pollution of their habitats. Several species are being raised in captivity as a conservation measure. Sturgeons are also highly prized as food fish, both for their meat (which may be smoked) and for their roe (caviar), which is one of the most valuable fish products in the world. Sturgeon farming is carried out in some Middle Eastern countries, in parts of Europe and the former Soviet Union and in North America (Le Francois *et al*. 2010).

Among the teleosts, the ostariophysans dominate the fresh waters of the world in terms of both numbers of species (about 7500) and individuals, accounting for about two-thirds of all freshwater fish species; they include the minnows, carps, loaches, piranhas, tetras, freshwater catfishes and electric eels. Culture of carps and freshwater catfishes dominates fish farming in fresh waters, and fish culture production as a whole. Although generally considered freshwater fish, about 120 ostariophysan species are marine; for example, the milkfish (*Chanos chanos*) is an important food fish in the Indo-Pacific region where it is farmed in brackish-water ponds and lagoons. The family comprising the carps and carp-like fishes (Cyprinidae) is the largest family of freshwater fishes, with about 2200 species and with its greatest diversity in Eurasia, followed by Africa and North America. Several species are popular as aquarium fishes, including the goldfish (*Carassius auratus*), koi carp (a variety of *Cyprinus carpio*), zebrafish (*Danio rerio*) and other rasboras. The zebrafish is now widely cultivated for use in laboratory-based research on subjects including developmental biology and genetics, toxicology and biomedicine. Box 1.1 gives more details of the species in this large group of teleost fish that are cultured and for which purposes.

The cichlids (Cichlidae) make up another family with many freshwater species (about 1400 species). There are almost 400 species in the Americas, but the great majority of cichlids occur in Africa and a few species are found in the Middle east and on the Indian subcontinent. Several cichlids are popular aquarium fishes; South American species include the freshwater angelfishes (*Pterophyllum* spp.), discus (*Symphysodon* spp.), oscars (*Astronotus* spp.) and convict cichlids (*Archocentrus* spp.), whereas amongst

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**Box 1.1** Further details of some cultured groups of Ostariophysi

See Tucker & Hargreaves 2004, 2008; Shelton & Rothbard 2006 and http://www.fao.org/figis for details

***Cyprinids*:** Several species of carp are farmed in South-east Asia, on the Indian subcontinent, and in Europe, but there is little interest in carp culture in North America. World-wide, the annual production of cyprinids is about 15–20 million tonnes. The common carp (*Cyprinus carpio*) is farmed in many countries and dominates cyprinid culture in Europe, making up about 64% of the approximately 225 000 tonnes of farmed cyprinids produced in that continent. A variety of cyprinid species, often referred to as Chinese carps, are farmed in large quantities in South-east Asia. These include grass carp (*Ctenopharyngodon idella*), mud carp (*Cirrhina molitorella*), silver carp (*Hypophthalmichthys molitrix*), bighead carp (*Aristichthyes nobilis*) and *Carassius* spp. (crucian carp and gibel carp). *Carassius* spp. are produced in several Asian countries and in Eastern Europe, but production is low outside China. Similarly, grass carp and bighead carp are farmed in over 20 countries, mostly in South-east Asia, but also in Europe and on the American continent, though fewer than 10 countries report production figures over 1000 tonnes. On the Indian subcontinent, Indian major carps, catla (*Catla catla*), mrigal (*Cirrhina mrigala*), rohu (*Labeo rohita*) and calbasu (*Labeo calbasu*) are farmed, along with some production of Chinese carps. The majority of carp farming takes place in ponds by extensive or semi-intensive methods, and pond-based, semi-intensive polyculture of cyprinids is the norm in many south-east Asian countries.

***Characiforms*:** The majority (about 1300) of characids are South American; some occur in Central America and the southern states of the USA and about 200 species occur in Africa. The order contains many popular aquarium fishes, including the tetras and silver dollars and some of the larger species are important as food fishes in certain South American countries; a few of these, such as *Colossoma* and *Brycon* spp., are farmed for human consumption.

***Siluriformes*:** There are almost 3000 species of catfishes, which mostly inhabit freshwater and as a group have a worldwide distribution, predominantly in South America, south-east Asia and Africa. Freshwater fish farming in the USA is dominated by catfish culture (family Ictaluridae) in the southern states bordering the Gulf of Mexico, with several species and their hybrids being cultured. Catfish farming in the USA is dominated by semi-intensive and intensive pond culture of the channel catfish (*Ictalurus punctatus)*. Catfish culture is widespread globally, being practised in several Asian, African and European countries. In these regions, farming tends to be based upon the rearing of native catfish species (families Siluridae, Pangasiidae, Clariidae). In South-east Asia, pangasius (*Pangasianodon hypophthalmus*) farming has undergone explosive growth, driven by a rapid expansion in Vietnam and other countries of the Mekong River basin (Thailand, Cambodia and Laos), but also in Indonesia, Malaysia, Bangladesh, Myanmar (Burma) and China. The development of pangasius farming has played an important role in the socioeconomics of rural communities in these countries, with most of the farmed pangasius being processed for export to markets in Europe, the Americas and countries of the former Soviet Union. Pond culture is the norm for the farming of catfishes, but there is some intensive cultivation of catfish in Europe, carried out in land-based, water re-use tank and raceway systems.

the African cichlids several species within the genus *Haplochromis* have attained popularity with aquarists. In parts of the world, some cichlids, commonly known as the tilapias, are important as food fishes. Tilapia farming has a long history, but has experienced a recent rapid expansion; within the space of two to three decades tilapias changed from being fish that were reared by poor farmers in developing countries for local consumption to being an important export commodity that is traded in global markets. Annual production of farmed tilapia is over 2 million tonnes and rivals or exceeds that of farmed salmonids, so tilapia is now familiar in international fish markets.

All salmonid species, about 70 in total, occur naturally in the northern hemisphere, but several species have been introduced to the southern hemisphere, where they are farmed or form the basis of recreational fisheries. There are both freshwater and anadromous species of salmonids, but some of the anadromous species also have populations that are confined to fresh waters. The farming of salmonids expanded rapidly in the late 20th century, with production reaching 1.5 million tonnes by the turn of the century and expanding further during the early years of the present century. Just over half of the production is Atlantic salmon (*Salmo salar*). Much of the remainder is rainbow trout (*Oncorhynchus mykiss*), global annual production of farmed rainbow trout being about 500 000 tonnes (http://www.fao.org/figis). Traditionally, the farming of salmon and trout has been

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carried out in Europe and North America, although Chile and Australia have become significant producers in recent years (http://www.fao.org/figis; Shelton & Rothbard 2006; Solar 2009; Le Francois *et al*. 2010). Atlantic salmon and rainbow trout are farmed primarily as food fish, but both species are sometimes used for supplementation to support recreational fisheries. The brown trout (*Salmo trutta*) is reared in several European countries for both food and supplementation. Several species of Pacific salmon, some charrs and whitefish are also reared, either directly for human consumption or for supplementing natural populations.

Representatives from several marine finfish families are also farmed, including sea breams and porgies (family Sparidae), drums and croakers (family Scianidae), sea basses (family Serranidae), the temperate basses (family Moronidae), Atlantic cod and sablefish (Gadidae) and marine flatfishes (families Scophthalmidae, Paralichthydae, Pleuronectidae and Soleidae; Stickney 2000; Tucker & Hargreaves 2008; Le Francois *et al*. 2010; http://www.fao.org/figis). Production of farmed marine species is generally moderate in comparison with the quantities of the major freshwater (cyprinids, freshwater catfishes and tilapias) and anadromous (salmon and trout) species that are produced by farming.

### 1.2.4 Kinds of culture systems

#### *Extensive and intensive fish culture*

Culture systems for finfish aquaculture can be classified on a continuum with extensive systems such as natural ponds that require little management at one extreme and intensive, closed, recirculating systems requiring continuous monitoring at the other (Figure 1.2; Tucker & Hargreaves 2008; Le Francois *et al*. 2010). As increasing control over the rearing environment is exerted by the farmer, culture intensity is said to increase, as does the production capacity of the system. The sophistication of the technology required to develop and operate a culture system is usually higher as intensification increases, though there can be variation even within a given type of culture system. As culture intensity increases, both initial and operating costs, as well as the chances of system failure, tend to rise. When fish are held at high stocking densities, there is greater dependence upon complex equipment and power supplies and a failure in the water supply will rapidly lead to deterioration in water quality, with the risk of death of the fish. Rearing conditions within closed, recirculating systems may be independent of the local climate and there may be strict control over water quality and other rearing conditions, but the risk of failure is increased and the margin of error reduced compared to low-technology systems.

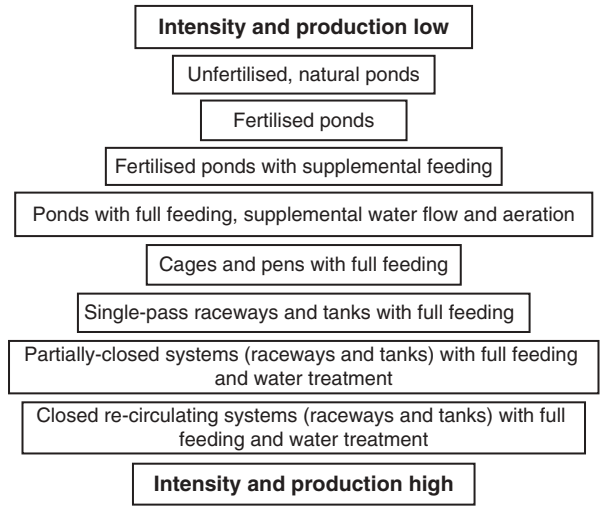


**Figure 1.2.** Schematic depiction of culture systems used for producing fish, classified in terms of intensity. Reproduced with permission from Le Francois *et al.* 2010.

Although culture systems vary in design and degree of intensification, all fish production systems have the common feature that they require abundant water of correct quality and temperature. Variation in water quality beyond acceptable ranges leads to reduced rates of growth of the fish, distress, increased incidence of disease outbreaks and in extreme cases mortality of the stock. Water characteristics are influenced by factors such as the type of production system, stocking density of the fish and the types and amounts of feed introduced into the system. Ponds, flow-through tanks and raceways rely on different amounts of water exchange and aeration to maintain water quality. When cages (or net-pens) are placed in the sea or lakes, water quality is maintained by the water exchange that results from water currents or tides. In water re-use and re-circulating systems, temperature and water quality parameters such as oxygen, carbon dioxide and ammonia concentrations, and pH are controlled mechanically or biologically (Tucker & Hargreaves 2008; Le Francois *et al*. 2010).

#### *Pond culture*

Natural earthen ponds, typical extensive production systems, are dynamic ecosystems under the influence of factors such as weather that are uncontrollable and

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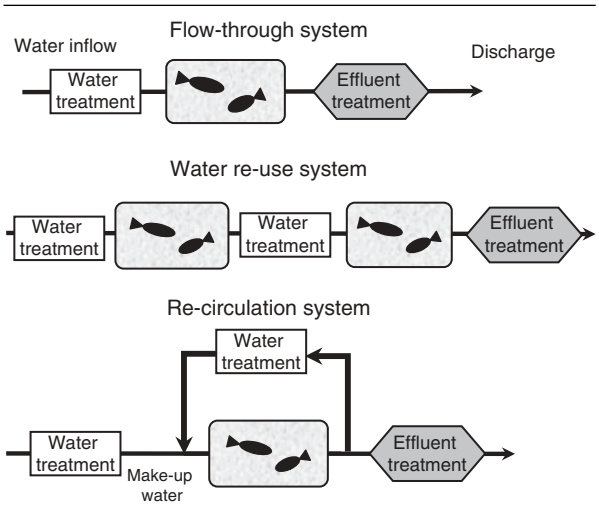


**Figure 1.3.** Schematic depiction of three water management systems used for producing fish. Reproduced with permission from Le Francois *et al.* 2010.

unpredictable and so are difficult to manage. Although earthen ponds are usually associated with extensive production, intensity of pond production varies depending upon external inputs and the effort expended in pond management. Intensification of pond culture increases from the unfertilized natural pond, through fertilized ponds and ponds with supplemental feeding to ponds with full feeding, aeration and rapid rates of water turnover (Figure 1.2). Pond carrying capacities and fish stocking densities rise as the level of intensification increases. Treatment of ponds with inorganic fertilizers that provide nitrogen, phosphorus and potassium, plant composts or animal manures will enhance growth of phytoplankton and this can lead to 5- to 10-fold increases in fish production relative to unfertilized natural ponds. 'Liming' with calcium compounds is also frequently carried out to regulate water pH and alkalinity (Boyd 1995; Tucker & Hargreaves 2008). In fertilized ponds the fish are wholly dependent upon consumption of natural prey organisms to support their growth. This type of pond culture has traditionally been used for the farming of cyprinids, such as common carp (*Cyprinus carpio*), grass carp (*Ctenopharyngodon idella*) and various species of Indian major and mud carps, for example, *Labeo, Catla* and *Cirrhina* spp.

The food base of the pond may be augmented by adding supplemental feeds, usually formulated from cheap feed ingredients, to supply the fish with additional nutrients and energy. The feeds may be deficient in some vitamins, minerals and other essential nutrients that the fish can obtain by feeding on the organisms present in the pond. In the most intensive form of pond culture, the fish are provided with complete feeds formulated to meet all their nutritional requirements, there is some water renewal in the pond and supplemental aeration is applied should hypoxic conditions arise. Such intensive pond culture is used in the farming of channel catfish (*Ictalurus punctatus*) in the southern states of the USA (Tucker & Hargreaves 2004, 2008).

### *Tanks and raceways*

Land-based culture systems usually use tanks and raceways of various sizes, connected to a water supply and drainage system. These are the rearing units within land-based flow-through (open) and recirculating (closed) culture systems (Figure 1.3; Tucker & Hargreaves 2008; Le Francois *et al.* 2010). Tanks, which may be square, rectangular or circular, are most commonly used in fish hatcheries for the rearing of larvae and juveniles, but may also be used for the on-growing of larger fish to market size. Tanks and raceways are in effect artificial ponds and streams that lack the complex biotic environment of natural systems and allow a great degree of control over the rearing environment. Flow-through systems require large quantities of water that are discharged after passing through the rearing units, whereas in a recirculating system more than 90% of the water may be recycled. In both flow-through and recirculating systems the water is pre-treated before it enters the rearing units; this includes settlement and filtration to remove particles of various sizes, treatment with ozone or UV light to kill disease organisms, heating or cooling and aeration or degassing. Effluent water from flow-through systems is usually treated prior to discharge. This often involves removal of solids such as waste feed and faeces, removal of excess dissolved nutrients and metabolic wastes and treatments to destroy potential pathogens (Figure 1.3). Treatment of effluent is mandatory in some countries where environmental regulations restrict the amounts of wastes allowed for discharge from a fish farm into the recipient water bodies (Tucker & Hargreaves 2008; Le Francois *et al.* 2010).

A raceway is a shallow longitudinal tank extended along the directional axis of the water flow. There is usually a continuous flow of water from one end to the other, adjusted to be sufficient to transport wastes and produce a self-cleaning effect. In a typical raceway, water quality degrades between input and outflow. In cross-flow raceways water is introduced along one side or both sides of the raceway and may be removed either from the

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opposite side or via a central drainage channel. In series and parallel raceway systems there is usually some re-use of water. The water flows into the raceways by gravity from a header pond and, after passing through the raceways, is discharged into a series of ponds. Here solid and dissolved wastes are removed and, in cases where the treated water is pumped back to the header pond for recirculation through the raceway system, aeration is carried out. The production of fish in raceway systems may be limited by dissolved oxygen and the accumulation of metabolic waste products.

Recirculating systems contain water treatment units that allow a large portion, often about 90%, of the water leaving the rearing units to be reconditioned and reused (Figure 1.3). Dissolved oxygen is the first limiting factor for production within such systems, so oxygen supplementation is required as part of the water treatment process. However, there is also the risk that metabolites and other wastes might accumulate to levels that would compromise fish growth and health. Recirculating systems often incorporate water treatment processes to control dissolved gases, feed waste, faeces and other solids, water pH, dissolved nitrogenous compounds and pathogens (Tucker & Hargreaves 2008; Le Francois *et al*. 2010).

#### *Cages and pens*

The terms 'cage' and 'pen' are often used synonymously, but a pen is sometimes defined as a system in which the base is formed by the bottom of the pond or the seabed. Pens of this type are used for the rearing of fish in several South-east Asian countries. Cages are enclosed by mesh screens on both the sides and the bottom and are usually open at the top to enable access for feeding, removal of dead fish and debris and for harvesting. Cages are open systems in contact with the surrounding water body, with water currents ensuring renewal of water and removal of metabolic wastes and faeces. Cages are relatively easy to construct and the cage culture of fish may represent a low-input farming practice with a high economic return. However, cages are vulnerable to natural hazards such as strong tides and storms and cage sites may also be vulnerable to deterioration in water quality resulting from oil spills and chemical pollution, for example (Beveridge 2004; Tucker & Hargreaves 2008).

Cage aquaculture may be extensive, semi-intensive or intensive depending upon the level of feed input. Extensive cage culture, in which the fish are reliant upon natural foods carried into the cage on currents, is generally restricted to highly productive tropical lakes, reservoirs and sewage-fed streams and rivers. This type of cage culture is used in the Philippines, China and Indonesia for farming some species of cyprinids and tilapias. Semi-intensive cage culture, in which fish are provided with low-protein feeds made from locally-available plants or agricultural by-products to supplement the intake of natural food organisms, is also largely restricted to tropical fresh waters, where it is a common method of rearing fish. Herbivorous, detritivorous, omnivorous and planktivorous tilapias and cyprinids are widely grown in this way. Intensive cage culture is the commonest method for farming high-value carnivorous species such as salmonids and a range of marine species such as the sea basses (*Dicentrarchus labrax* and *Lates calcarifer)* and sea breams and porgies (Sparidae). In intensive cage culture the fish are provided with high-protein, nutritionally complete feeds and stocking densities are generally much higher than in extensive and semi-intensive culture (Beveridge 2004; Tucker & Hargreaves 2008).

## 1.3 INTRODUCING THE SPOTLIGHT SPECIES

Throughout this book a small number of important culture species, or species groups, will be brought into the spotlight, with a focus on their biological characteristics and behaviour. These species have been selected as examples from the groups of fish that are reared for different purposes, including those reared directly as food for human consumption, for supplementation or conservation purposes, as ornamentals and for use in research. The selected species are introduced here, with brief presentations of their general biology and commercial importance.

### 1.3.1 Fish farmed for the table

Concentrating on finfish species that are produced for food in relatively high volume, the selected representatives are a cold-water and anadromous species (Atlantic salmon), a cool-water and freshwater or anadromous species (rainbow trout), a temperate and marine species (European sea bass) and a warm-water species found in fresh water (Nile tilapia).

#### *Atlantic salmon (Salmo salar)*

The Atlantic salmon is one of five representatives of the genus *Salmo* (family Salmonidae). It has its natural geographic distribution on both sides of the Atlantic Ocean in the northern hemisphere. The Atlantic salmon is usually anadromous, although there are some non-anadromous freshwater populations. Both within and among populations there are differences in the length of time spent in fresh water prior to migration to sea (following the parr–smolt transformation), in the time spent at sea, age-at-maturity and post-spawning survival (Klemetsen *et al*. 2003; Solar

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2009). Atlantic salmon usually mature after one to three winters at sea, but some of the male salmon mature (as parr) without having undertaken a migration to the sea. This means that the salmon show a wide range of ages and sizes at maturity and individuals with markedly different ages at maturity may occur within the same population. Salmon spawn in fresh water during the autumn and early winter, with the sea-run maturing adults, which generally weigh 1–6 kg, entering fresh water in summer, a few months before they will spawn (Pennell & Barton 1996; Klemetsen *et al*. 2003). The eggs, which are relatively large, are laid in a series of nests (called a redd) excavated in coarse sand or gravel on the bed of a relatively swift-flowing river. The eggs incubate over winter and hatch in spring. The fish are 15–25 mm in length at hatching and have a large yolk sac that acts as a source of nourishment when they are still in the gravel redd. When most of the yolk has been used the young fish, called alevins, emerge from the gravel (swim-up phase) and start to feed on small planktonic organisms, and then they expand their diet to include insect larvae and other organisms that make up the aquatic drift (Gibson 1993).

Life in fresh water, during which the fish are called parr, can last from 1 to 8 years, after which the majority of the fish undergo the parr–smolt transformation in preparation for migration to the sea. Some male parr do not undergo the parr–smolt transformation, but mature instead, so there are more females than males amongst the fish that migrate to sea as smolt. The smolts usually migrate downstream and enter seawater during May or June. During the marine phase of their life, Atlantic salmon feed predominantly on crustaceans and small, pelagic fish. Some Atlantic salmon return to their native rivers after spending one winter at sea; these fish are known as grilse and are usually 1.5–4 kg in body weight. In some populations the majority of fish return as grilse, but most salmon return to fresh water as maturing individuals after two or three winters at sea and some may remain in the sea for up to 5 years (Pennell & Barton 1996; Klemetsen *et al*. 2003). The Atlantic salmon is a fish of considerable economic importance and introductions to Australia (Tasmania) and Chile have given rise to salmon aquaculture in these two countries. At present, salmon are farmed in northern Europe, Tasmania, Chile and North America, particularly Canada, with annual aquaculture production exceeding 1 million tonnes. Rearing methods are generally intensive and similar wherever salmon farming is practised; thus egg incubation usually takes place in trays with flowing water, start-feeding of alevins, rearing of parr, and smolt production in tanks supplied with abundant fresh water, followed by on-growing to market size (3–7 kg) in sea-cages (Pennell & Barton 1996; Stead & Laird 2002; Solar 2009; Le Fancois *et al*. 2010).

### *Rainbow trout (Oncorhynchus mykiss)*

The Pacific salmons and trouts (genus *Oncorhynchus*, family Salmonidae) are anadromous, occasionally freshwater, fish that are naturally distributed in the North Pacific region. The natural distribution of the rainbow trout extends from Baja California through Alaska and the Aleutian Islands in the Americas, to the Kamchatka Peninsula and rivers that drain into the Okhotska Sea on the Asian side of the Pacific Ocean (Pennell & Barton 1996). Although the rainbow trout has its natural distribution in countries that border the North Pacific it has been introduced to so many other regions of the world that it is now virtually cosmopolitan (Lever 1996; Pennell & Barton 1996; Solar 2009). The successful introduction of this species to many areas outside its native range results from the fact that the rainbow trout is relatively hardy, is highly esteemed as a sport fish, is considered a good food fish and adapts well to culture. There is widespread cultivation of rainbow trout, either directly for human consumption or for stocking purposes, and it is a valuable commodity in many countries with a temperate climate.

Rainbow trout are usually considered to be freshwater fish, but many populations have some fish that are anadromous, called steelhead because they develop a silvery body colour. Steelhead trout spend 1–2 years in fresh water and then migrate to the sea where they spend 1.5–3 years before migrating back to fresh water to spawn. They do this during the spring when water temperature rises to 6–7 °C, with the eggs being deposited in gravel redds in a stream-bed. Depending upon her size, age and whether or not she is anadromous, a female rainbow trout produces 300–3000, relatively large eggs that hatch after about 40 days at 8 °C to give young that are about 15 mm in length. The young fish remain in the redd until their yolk is almost exhausted and then emerge and start to feed on small zooplanktonic organisms. As they grow the young fish broaden their diet and eat small aquatic insects, and then graduate to terrestrial insects and small fish. The fish generally mature at an age of 3 years, lifespan is 4–10 years and size may vary from 200 g to 3–5 kg, depending upon whether the fish are of the freshwater form and live in a small stream, or are of the anadromous, sea-going steelhead form. Most rainbow trout farming is carried out in fresh water in ponds, tanks and raceways, with the production of fish weighing 300–350 g and 600–750 g tending to dominate, but there is some sea-cage culture to produce larger fish weighing 2.5–3.5 kg.

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The annual global production of rainbow trout is about 500 000 tonnes, with the major trout-producing countries being France, Italy, Spain, UK, Norway, Denmark, Chile, USA and Japan (Pennell & Barton 1996; Stickney 2000; Tucker & Hargreaves 2008; Le Francois *et al*. 2010).

***European seabass (Dicentrarchus labrax)***

The European seabass, one of six members of the family Moronidae, is primarily a marine fish, but it is sometimes found in brackish- and fresh water; its habitats include coastal waters, estuaries, lagoons and rivers. It is found in the waters in and around Europe, including the eastern Atlantic Ocean, from Norway in the north to Senegal in the south, in the Mediterranean Sea and in the Black Sea (Pickett & Pawson 1994). The European seabass is highly regarded as a food fish, particularly in Mediterranean countries, and the fish fetches high prices in international markets. The fish can tolerate a wide range of temperatures and salinities, but although it is often found in water of low salinity, spawning takes place in water of salinity close to that of full strength seawater.

Spawning takes place between December and March in the Mediterranean basin, but somewhat later (March–June) towards the northern limits of the species distribution, with spawning and egg development usually taking place at 9–15 °C. During the spawning season a large female will produce several hundred thousand small eggs that hatch after a few days to give 4–4.5 mm larvae. A few weeks after hatching young juveniles start to congregate close to shore and migrate into warm estuaries, bays, back-waters and harbours. Here they form shoals and feed on small crustaceans. As they increase in size they also include larger crustaceans, polychaetes, cephalopods and small fish in their diet. The male European sea bass may mature at 2–3 years of age, females usually one year later and most will be mature by the time they reach an age of 4–5 years (Pickett & Pawson 1994). The fish can reach an age of 30 years, and large individuals can weigh up to 10 kg.

The fish has considerable importance in Mediterranean aquaculture, with Greece, Turkey, Italy, France, Spain, Croatia and Egypt all having many European seabass hatcheries and on-growing farms. On-growing is generally carried out in sea cages, but some fish are held in lagoons and land-based culture systems are sometimes used for the intensive rearing of the species. Under farming conditions the fish are most often fed dry pellet feeds that are relatively rich in both proteins and lipids. Farmed European seabass are usually marketed at a size of 250–450 g, and the time required to reach this size is 20–24 months in the cooler regions of the western Mediterranean, but is reduced to 14–15 months in the warmer waters along the African coastline (Moretti *et al*. 1999; Theodorou 2002; Le Francois *et al*. 2010). Farmed populations often have a high percentage of males, the result of a pronounced environmental influence on sex differentiation (Chapters 2 and 10). Male-biased populations are undesirable because the males grow slower and mature earlier than do females. Under farm conditions most males mature at an age of 2 years, when they are about 300 g in weight, but some males mature during their first year of life, when they weigh no more than 50–70 g (Moretti *et al*. 1999; Theodorou 2002; Le Francois *et al*. 2010).

***Nile tilapia (Oreochromis niloticus)***

The Nile tilapia (family Cichlidae) is distributed throughout tropical and subtropical Africa, in the Nile River basin and in the Volta, Gambia, Senegal and Niger River watersheds of West Africa. It is also native to a number of large lakes and their feeder rivers and streams (Beveridge & McAndrew 2000; Lim & Webster 2006). Several natural populations are under threat as a result of habitat destruction, overfishing or the introduction of exotic and non-native species, such as the predatory Nile perch (*Lates niloticus*). The Nile tilapia has been introduced to many areas outside its natural range, both on the African continent and further afield; for example, it was introduced to the USA via Brazil and there have been introductions to at least 60 countries. Farming of Nile tilapia is carried out in over 50 countries, with the major producers being China, Egypt, Philippines, Indonesia, Thailand and Brazil. In some areas where it has invaded natural waters it is considered a pest (Lever 1996; Beveridge & McAndrew 2000; Lim & Webster 2006; Le Francois *et al*. 2010).

The Nile tilapia is a mouth-brooder, with the female incubating the eggs within her buccal cavity. The optimum spawning temperature is 25–30 °C. There is sexual dimorphism, with the male being larger than the female, and age and size at sexual maturation varies according to growth conditions. For example, in the large lakes of Eastern Africa the fish may mature at an age of about 1 year, and 350–450 g, but when held in farm ponds fish of the same populations may mature after 5–6 months at a size of about 200 g. Depending upon her size, a female will produce 50–2000 medium-sized eggs at each spawning, the eggs hatch after 2–3 days and remain within the buccal cavity of the female for an additional 6–8 days until the young fish have exhausted their yolk supply. This period of mouth-brooding, which lasts approximately 10 days, is followed by a short nursing period, during which the female continues to protect her offspring even though they are swimming

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freely and feeding. The complete reproductive cycle lasts 4–6 weeks and a female may spawn 6–11 times per year under suitable environmental conditions (Beveridge & McAndrew 2000; Lim & Webster 2006).

The Nile tilapia feeds on a wide variety of foods, including detritus and aquatic plants, plankton, small aquatic invertebrates and fish larvae. When farmed, the fish may be reliant on natural prey organisms in the farm pond or they may be provided with formulated pellet feeds. Nile tilapia are tolerant of changes in many environmental factors, including temperature, dissolved oxygen, ammonia and salinity, so they are extremely hardy and are easier to rear than other commonly-cultured fish species. Farming of Nile tilapia is carried out using a variety of methods, ranging from extensive pond culture to intensive farming in land-based, re-circulation systems. There has been some selective breeding to develop stocks that perform well under certain culture conditions; the GIFT (Genetically Improved Farmed Tilapia) programme is probably the most ambitious, and best-known example of the genetic improvement efforts (Beveridge & McAndrew 2000; Lim & Webster 2006; Le Francois *et al*. 2010).

### 1.3.2 Fish farmed for supplementation programmes or conservation

Several freshwater, anadromous and marine fish species are produced for supplementation purposes on a variety of scales. Some operations may be of limited proportions. For example, an individual farmer or small co-operative may produce fish for the stocking of ponds or lakes that are to be used as a source of income from fee-fishing and put-and-take fisheries and angling societies may operate hatcheries for the production of fish for stocking into lakes, canals and river reaches. These operations often involve the production of salmonids, such as rainbow trout, brown trout (*Salmo trutta*) or brook charr (*Salvelinus fontinalis*), sunfishes (*Lepomis* spp.) and basses (*Micropterus* spp.) of the family Centrarchidae, or a variety of so-called coarse fishes, such as the common carp (*Cyprinus carpio*), tench (*Tinca tinca*) and pike (*Esox lucius*). Larger-scale production may be carried out under the auspices of district or regional authorities for supplementing fish populations in regulated water-courses, or in support of local fisheries and sea-ranching operations. An example of this type of activity is the production of Pacific salmon species on the western seaboard of the USA for stocking dammed rivers and in Japan for sea-ranching. The Pacific salmons are considered in some detail throughout this book. Captive rearing may also be carried out to replenish populations that do not reproduce well in the wild, or to re-stock waters in which fish populations have been eliminated or drastically reduced in size due to severe, but transient, habitat deterioration. Finally, some species have been taken into captivity as a conservation measure in an attempt to prevent extinction of threatened local stocks, or in some cases species. The captive rearing of sturgeons is, in part, designed to fulfil this role, as is the cultivation of several species of seahorses. The seahorses are another group that will be a focus of attention throughout this book.

#### *Pacific salmons (Oncorhynchus spp.)*

Salmon with natural distributions in waters that drain into the Pacific Ocean are members of the genus *Oncorhynchus*, which also includes a number of trout species (Ruggerone *et al*. 2010). The ranges of the different species extend from the Bering Sea, southward down Asian coastal areas to Japan and Korea in the west and along the Alaskan, Canadian and US coasts to the state of California on the eastern side of the Pacific basin. Pacific salmon are an important economic resource for countries that border the North Pacific Ocean. Salmon of several species are fished in coastal waters by Canada, USA, North and South Korea, Japan and Russia and there is also a more limited high-seas fishery (Groot & Margolis 1991; Pennell & Barton 1996; Stouder *et al*. 1997; Quinn 2005). Seven species of Pacific salmon are recognized; sockeye (*O. nerka*), pink (*O. gorbuscha*), chum (*O. keta*), chinook (*O. tshawytscha*), coho (*O. kisutch*), masu (*O. masou*) and amago or biwamasu (*O. rhodurus*). Natural reproduction of the first five species has been recorded on both the Asian and North American side of the Pacific Ocean, but spawning populations of the masu and amago salmon only occur in Asia.

Pacific salmon spawn in gravel beds in rivers, streams, or along lake-shores and they generally migrate to sea after a short freshwater life. Amongst the species of Pacific salmons there is considerable variation in the time spent in fresh water prior to parr–smolt transformation, and also in the length of residency in the marine environment before they mature and return to fresh water to spawn. For example, pink and chum salmon normally migrate downstream to the sea within 2–3 months after hatching, whereas young sockeye salmon may spend up to 5 years in fresh water before migrating to the sea. Pacific salmon are widely distributed in the North Pacific Ocean and Bering Sea during their marine residency and most perform extensive migrations while at sea. Upon maturation, after 1 to 7 years at sea depending upon species, the fish usually return to their natal rivers to spawn. Spawning occurs during autumn and early winter, after which the fish usually die; in other words, they are semelparous. Amago and masu may be

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exceptions because some fish spawn more than once. Pacific salmon are distinctive because of their semelparity and also because they produce relatively few, large eggs compared with other fish species (Groot & Margolis 1991; Pennell & Barton 1996; Quinn 2005). The number and size of eggs produced varies among species, among populations within a given species and also among females within a population, depending on their size and age, but rarely exceeds a few thousand. The young fish are generally about 20 mm in length at the time of hatching and they survive on the yolk sac for some time before starting to feed. The food eaten reflects the types and abundances of prey organisms present in particular habitats. Insects and insect larvae are the main prey of juvenile salmon in streams and rivers, zooplankton, insect larvae and small fish are eaten by lake-dwelling Pacific salmon, and large zooplanktonic organisms, fish and squid are consumed by the larger salmon when they are in the ocean (Groot & Margolis 1991; Pennell & Barton 1996; Quinn 2005).

Populations of several Pacific salmon species are under threat of extinction because of habitat loss, due to water diversion, damming and urban development, or habitat deterioration as a result of logging and the discharge of industrial and agricultural effluents. Restoration programmes have been initiated in several areas in an attempt to counteract these declines and to conserve these at-risk populations and often include a combination of watershed management and release of artificially-propagated fish (Groot & Margolis 1991; Pennell & Barton 1996; Stouder *et al*. 1997; Quinn 2005; Araki *et al*. 2008; Nielsen & Pavey 2010). As such, the vast majority of the cultivation of Pacific salmon is for supplementation of existing populations, but there is also farming of some of the species for stocking water-courses that lack natural populations, for sea-ranching, and for sea cage culture of fish for human consumption. For example, there is some sea cage culture of chinook salmon in Canada and both Chinook and coho salmon have been introduced into Chile, where they are farmed as food-fish.

***Seahorses (Hippocampus spp.)***

The seahorses, which along with the pipefishes make up the family Syngnathidae, are represented by almost 35 species of relatively small (3–25 cm in length, depending upon species) marine fishes within the genus *Hippocampus.* The name seahorse arises because of the equine appearance of the head. Seahorses are found in shallow tropical and temperate waters throughout the world, where they prefer to live in sheltered areas such as seagrass meadows, in amongst the submerged roots of mangroves and in the protected areas of coral reefs (Koldeway & Martin-Smith 2010; http://seahorse.fisheries.ubc.ca). Seahorses swim in an upright position using undulations of the dorsal fin. The small pectoral fins located close to the head are used for steering and in making fine positional adjustments. Seahorses are incapable of swimming rapidly and the fish often attach themselves to strands of seagrass, algae or mangrove roots by means of their flexible, prehensile tail. When attached to underwater vegetation they are well-camouflaged as a result of their grey–brown to greenish body patterns. Seahorses have elongated snouts, but very small mouths and adopt suction feeding to capture zooplankton, such as small crustaceans and fish larvae. The eyes of the seahorses can move independently, which may aid in both locating prey and the detection of predators. The males tend to remain on small home ranges, whereas the females range more widely. Prior to spawning a pair may engage in courtship for several days and then the female deposits a clutch of eggs in the brood pouch of the male. The male fertilizes the eggs as they are being transferred to his brood pouch and the fertilized eggs eventually become embedded in the pouch wall where they are held during incubation. The gestation period is generally about 2–4 weeks and the number of offspring produced by most species is 100–200 (Koldeway & Martin-Smith 2010). The small seahorses are expelled from the brood pouch by a series of quite powerful muscular contractions and after release of the offspring from the pouch the period of parental care is at an end. Some species of seahorses are bred in captivity to supply the aquarium trade and others are reared as a conservation measure. When held in captivity, the fish may be fed on live zooplankton, such as brine shrimp (*Artemia salina*), or frozen crustaceans, such as copepods (Copepoda) and mysids (Mysidacea; Koldeway & Martin-Smith, 2010; http://seahorse.fisheries.ubc.ca).

### 1.3.3 Fish farmed as ornamentals and for research

Many small, brightly coloured warm-water teleosts have become popular with aquarists. Most of these aquarium species are small carp-like fishes (Cypriniformes), characins (Characiformes), tooth-carps (Cyprinodontiformes) and cichlids (Cichlidae) that are displayed in tropical, freshwater aquaria in homes and work-places around the world. A few of these species, including the goldfish (*Carassius auratus*), zebrafish (*Danio rerio*) and guppy (*Poecilia reticulata*), have also been widely adopted for use in biological and medical research. These species are used for the investigation of problems relating to neurophysiology, sensory physiology, the regulation of

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feeding, reproductive and developmental biology, genetics and behavioural ecology. The zebrafish and guppy are two of the species spotlighted for attention in this book. The koi carp is larger than most other freshwater ornamentals and is the third freshwater fish considered here. Finally there are a few tropical marine species that are cultured for the aquarium trade; amongst these the clownfishes are the selected representatives for more detailed analysis.

***Koi carp (Cyprinus carpio)***

Koi carp is the name given to some aberrant, genetically selected forms of the common carp (*Cyprinus carpio;* family Cyprinidae). Koi is the Japanese for carp and it might be more correct to call these fish by their Japanese name *nishikigoi*. Being derived from the common carp, koi carp are larger than most other ornamental species and are usually kept in outdoor ponds in parks and gardens. The koi was originally developed from the common carp in China and was later imported into Japan, where it became popular as an ornamental species. To-day koi have a world-wide reputation and can command very high prices from devotees. Most koi are still produced in Japan, but there is increasing interest in many countries in selective breeding of these fish. A variety of colour patterns have been developed and these are classified according to a Japanese system devised for show purposes, the names often reflecting the history of the particular variety concerned or its place of origin. The different varieties combine a single body colour with superimposed patches of white, black, red, yellow, blue and orange, together with variations in scale patterns. Newer developments include the introduction of varieties with particular fin shapes and body morphology, as in veiltail and hifin koi. In order to be seen to advantage, the fish must be attracted close to the water surface, so they are usually fed on floating flake and pellet feeds, sometimes supplemented with pieces of fruit and vegetables. Koi carp are hardy, being relatively tolerant of low dissolved oxygen and a wide range of temperatures, although they thrive best at 20–25 °C. At spawning the females produce several thousand small eggs that develop a sticky outer coat and become attached to underwater plants. The eggs hatch after a few days into larvae that are about 5 mm in length and that start to feed on small planktonic organisms when they are 6–7 mm. The koi may not breed 'true', so many of the young fish and juveniles will usually be culled, because they do not develop the colour pattern considered desirable by the producer and potential purchasers. The koi carp is often long-lived and there are reports of fish that have achieved ages of 100–200 years (Purdom 1993; Billard 1999).

***Zebrafish (Danio rerio)***

The zebrafish or zebra danio is a small (4–5 cm), distinctive and brightly-coloured, rasbora (family Cyprinidae). It is native to the fresh waters of India and Bangladesh, where it is found in vegetation-rich, still or slow-flowing waters, such as streams, canals, ditches, ponds and rice fields. It is a popular aquarium fish and spawns readily in captivity, scattering the eggs amongst underwater vegetation. Although the fish can tolerate a wide range of temperatures, the water must be over 24 °C, and ideally 28–29 °C, for spawning to take place. Females can lay clutches of a few hundred eggs at 2–3 day intervals, the eggs hatching after 2–3 days. Zebrafish larvae are quite adept at swimming by day 4 after egg fertilization (dpf), and they readily capture prey by 5–6 dpf. In the wild, zebrafish feed on zooplankton and small insects, but in captivity they are usually given flake food or *Tubifex* worms. The fish generally have a life-span of 2–3 years. A prominent social behaviour of zebrafish is shoal formation (Chapter 8) and shoaling preferences are determined at a young age. The ease with which the zebrafish can be raised in captivity, coupled to its short generation time of 3–4 months, has led to it being adopted as a model system in a number of biological disciplines (Westerfield 2000; Detrich *et al*. 2004). The zebrafish was first used in studies of genetics and then became popular for the study of developmental biology, because the embryos and larvae are transparent until about 6 dpf, so organogenesis and tissue differentiation are easily observed. A large number of zebrafish mutants, with a wide range of phenotypes, have been isolated and described, with several of these being used for research purposes. Recently, much information about the species has been made accessible (www.zfin.org) and the zebrafish is now widely used in biomedical research, including neurophysiology, in ecotoxicology and in studies of behavioural ecology (Lieschke & Currie 2007; Spence *et al.* 2008).

***Guppy (Poecilia reticulata)***

The guppy, a live-bearing toothcarp, is one of about 300 species within the family Poecilidae, most of which occur in tropical and subtropical regions of the Americas. The guppy is native to Trinidad, Barbados and many other Central American islands and is also found in Venezuela, Guyana and northern Brazil. It has been introduced to many tropical and subtropical regions as a controller of the larval stages of malaria-carrying mosquitos (Lever 1996). In its native habitat it lives in fresh and brackish water and can be found in streams, ditches, small canals and drainage channels and pools. The guppy will eat a wide range of foods, including freshwater algae, insect larvae, small

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crustaceans and fish eggs and larvae, and it is sometimes cannibalistic. Wild male guppies, which grow to about 3 cm in length, have a dull olive-green or brown background colour with some coloured spots and the body sides shimmer with metallic greens and blues. The colour patterns of the males are highly varied, not only between populations across the species' geographic distribution range, but also within populations. This variability attracted the attention of geneticists, and made the guppy an early model species for the study of inheritance mechanisms. The guppy is still widely used in genetics research and also has a central place in studies of evolutionary ecology and fish behaviour (Purdom 1993; Magurran 2005).

The attractive appearance of the male fish, along with the ease with which the species can be reared in captivity, resulted in the guppy becoming a very popular aquarium fish following its introduction to Europe by the Reverend R.J.L. Guppy in 1866. In the intervening years aquarists have produced a wide variety of forms that differ in colour patterns and tail fin morphology and the guppy is now probably the most popular tropical aquarium fish in the world (Purdom 1993; Lever 1996). In contrast to the males, the females are rather dull in colour, being grey dorsally and lighter ventrally. Females grow to about twice the length of the males, reach sexual maturity at an age of 3–4 months and may survive for 5–6 years in well-tended aquaria. The guppy is a live-bearer and the male has the third, fourth and fifth rays of his anal fin elongated to form a copulatory organ, the gonopodium, that is used to transfer a spermatophore, a gelatinous ovoid structure that contains large numbers of sperm, to the cloaca of the female. The release of sperm from the spermatophore is slow and a female can produce several litters of offspring, often 6–8, following a single mating. The eggs are fertilized and are incubated within the ovarian cavity. After the female guppy has been inseminated a dark area near the anus increases in size and darkens to form the gravid spot. The gestation period is generally 21–35 days, litters being produced at 4–5 week intervals at 20–25 °C, but guppies prefer water temperatures of about 27 °C for reproduction. Just before birth, the eyes of the young fish may be seen through the translucent skin of the abdomen of the female. At birth the protective envelope that surrounds the embryo bursts and the young fish is released. Litters range in size from 10–100, but usually around 30 offspring are produced in a litter. The young are capable of swimming from the moment of birth and they start to feed almost immediately. They are able to feed on small waterfleas (*Daphnia* spp.), *Artemia* nauplii and finely ground flake foods.

***Clownfishes (Amphiprion spp.)***

The clownfishes, or anemonefishes, are a group of about 27 species of relatively small (10–18 cm in length, depending upon species) damselfishes (family Pomacentridae) of the genus *Amphiprion.* They occur on coral reefs in coastal areas of the Indo-West Pacific region. They are called clownfishes because they have a rather garish, brightly-coloured mottled appearance that resembles the dress of a circus clown, or harlequin. The fish associate with and usually live amongst the tentacles of a large sea anemone (Anthozoa, Cnidaria), which they defend, remaining with a single host throughout life and rarely moving more than a few metres away from the host (Spotte 1992; Tucker 1998). The relationship between the clownfish and the anemone (from which the fish get their alternative name) is considered a symbiotic and mutualistic one, because the fish receives protection by hiding within the stinging tentacles of the anemone and may also obtain some food by taking prey captured by the anemone. In return, the clownfish remove debris and parasites from the anemone, attack small fish that may approach the anemone to damage its tentacles and the nitrogenous excretory products of the fish may stimulate the growth of symbiotic algae in the tissues of the anemone. Anemones that have clownfishes associated with them grow faster, reproduce more frequently and suffer less damage than do anemones that lack symbionts.

Clownfishes are sequential, protandrous hermaphrodites (Chapters 2 and 10), starting life as males and later changing sex to become females. They usually live in small groups comprising two large and several small individuals. Only the two largest fish within a group are sexually mature; the largest fish is a mature female, the next largest is a mature male and all the other fish are immature males. Although the small fish may be almost as old as the two largest fish, the behavioural dominance of the mature pair prevents the immature males from growing larger and maturing. When the female dies, the mature male changes sex to become female and one of the immature males, generally the largest of these, increases in size and matures to take over the role as the mature male within the group. Female clownfish lay their eggs on the coral beneath the anemone and when the eggs hatch, some 6–10 days later, the larvae enter the plankton and drift away from the anemone inhabited by their parents. When they have grown large enough to settle out of the plankton, the young fish are attracted to reefs and anemones and by chemical signals secreted by other clownfishes, but are repelled by the scent of close relatives (Dixson *et al*. 2008; Munday *et al*. 2009).

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This means that the young fish will not settle on the same anemone as family members, so the clownfishes associated with a particular anemone are not closely related to each other and inbreeding is avoided. In the wild, clownfishes feed on a mixture of algae, small molluscs and crustaceans, but in captivity are often fed on flake food, small pellets, or live or frozen zooplankton. Clownfish were the first species of ornamental marine fish to be bred in captivity and they are currently raised for the marine aquarium trade by a small number of farmers, particularly in the USA (Spotte 1992; Tucker 1998).

## 1.4 ABOUT BEHAVIOUR

The previous sections have dealt with the first topic in the title of this book, namely aquaculture. The descriptions of the spotlight species include information on topics such as what the fish eat, how they eat it, how much they move about and how they breed. These are aspects of the second topic in the title, namely behaviour, which is discussed in more detail in this section.

### 1.4.1 What behaviour is and why biologists are interested in it

The term 'behaviour' refers to what an animal does or the movements or actions it makes in response to external or internal stimuli. As discussed in Chapter 3, animal behaviour is difficult to study because it is ephemeral, usually leaving no trace once an action has been performed, because it is readily modified by past and present circumstances and because its causes and consequences are complex. Nevertheless, it is important to understand why animals behave as they do, because it is through its behaviour that an animal interacts with and adapts to its environment, providing a link between physiological and ecological events. For example, when a three-spined stickleback (*Gasterosteus aculeatus*) encounters a potential predator such as a pike, it stops feeding, raises its protective spines and starts cautiously inspecting the larger fish. Depending on circumstances, it may then move slowly away from the predator, possibly to join a group of other sticklebacks, or may escape rapidly to shelter. These responses are accompanied by striking physiological changes (Bell *et al.* 2007), but the key responses are behavioural. On a larger spatial and temporal scale, fish movements are often finely tuned to local temperature regimes. For example, European seabass move horizontally and vertically through the seas tracking water of 10 °C; this is the optimal temperature for maturation (Metcalfe *et al.* 2008), so the behavioural response to water temperature helps to determine patterns of reproduction.

Understanding behaviour is also important from an applied perspective. For example, fish are very sensitive to variation in water quality and behavioural changes are among the first visible responses to adverse conditions, so monitoring fish behaviour can provide a valuable bio-indicator and early warning of, for example, water-borne pollutants. Three-spined sticklebacks form larger shoals when exposed experimentally to certain pollutants (Wibe *et al*. 2002); this may be because the pollutants impair the fishes' ability to escape, increasing their predation risk and causing them to seek safety in numbers (Chapter 8). Male three-spined sticklebacks exposed to endocrine-disrupting, oestrogenic chemicals show reduced aggression compared to control fish (Bell 2002). Both these behaviour patterns are conspicuous and relatively easy to monitor, so could provide useful bio-indicators for such pollutants.

### 1.4.2 Some basic behavioural biology

Researchers from a number of disciplines, including psychologists, veterinarians, anthropologists and biologists, are interested in behaviour. The modern approach to the biological study of behaviour has a number of special features highlighted by one of its Nobel Prize-winning founding fathers, Niko Tinbergen, in his book *The Study of Instinct* (1951). Tinbergen stressed the fact that as far as possible animals should be studied in natural conditions and that a complete understanding of what animals do can only be achieved when studies of the causes and development of behaviour are integrated with studies of its evolutionary history and consequences for Darwinian fitness. This section reviews briefly the picture that has emerged from this multi-faceted approach to the study of behaviour, as a background to consideration of specific behavioural systems covered in later chapters.

#### *The causes of behaviour*

One strand of research into the biology of animal behaviour involves investigating the mechanisms that control it, including the stimuli that determine whether or not a particular action is performed and how these stimuli interact with the internal state of the animal concerned.

As described in Chapter 2, fish are able to detect stimuli in a number of different modalities and their role in the control of specific behaviour patterns is considered in some detail in later chapters. In general terms, stimuli may come from the animal's non-social environment, for example water temperature and chemical and visual cues arising from potential food. Stimuli may also come from the social environment, such as the sight, sound or smell of conspecifics. Broadly speaking, such stimuli may either increase

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the chances that an animal will perform a particular action or they may inhibit it. Whether or not a given behaviour is performed at a given time depends on the combined action (positive and negative) of the stimuli impinging on the animal. For example, among the amino acids, cysteine stimulates feeding in many fish, whereas arginine inhibits feeding (Kasumyam & Doving 2003; Chapter 6); whether a food item containing both chemicals is eaten will depend on their relative proportions. Considering stimuli from the social environment, when two male cichlid fish (*Cichlasoma centrarchus)* fight they make sounds by grinding their pharyngeal teeth together. Short sounds with long gaps stimulate listening rivals to attack, but long, rapidly repeated sounds inhibit attack (Chapter 9). At the same time, larger males are less likely to be attacked than smaller ones. Whether a male *C. centrarchus* gets into a fight with a particular rival depends on the balance between such attack-eliciting and attack-inhibiting cues.

The effects of external stimuli provide just one component of the mechanism that controls behaviour, because animals do not always react identically to the same stimulus or set of stimuli. For example, depending on the time that has elapsed since its last meal, a fish may bite vigorously at or ignore identical food items; such altered responses relate to changes in internal state. At a certain level of knowledge, behavioural biologists often find it useful to explain such changes in responsiveness in terms of hypothetical entities at a behavioural level. For example, they might ascribe changes in response to food to differences in motivational state (hunger) and try to deduce the nature of such differences from behavioural evidence. In the case of feeding, many cases of altered responsiveness to food can be explained in physiological terms (Chapter 7) and the motivational concept of hunger may soon become redundant. For more complex behaviours, especially those involving other animals, much less is known about the underlying physiological processes. In the case of aggression, for example, during the course of a fight how one fish responds to the sight and sound of a rival can change dramatically, from attacking to fleeing. The nature and timing of such changes depends on many features of the two combatants, including their past history and current nutritional state, as well as on events occurring as the fight progresses. Although something is known about the neuro-endocrine processes that accompany such changes (Chapter 9), the concept of aggressive motivation is still a useful way of conceptualizing the alterations taking place inside the animals concerned. Understanding the mechanisms that control behaviour is clearly important for fish culture, telling us, for example, what makes a fish eat a particular food item at a particular time and why one fish chooses to attack its companions.

### *How behaviour develops*

An important and challenging area of behavioural research concerns the way in which behaviour develops as the fertilized egg becomes a free-living individual that grows and matures into an adult. This involves, amongst other things, the sequential expression of the genes that an individual inherits from its parents. Under the influence of changing patterns of gene expression, sense organs, nervous system, endocrine glands and muscles develop; in other words, the young animal acquires the machinery for behaviour. Provided it lives in broadly favourable conditions, these systems develop routinely and will be at work in cases when animals show normal, species-specific behaviour without having had the opportunity of observing other animals. For example, juvenile Atlantic salmon reared from hatching on artificial feed and then offered a choice of food types show similar prey preferences in terms of colour and shape to those of their wild counterparts (Chapter 5). Male three-spined sticklebacks raised in isolation with no opportunity to interact with other fish build nests when they come into breeding condition and display species-typical aggressive behaviour when they encounter a rival male (Wootton 1984). Genetic differences between animals can alter developmental processes, resulting in individual differences in the mechanisms that underpin behaviour and in the behaviour itself. For example, interspecific crosses between goldfish, which find the amino acid proline aversive, and common carp, which show a positive preference for this substance, have revealed that the differences are inherited through the male line (Chapter 6), while genetic elements on the Y chromosome of guppies are responsible for marked differences in male aggressiveness (Chapter 9).

The term ‘innate’ is often used to describe behaviour that develops normally in the absence of specific environmental inputs and experiences. This is a useful term that draws attention to the fact that quite complex behaviour can be ‘hardwired’, but leads to problems if it is taken to mean that the behaviour concerned is not subject to any environmental modification. This is clearly not the case, because the way behaviour develops is profoundly influenced by the environment experienced by the developing animal from the point of fertilization onwards. In some cases, the influential factors are very general, as when aggressiveness in adult zebrafish depends on the amount of dissolved oxygen experienced by larval fish (Chapter 9). In other cases, behavioural changes come about through

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the effects of specific experiences, contingent on the results of behaviour performed in the past. In other words, both juvenile and adult fish are capable of learning. This is, defined as long-term changes in the probability of showing a particular response to a particular stimulus over successive associations between stimulus and response, sometimes depending on positive or negative reinforcement. Indeed, most of the kinds of learning of which mammals are capable have been demonstrated in fish (Table 1.1).

Differences experienced during development, from general effects of water quality through to highly specific learning opportunities, combine and interact with inherited differences to determine how juvenile and adult animals behave. For example, male three-spined sticklebacks typically chase and retrieve their fry when these first start to leave the nest. The main function of this behaviour by the male is to keep the fry safe, but the fry try to avoid their father and this has the additional consequence of giving them practice in escaping from a larger fish. Sticklebacks that have been reared by their father show better-developed escape responses when subsequently faced with a piscivorore such as a pike than do those deprived of the experience of being chased by their father. However, this is only true for fish originating from places where such predators are abundant; fish from sites lacking piscivores show poorly developed escape responses regardless of how they were reared. In this case the experience of being chased by their father interacts with inherited differences in propensity to learn from an aversive experience (Tulley & Huntingford 1987). The factors that influence how a young animal develops and how it eventually behaves may act across generations. For example, both the nutritional and hormonal state of gravid fish is known to influence the composition of their eggs and the performance of their young (Chapter 2). The eggs of stressed female coral reef fish (*Pomacentrus amboinensis*) often contain more cortisol and produce smaller offspring than do those of unstressed females (McCormick 1998, 1999). Early exposure to high levels of cortisol potentially has a number of effects on subsequent behavioural capacities in fish; for example, brown trout as ova exposed to cortisol show impaired learning abilities compared to untreated fish (Sloman 2010). As such, there would appear to be plenty of scope for cross-generational effects on the development of fish behaviour.

Understanding how such interacting genetic and environmental effects determine the way behaviour develops is important for fish culture, potentially allowing farmers to predict and control the behaviour of their stock. For example, knowing how genes generate behavioural differences may allow farmers to select stock with desirable behavioural traits, while knowing how early experience affects the way fish behave may allow them to improve the behavioural capacities of fish cultured for release into the wild.

### *How behaviour contributes to fitness*

One reason biologists study behaviour is an interest in the link between behaviour and Darwinian fitness, defined as the relative contribution of an individual to the gene pool of the next generation(s). An important distinction to be made when considering Darwinian fitness is between naturally selected and sexually selected traits. Naturally selected traits are those that contribute to survival and/or to some aspects of reproduction, such as producing gametes in the correct season and ensuring that any resulting young survive. Sexually selected traits are those that contribute to fitness through improved competition over mates, either by increasing an animal's ability to fight off rivals or by making it particularly attractive to potential mates (Chapter 10). While sexually selected traits increase the chances of obtaining mates, they may also reduce survival, as when visually-hunting predators home in on courting fish. Natural selection and sexual selection may therefore be in conflict, although both contribute to overall Darwinian fitness and both must be considered for a full understanding of how selection has moulded the behaviour of fish, in the wild or in culture.

The subdiscipline of behavioural ecology has developed as a result of this strong interest in the link between behaviour and fitness, the aim being to identify the fitness-related consequences of behaving in a particular way. Some such consequences are beneficial; for example, by foraging in areas of high prey density, fish obtain the nutrients they need for survival, growth and, ultimately, reproduction; sticklebacks get plenty to eat if they forage on dense swarms of zooplankton that are easy to see in clear water. At the same time, there are fitness-related costs of particular actions; movement requires energy and some behaviour patterns involve a risk of physical injury or an increased risk of predation. Behavioural ecologists seek to identify and measure these costs. For example, when feeding on prey in a group, foragers must concentrate in order to follow one particular prey and have reduced ability to detect signs of danger; sticklebacks foraging on dense zooplankton swarms are less vigilant than those foraging on single prey. Animals adjust their behaviour flexibly depending on the balance between such costs and

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**Table 1.1.** Examples of some of the different kinds of learning demonstrated by fish.

| | Definition | Fish example | Reference |
|---|---|---|---|
| Habituation | Waning responsiveness after repeated exposure to an initially-effective stimulus that is not followed by positive or negative experience. | Minnows (*Phoxinus phoxinus*) cease to show fright responses to a model of a predatory fish and the less realistic the model, the more rapidly the response wanes. | Magurran & Girling 1986 |
| Imprinting | Development of preferences for a category of animal or location through experience of that animal or location at a specific period during development. | Lake Victoria cichlids (*Mbipia* sp.) tend to mate preferentially with partners with the same colour patterns as the adults that reared them. | Verzijden & Ten Cate, 2007 |
| | | Salmon (*Salmo salar*) prefer the scent of water from the river in which they were reared around the time of smolting. | Stabell 1984 |
| Pavlovian conditioning | Formation of an association between an initially neutral (conditioned) stimulus (CS) when repeatedly paired with a biologically-relevant (unconditioned) stimulus (US), so that the normal, unconditioned response to the US is shown to the CS. | Atlantic cod (*Gadus morhua*) held in culture conditions learn rapidly to associate a flashing light with the delivery of food after as as much as 1 minute's delay and swim towards the feeding area in anticipation of food delivery. This association is remembered for at least 3 months. | Nilsson *et al*. 2008 |
| Operant conditioning | Increase in the probability of performing a particular behaviour when that behaviour results in a positive experience and decrease when it results in a negative experience. | Common carp (*Cyprinus carpio*) learn to press a lever if this is followed by food delivery. | Wright & Eastcott 1982 |
| | | Sticklebacks (*Gasterosteus aculeatus*) learn to avoid a previously-favoured feeding patch if they experience a simulated predatory attack in that location. | Huntingford & Wright 1992 |
| Social learning | Acquisition of new information or learning of new behaviour patterns through observation of or interaction with social companions. | French grunts (*Haemulon flavolineatum*) in unfamiliar locations learn routes between resting sites and feeding grounds by following and copying experienced resident fish. | Helfman & Schultz 1984 |

benefits. For example, when undisturbed sticklebacks are offered a choice of zooplankton swarms of different density, they feed preferentially on the densest swarm. However, when foraging under a perceived risk of predation, they switch to feeding on less dense swarms and isolated individual prey. Thus they select an option that allows them feed, albeit at a reduced rate, while also watching for predators (Milinski & Heller 1978). This is

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almost certainly not the result of any conscious thought on the part of the animal concerned; instead it is the result of mechanisms produced by natural selection acting over evolutionary time.

Sometimes the costs and benefits of behaving in a particular way are not fixed, but depend on environmental circumstances; in the case of social behaviour, this includes how other animals behave. For example, the benefits of fighting come in the form of better access to valuable resources, whereas the costs lie in the fact that fighting is energetically expensive, imposes a risk of injury and makes the combatants vulnerable to predation (Chapter 9). Whether the benefits of fighting outweigh its costs will depend on, among other things, just how aggressive potential opponents are. When faced with many fierce opponents, the risk of getting injured may increase to the point at which this outweighs the advantages of winning a fight, so avoiding fights becomes the best option. The fitness arithmetic may be complex, but the main message is that frequency-dependent and environment-dependent costs and benefits serve to maintain adaptive behavioural variability within populations. Although such considerations seem a long way from the fish farm, an understanding of how fish adjust their behaviour to its costs and benefits can be useful. For example, holding fish in a directional current rather than in still water means that they expend more energy if they fight. Raising the cost of fighting in this way makes them less aggressive, reducing fin damage and promoting efficient growth (see below).

### *The phylogenetic history of behaviour*

Continuing with an evolutionary theme, Tinbergen was interested in the phylogenetic history of behaviour, or how it changes over evolutionary time. This is important because the evolutionary history of an animal group determines the behavioural options open to it. Modern fish belong to an aquatic lineage and have adaptations for an aquatic lifestyle that determine how they behave. For example, water is a good medium for transmitting mechanical vibrations, fish have sensory systems for detecting vibrations (Chapter 2) and mechanosensory cues are important stimuli that influence their behaviour. The phylogenetic history of behaviour may also seem far removed from the fish farm, but understanding how behaviour has changed through evolutionary time and the genetic alterations that have accompanied such changes may in the future help in the design of targeted selective breeding programmes in fish that are cultured for specific purposes.

Behaviour does not appear in the fossil record, but in some instances its consequences may be detected in fossils. For example, feeding on planktonic as opposed to benthic prey leaves different patterns of wear on the teeth of three-spined sticklebacks and in fossil sticklebacks these can be used to reconstruct the feeding habits of fish of known geological age. Fossil fish that fed on benthic or pelagic prey usually also show the morphological traits known to be associated with these two feeding modes in living sticklebacks (Chapter 5). Evidence from the teeth of fish from one historical sequence suggests that a shift from pelagic to benthic feeding may have occurred some 100 years before any morphological changes. If correct, this provides an example of a behavioural shift (a change in feeding habit) initiating a process of rapid evolutionary change (Purnell *et al*. 2007). Such cases are rare, however, and reconstructing the phylogenetic history of behaviour mostly involves comparing equivalent behaviour in living species whose phylogenetic relationships are well known.

The advent of molecular biology has meant that genetic and genomic resources can be used to identify the chromosomal events that have been responsible for evolutionary change. To date, such studies have focused on morphological traits, but there is little doubt that the molecular changes that underlie the evolution of behavioural traits will eventually be identified. In addition, some well-studied morphological cases have clear implications for behaviour. For example, three-spined sticklebacks are named after their sharp spines, which have evolved from the rays in the dorsal and pelvic fins and protect the fish from attack by piscivorous vertebrates (Chapter 8). In a number of populations, the pelvic spines have been lost, probably as an evolved adaptation to a change in predation regime (Reimchen 1980). The genome-wide linkage map for sticklebacks shows that spine loss is linked to a specific chromosomal region containing genetic elements that are involved in the development of the hind limbs in mammals (for example, *Pitx1*) and that are also present in the ancestral, marine form of three-spined stickleback. Visualization of *Pitx1* during development shows that expression of this gene is missing in the prospective pelvic region of sticklebacks with pelvic spine loss, though it is present in other parts of the body. The same gene is associated with spine loss in sticklebacks from several different populations in which this trait has evolved. It seems that tissue-specific changes in gene expression, probably due to changes in regulatory factors near the *Pitx1* locus, were responsible for the parallel microevolution of pelvic spine loss in sticklebacks (reviewed in Kingsley & Peichel 2007). Similar studies are

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also elucidating, for example, the genetic mechanisms involved in the switch from pelagic feeding to benthic feeding and vice versa (Schluter *et al*. 2010).

Such research sheds light on the genetic processes that have been responsible for evolutionary change, but at present studies of the molecular genetics of behavioural evolution are at a very early stage. For this reason, questions about the phylogenetic history of behaviour are not pursued further in the specific behavioural chapters of this book. However, the possibility of using knowledge about how genetic alterations at the molecular level underpin the evolution of behaviour and related traits in targeted selective breeding programmes is considered further in Chapter 11.

### 1.4.3 How complex is fish behaviour?

Recently, there has been much discussion about just how complex fish behaviour is, mainly in the context of whether fish are conscious and sentient and so have the capacity for suffering. This reflects increasing concerns about the welfare of fish. The view that fish do not have the capacity for suffering, clearly articulated by Rose (2002, 2007), is based on the fact that the fish brain is small compared to that of mammals and lacks part of the cerebral cortex (the neo-cortex) that is the seat of many higher mental processes. In addition, according to this view, fish have little capacity for learning and they also have a short memory span. While they have the machinery to detect and respond to harmful stimuli and potentially dangerous events, it is considered that such responses are little more than simple reflexes with no emotional content.

Others have argued against this view (for example, Chandroo *et al*. 2004; Braithwaite & Huntingford 2006; Braithwaite, 2010), partly because of a high degree of homology and functional equivalence between the brains of fish and mammals, despite marked differences in size and in the processes of brain development in these two groups. Two parts of the forebrain (Chapter 2) are involved in generation of emotion and in learning in mammals; these are the amygdala and hippocampus, respectively. Homologues of these structures exist in the forebrain of fish; lesion of the amygdala-equivalent impairs the ability for avoidance conditioning in fish, while lesion of the hippocampus-equivalent impairs spatial learning (Rodriguez *et al*. 2006). As such, the fish brain has structures homologous to those involved in generating emotions and in complex learning processes in mammals and these also seem to serve similar functions. On this basis, it seems risky to conclude that all features of consciousness or sentience are ruled out in fish because of the nature of their central nervous system.

Considering the view that fish behaviour is simple and reflex-based, the evidence points to the contrary. For example, fish have a well developed capacity for learning (Brown *et al*. 2006), including the rapid formation of long-lasting memories of aversive events such as an attack by a predator (Chapter 8), the formation of mental maps (Chapter 4) and the ability to make complex decisions based on past social interactions with recognized individuals (Chapter 9). To give a striking example of how complex fish behaviour can be, when the prey of a Red Sea grouper (*Plectropomus pessuliferus*) escapes into a crevice, the grouper may recruit a moray eel (*Gymnothorax javanicus*) to flush the prey out. The eel is alerted by a set of specific signals and led by the grouper to the hiding place of the prey. When the prey is flushed out, the eel and grouper each catch and eat it on about 50% of these co-operative hunting sorties. It is not yet clear just how this complex interaction has developed, though a combined process of individual learning and cultural transmission through observational learning has been suggested. Such joint hunting requires complex, context-specific foraging decisions, awareness of the capacities and likely future behaviour of the other fish and coordination of behaviour based on effective communication between grouper and eel. Indeed, this example has been used to argue for 'Machiavellian intelligence' in fishes (Bshary 2006).

There is an extensive literature on the problems associated with identifying states of consciousness and on the different levels of consciousness that exist (reviewed by Braithwaite 2010). Access consciousness refers to the ability to generate a mental image or representation of the world, combining information from different sources and used to guide behaviour. The ability of fish to form mental maps and to predict what individual companions will do based on past experience points to the existence of this level of consciousness in fish. Phenomenological consciousness refers to the ability to experience feelings and emotions arising from events in the external world. The position here is still uncertain; however, the fact that the ability of fish to develop conditioned avoidance responses disappears when the amygdala-equivalent is destroyed (Rodriguez *et al*. 2006) suggests that the mechanisms that generate emotions in mammals also function in fish. Finally, monitoring and self-consciousness refers to the capacity for reflecting on one's own actions and for basing decisions on considered scenarios; co-operative hunting by groupers and eels may possibly represent an example of consciousness at this level.

Clearly, there is still much to be learned about the mental and emotional life of fishes and it is likely that the capacity

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for consciousness in fish will be less developed than and different from our own. Nevertheless, in the opinion of the editors of this book, accumulating evidence of complex behavioural abilities and mental states in fish supports the position that fish are sufficiently complex in brain structure and behavioural function for the term "welfare" to be applicable.

## 1.5 FISH WELFARE

### 1.5.1 Definitions of welfare

The subject of fish welfare is complex and controversial, but is one that is becoming increasingly important as a result of rising public concern and of the regulations and legislation that have been introduced in response to this concern. It is clear that many aspects of fish culture, whether this be for food, supplementation and conservation, scientific research or the ornamental trade, can potentially compromise welfare, both in the fish that are cultured and in those with which they may interact (Braithwaite & Salvanes 2010). Fortunately, those who culture fish have ways of detecting when welfare is compromised and a number of strategies are available to them for mitigating any adverse effects. These topics are discussed briefly here.

Much of the controversy surrounding the welfare of cultured fish arises from the fact that there are different ways of defining welfare, placing emphasis on different aspects of the biology of the animals concerned. According to one school of thought, an animal experiences good welfare if it can adapt to its environment and is in good health, with all its biological systems functioning appropriately. According to such *function-based* definitions, animals that are in poor health have poor welfare by definition, and the converse. While most would agree that good health and proper functioning of body systems is necessary for welfare, many would feel that they are not sufficient and that welfare may be compromised in a perfectly healthy animal, for example if a social animal is housed in isolation. Such concerns can be accommodated by definitions that equate good welfare with an animal being free from negative experiences, such as pain, fear and hunger, and having access to positive experiences, such as social companionship. Such *feelings-based* definitions are based on the assumption that the animal concerned is conscious or sentient (see above) and suggest, for example, that it does not necessarily matter if an animal is thin or injured, provided that this does not generate negative feelings and emotions. For example, wild male salmon fighting to gain access to spawning females after having swum hundreds of miles up-river without feeding (Chapters 9 and 10), have markedly depleted energy reserves and may be injured. However, these are fitness costs incurred in the interest of gaining fitness benefits; the fish are highly motivated to migrate, fight and breed and their resulting poor condition should not be regarded as indicative of poor welfare.

This relates to the third way of defining welfare, namely that it requires an animal to be able to lead a natural life, expressing the same kinds of behaviour as it would in the wild and meeting what are sometimes called its 'behavioural needs'. Such a *nature-based* definition assumes that welfare is compromised if a captive animal is not able to show the full repertoire of behaviour that it would show in the wild. Most would agree, for example, that the welfare of a social animal is likely to be compromised if it is deprived of the opportunity to interact with conspecifics. It is less obvious (though not impossible) that animals in some sense need the opportunity to respond to predators, to take part in fights or to experience periods of fasting and will suffer if denied such opportunities.

None of these three approaches to animal welfare is inherently correct or incorrect; instead they emphasize different aspects of a complex topic and all throw light on a complex phenomenon. However, there is tension between the definitions. For example, on a function-based approach, a thin salmon with injuries experiences poor welfare. On a nature-based approach, if it has been fighting for breeding opportunities, it experiences good welfare. On a feelings-based approach, the fish may experience good or bad welfare depending on the sensations and emotions generated by depleted nutrient reserves and injuries. Feelings-based and nature-based definitions probably capture best the aspects of welfare that most concern the general public; functions-based definitions tend to suit veterinarians and scientists best, because these refer to aspects of animal biology that are amenable to quantitative study.

### 1.5.2 Identifying and measuring welfare

Welfare encompasses the comprehensive state of the animal, both bodily and mental, and requires that the animal is in good health, can adapt to its environment, is able to express the same kinds of behaviour that it would in the wild and does not have unduly negative experiences, such as pain and fear (Dawkins 2006; Branson 2008). Accordingly, welfare will vary over a continuum from good to very poor and studies of welfare will be most effective if a wide range of measures of welfare is used (Broom & Johnston 1993). The study of animal welfare therefore requires an interdisciplinary approach, bringing together, for example, physiology, veterinary science and behavioural sciences.

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There are many possible indicators of poor welfare, the value of which depends on how welfare is defined (Table 1.2). These include poor physical health, which can usually be recognized relatively easily, as well as other measures that relate to poor health, such as immune suppression, that are less obvious to the casual observer and may only be revealed by advanced analytical techniques. Several physiological measures have been used in welfare assessment, including gill ventilation and heart rate and levels of hormones in the blood, especially cortisol, a major stress hormone in fish (Ashley 2007; Branson 2008). Although these are all objective, quantitative measures, they are part of the wider set of responses by which a fish responds to changes in its environment (Chapter 2) and can be difficult to interpret in welfare terms. For example, cortisol is an important mediator of salt and water balance in marine fish and is required for anadromous salmonids to complete the parr–smolt transformation. Further, mating contests will often result in plasma cortisol concentrations being elevated, but these are not necessarily a sign that the fish is in a state of poor welfare. When used as a tool for welfare assessment, physiological measures must be interpreted with reference to the environmental context in which they are collected, otherwise they may be misinterpreted. With this caveat, it is possible to use physiological measures, preferably together with other measures, to provide an assessment of welfare (Huntingford *et al*. 2006; Ashley, 2007; Branson 2008).

The behaviour of an animal can be observed directly and non-invasively and behavioural assessment of welfare has the potential advantages that it reflects ambient conditions, both internal and external, from the perspective of the animal (Dawkins 2006). Potential behavioural indicators of poor welfare include natural signals of stress or distress and the performance of abnormal behaviour and persistently repeated actions (stereotypies). For example, African catfish (*Clarias gariepinus*) held in groups in laboratory aquaria may show stereotypic behaviour in the form of continuous circling in a small area of the holding tank for minutes at a time, especially during the night when these fish are normally active (Rueda 2004). As an example of natural signs of stress and distress that can be used as welfare indicators, in salmonid fishes, the colour of the body and of the ring around the eye darken in response to various stressors and also act as social signals; for example, these patterns are typical of fish that have lost fights and serve to inhibit further attack (Chapter 9). Colour patterns can also be used as a sign of trouble by fish culturists, sometimes indirectly reflecting plasma cortisol levels in the fish concerned (Kittilsen *et al*. 2009). These are normal, adaptive responses to challenge, but abnormal behaviour can also indicate poor welfare. For example, Atlantic cod (*Gadus morhua*) that have been raised through the water column too rapidly suffer swim bladder damage, which is evident from erratic, abnormal swimming (Brown *et al*. 2010), and one response of rainbow trout to noxious stimuli applied to their mouth is to perform regular rocking movements that are not normally seen in this species (Sneddon *et al*. 2003).

A potentially fruitful approach to assessment of welfare in intensively cultured fish is to use the anticipatory response in fish that have been trained in a Pavlovian paradigm, for example to associate a flashing light in one part of a holding tank with the imminent presentation of food in another part. Various species, including Atlantic cod and Atlantic salmon for example, learn this association and towards the end of the period between the appearance of the flashing light and the delivery of food they move towards the area where the food will appear; in other words they show anticipation of the reward. When Atlantic salmon post-smolts are stressed, cortisol levels and oxygen consumption rates increase and feeding anticipation is suppressed. It takes longer for the conditioned anticipation response to reappear than it does for the other indicators to return to base line, suggesting that this behaviour is a sensitive indicator of welfare status. Conditioned anticipatory behaviour can be identified by computer analysis of video sequences of groups of fish held at high densities (Chapter 3) and so can potentially provide a practicable, non-invasive indicator of welfare in intensively farmed fish (Folkedal *et al*. 2011).

Studying behavioural choices and preferences is particularly important in the context of welfare research, since this is one of the few ways of gaining objective data about how fish respond to, and possibly feel about, particular experiences. For example, in some studies fish have been given a choice between staying, unfed, in shelter or emerging to feed in an exposed area; how they apportion their time gives information on the relative importance to the fish of security as opposed to food. It can also be used to probe more complex aspects of behaviour and welfare. For example, rainbow trout quickly learn to emerge from shelter when a light flashes to signify that food is about to be given. After application of a noxious stimulus such as bee venom to their snout, the fish tend to stay in the shelter while the light flashes rather than emerge to feed and this persists until the effects of the venom have worn off (Sneddon *et al*. 2003; Braithwaite 2010). Such results indicate that responses to noxious stimuli are not just reflexes, but include changes in behavioural priorities. Use of preference tests to study welfare is based upon the

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**Table 1.2.** A summary of some commonly-used indicators of fish welfare, with comments on what they might potentially tell us about welfare, according to the three different ways in which this is commonly defined.

| Welfare indicator | Function-based definitions | Feelings-based definitions | Nature-based definitions |
|---|---|---|---|
| Physical status | | | |
| Injury & disease status | Indicative of capacity for effective functioning | Currently no clear understanding of how fish experience good or poor health | Injury & disease are natural, so their occurrence at approximately normal levels does not indicate impaired welfare |
| Immune status | Indicative of capacity for effective functioning | Currently no clear understanding of how fish experience altered immune status | Variable immune status is natural, so does not in itself indicate impaired welfare |
| Nutritional status | Indicative of capacity for effective functioning | Currently no clear understanding of how fish experience altered nutritional status | Fish make natural choices that reduce nutritional reserves, so poor nutritional status does not in itself indicate impaired welfare |
| Growth | Indicative of capacity for effective functioning | Currently no clear understanding of how fish experience different rates of growth | Not all wild fish grow to capacity, so poor growth does not in itself indicate impaired welfare |
| Reproduction | Indicative of capacity for effective functioning | Currently no clear understanding of how fish experience achieving or not achieving reproductive status | Fish are naturally selected to maximise lifetime reproductive output, so poor breeding may be unnatural and indicate poor welfare |

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| | | | |
|---|---|---|---|
| Physiological status | | | |
| Metabolic state[1] | Indicative of capacity for effective functioning | Currently no clear understanding of how fish experience altered metabolic state, whether acute of chronic | Variable metabolic state is natural, so is not in itself indicative of poor welfare |
| Stress hormone production[1] | Indicative of capacity for effective functioning | Currently no clear understanding of how fish experience altered levels of cortisol or adrenaline, whether acute or chronic | Production of stress hormones is natural, so acutely elevated cortisol is not in itself indicative of poor welfare. |
| Brain biochemistry | Indicative of capacity for effective functioning | Bioamine systems mediate reward and punishment, so brain biochemistry may reflect what fish experience | Variable brain biochemistry is natural, so in itself is not indicative of poor welfare |
| Gene expression | Potentially indicative of capacity for effective functioning | Differential expression of genes (e.g. relating to brain reward and punishment systems) may reflect what fish feel | Altered patterns of gene expression are natural, so are not in themselves indicative of poor welfare |
| Behavioural status | | | |
| Natural signs of distress | No clear link to capacity for effective functioning | If distress responses are not just reflexes, they indicate poor welfare | Distress responses are natural acts, so not necessarily indicative of poor welfare |
| Stereotypical behaviour | Potentially indicative of failure of normal coping systems | If stereotypies reflect frustrated motivation, they may reflect poor welfare | Wild fish tend not to perform stereotypies, so these are unnatural and indicative of poor welfare |
| Full natural repertoire | No clear link to capacity for effective functioning | If fish are strongly motivated to perform specific actions, an incomplete repertoire may indicate poor welfare | By definition, inability to perform a full natural behavioural repertoire indicates poor welfare |
| Preferences in choice tests | No clear link between preferences and functioning | Whether or not fish choose what is good for they, they do choose what they want | Spontaneous, natural choices by fish can indicate events and circumstances that promote/impair their welfare |

[1]While acute metabolic activation or secretion of stress hormones reflect effective coping and so good welfare, long-lasting activation or chronically elevated stress hormone levels probably indicate failure to cope and hence poor welfare. There is currently inadequate information about the the threshold metaboloic rate or hormone level that tips fish from good to poor welfare.

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assumption that animals will choose conditions that are beneficial to their physical well-being. This may not always be the case, leading to some problems when trying to use and interpret the results of free-choice experiments in welfare measurement and assessment (Dawkins 2006).

### 1.5.3 Talking a common welfare language

Reaching a consensus about what constitutes good welfare is not easy, because the term means different things to different people (Dawkins 2006; Huntingford *et al*. 2006; Ashley 2007; Branson 2008). For example, farmers usually equate welfare with a healthy stock, so would argue that good welfare is a characteristic of fish that are healthy and are growing well and efficiently. On the other hand, some people would claim that criteria for good welfare are met only if the fish is able to carry out its normal behaviour patterns without undue constraint and that it is able to live a natural life (Dawkins 2006). Although there is some overlap between these two standpoints, they are not completely compatible. For example, the fact that a fish has the opportunity to perform natural behaviours need not imply that its welfare is optimal and the performance of some types of natural behaviour may be detrimental to health and growth. These may include interactions with predators that invoke emergency or escape reactions and lead to reductions in feeding and growth (Chapter 8) and damaging behaviours arising from competition and aggression (Chapter 9).

A particularly controversial issue is whether fish are sentient, conscious animals; if they are not, using a feelings-based definition for fish welfare is inappropriate. As discussed above, evidence for sentience in fish is equivocal, although it is clear that the behavioural capacities of fish are complex. In addition, some scientists hold the view that, because feelings are subjective experiences, welfare defined in terms of feelings cannot be monitored or studied objectively (Arlinghaus *et al*. 2007). Carefully designed behavioural tests can help to probe the mental states and experiences of fish (Huntingford *et al*. 2007; Braithwaite 2010), but the results may not be easy to interpret or to apply in culture conditions. The working position taken in this book is that fish have sufficiently complex mental capacities that welfare, including those aspects that relate to feelings, is an appropriate and meaningful concept, while recognizing that our understanding of this issue may well change with further research. Pragmatically, given the fact that much fish culture is at an early stage in development in which welfare and production usually go hand in hand, at this time whether welfare is defined in terms of feelings or function is unlikely to make much difference to behaviourally based recommendations for improvement.

## 1.6 DOMESTICATION, CAPTIVE REARING AND BEHAVIOUR

### 1.6.1 Domestication and captive rearing

There are many striking differences in the conditions experienced by wild fish in their natural habitat and fish reared in culture. Cultured fish are physically constrained in environments that are impoverished in many ways, they usually experience unnaturally high densities, are often provided with an abundant and predictable supply of food and are protected against predation and certain diseases. Such differences can cause the phenotypic traits of fish reared in culture, including their behavioural responses, to deviate from those of wild fish (Einum & Fleming 2001; Huntingford 2004; Jonsson & Jonsson 2006; Araki *et al*. 2008; Belk *et al*. 2008; Nielsen & Pavey 2010). As described in Section 1.4.2 in the specific context of how behaviour develops, two main forces shape the phenotypic traits of fish in culture. On the one hand there are effects arising from the programmed expression of the genes they inherit from their parents and on the other hand there are plastic responses to the environment experienced both during development (including the prenatal environment) and as adult fish. In addition, there are interactions between these two inputs, as when fish with different genotypes are differentially susceptible to environmental factors or when the effects of different genes are only expressed in particular environments. Such processes are important in aquaculture, since many desirable traits are likely to be altered by artificial culture, contributing to the process of domestication and to the tricky issue of the impact of farm escapees on native populations. From a different perspective, aquaculture offers an excellent means of studying genetic and environmental effects on development in fish and evolutionary processes in general, because of the marked changes in selective pressures (intentional and unintentional) that accompany the introduction of fish into culture.

Fish within a species and population vary considerably in morphology, physiology and behaviour and such differences are sometimes inherited. Not all fish flourish in culture systems and differential mortality of fish with different phenotypes may result in different distributions of traits in wild-reared and captive fish of the same stock after a single generation of captive rearing. Over successive generations, the same process can result in long-term inherited differences between wild and cultured stocks arising either through domestication or as a by-product of selective breeding for desirable traits such as fast growth,

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or both. Thus, domestication involves changes in the intensity of selection on different traits. In some cases there is a relaxation of selection that would occur in the wild, such as predation and death by starvation; selection on other traits, for example the ability to compete for resources, may be intensified. As a consequence, domesticated animals will differ from wild, ancestral stock in morphology, physiology and behaviour, perhaps to so great an extent that they will be unable to survive in the wild, in absence of husbandry and protection by humans. Effects of domestication on a given trait can, in principle, be demonstrated by rearing cultured and wild fish from the original founder population in identical conditions and then comparing them with respect to the trait(s) under investigation. Ideally, to rule out maternal effects (Chapter 2), the wild and cultured strains should be reared in captivity for at least one generation before making comparisons. This is rarely possible for long-lived species such as salmonids, but can be achieved relatively easily with short-lived species such a zebrafish. In addition to inherited effects, the strikingly different environments experienced by wild and captive reared fish during development may generate non-inherited differences in behaviour. Such effects of captive rearing can be demonstrated by rearing fish of the same stock either in the wild or in culture conditions and comparing their behaviour, with the proviso that any differences may also be due to differential mortality by behavioural phenotype during the rearing process.

### 1.6.2 Selective breeding

Domestication is probably an unavoidable consequence of artificial propagation, exerted by holding fish in an unnatural environment, by unintentional non-random choice of broodstock and by patterns of survival that differ from those seen in the wild. In addition, where fish can be reared in culture over their whole life cycle, farmers can influence the process of domestication by intentionally selecting for particular traits. The goals of selective breeding of animals farmed for food include altering their characteristics to give more effective and profitable production, a major goal of farm animal breeding for many decades. However, there may be negative side effects associated with this form of selection. For example, selection for fast growth, improved utilization of feed or increased resistance to disease can also have an influence upon other traits, such as reproductive capacity and aggressive behaviour (Dunham 2004; Gjedrem 2005; Bartley *et al*. 2009).

One possible way to improve production of farmed fish without embarking on long-term selective breeding is to perform interspecific hybridization (Le Francois *et al*. 2010). Hybridization has been carried out on all major groups of fish farmed for human consumption and some hybrids are the choice for commercial culture. Examples include a hybrid between Thai (*Clarias macrocephalus*) and African catfish (*Clarias gariepinus*), which combines the better eating qualities of the Thai catfish with the more rapid growth of the African species, and the sunshine bass, a hybrid cross between female white bass (*Morone chrysops*) and male striped bass (*M. saxatilis*), which is more tolerant of extremes of temperature and dissolved oxygen than either of the parental species (Lim & Webster 2006; Le Francois *et al*. 2010). Gene transfer is another possible way of circumventing the need for a long-term selective breeding programme for stock improvement and over 35 fish species have been used in different types of gene transfer studies. Potentially, genetic manipulation could be used to enhance disease resistance, alter the digestive capacity of the fish or modify metabolic pathways that influence flesh composition (Beardmore & Porter, 2003; Devlin *et al.* 2006; Hu & Zhu, 2010). To date, no transgenic fish have been adopted for the commercial production of food, although transgenic zebrafish that express green, red or yellow fluorescent proteins are being sold to aquarists under the tradename GloFish. The situation may well change soon, as permission has been sought in the United States for the use of growth-hormone transgenic salmon.

### 1.6.3 Are cultured fish domesticated animals?

Few of the fish species that are currently farmed have been subjected to long-term, directed genetic selection to alter and improve production traits and most selection programmes are at a very early stage (Dunham 2004; Gjedrem 2005; Shelton & Rothbard 2006; Bartley *et al*. 2009). Only a handful of fish species can be considered as being completely domesticated and the majority of farmed fish species can be classified as what Balon (2004) has called ‘exploited captives’, so there is considerable potential for improving production of farmed fish by selective breeding (Dunham 2004; Gjedrem 2005; Bartley *et al.* 2009). Such efforts are likely to benefit considerably from the application of molecular genetic technologies; for example, molecular markers that relate genotype to particular production traits could be used in pinpointing genetic loci of economic interest and allow genetic characterization of potential broodstock (Dunham, 2004; Gjedrem 2005; Liu 2007; Nielsen & Pavey 2010; Thomson *et al*. 2010).

Many stocks currently used in fish production have been derived from very small founder populations and several

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suffer from genetic bottleneck effects (Beveridge & McAndrew 2000; Dunham 2004; Gjedrem 2005; Bartley *et al*. 2009). Genetic deterioration may be widespread owing to extended periods of poor broodstock management, but identification of genetic lineages and estimation of the level of inbreeding are still in their infancy (Dunham 2004; Gjedrem 2005; Liu 2007; Nielsen & Pavey 2010; Thomson *et al*. 2010). In addition, knowledge about the genetic structure of natural populations of farmed fish species is extremely limited. Although such populations potentially represent genetic reservoirs that could be tapped to improve the performance of cultured fish, they are potentially at risk as a result of a reduction in genetic integrity through excessive stocking with fish raised in hatcheries for supplementation programmes (Araki *et al*. 2008; Nielsen & Pavey 2010) or through interactions with escaped fish that are farmed for food (McGinnity *et al*. 2003; Hindar *et al*. 2006).

### 1.6.4 Behavioural responses to domestication and selective breeding

In general, an animal that is domesticated is likely to possess character traits that facilitate adaptation to the captive environment, including traits related to behaviour, such as attenuated stress responses and increased tolerance of conspecifics (Diamond 2002; Mignon-Grasteau *et al.* 2005; Jensen 2006). When fish are bred to be companion animals, pets or ornamentals, the main selection criteria may include selection for particular colour patterns, which may affect behaviour, and a reduced reactivity to humans. Inherited effects of domestication on behaviour have been demonstrated in a number of fish species. For example, when reared under the same conditions for several generations, ruling out effects of maternal nutrition, zebrafish from domesticated strains grow faster and behave differently from fish of wild origin in several ways (Wright *et al*. 2006).

Some of the concern about the use of transgenic fish for food production relates to the potential environmental impacts should such fish escape or be inadvertently released. Part of the assessment of the risk imposed by transgenic fish involves a comparison of their characteristics with those of both the founder hatchery population and wild-type fish of the same species. Not unexpectedly, transgenic fish with enhanced growth hormone differ from the founder population and wild-type fish in a variety of characters that relate directly to feeding and growth. However, there are other differences; for example, transgenic fish of several species tend to swim higher in the water column than non-transgenic conspecifics, have poorer swimming ability and suffer higher mortality from predatory attacks (Devlin *et al*. 2006; Le Curieux-Belfond *et al*. 2009; Hu & Zhu 2010). Such differences potentially influence the capacity of the fish to survive in the wild and to interact with wild fish to the detriment of local populations. This has led to calls for stringent control of the use of transgenic fish in research, including the establishment of secure methods of containment.

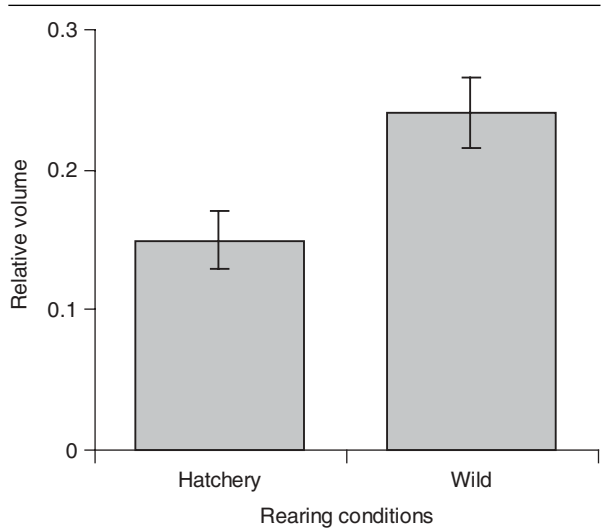


**Figure 1.4.** Relative volume of the telencephalon ($mm^3$/mass g) in Chinook salmon reared in the wild and in conventional hatchery raceways. Values are plotted as mean ± SEM. Adapted from Kihslinger *et al*. 2006.

### 1.6.5 Captive rearing and fish behaviour

The very different environment experienced by wild and cultured fish can have profound effects on a variety of developmental processes and so can potentially produce non-inherited differences in behaviour between wild and captive fish. Captive environments usually lack the complexity of those experienced by fish in the wild and a number of studies have shown that captive rearing alters brain development in fish. For example, the optic tectum and telencephalon of captive-reared rainbow trout (Marchetti & Nevitt 2003), Chinook salmon (Figure 1.4; Kihslinger *et al*. 2006) and guppies (Burns *et al*. 2009) are significantly smaller than those of wild fish. Although the relationship between the size of a particular brain region and its function is complex (Healy & Rowe 2007), given such striking differences it is perhaps not surprising that many behavioural differences have been reported between

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captive-reared and wild fish. These include differences in learning ability and in the expression of a range of behaviours, including exploration of novel surroundings and the propensity to join shoals of conspecifics (Burns *et al*. 2009; Chapman *et al*. 2010). Such differences are explored in more detail in the relevant later chapters.

## 1.7 CRITERIA FOR EFFECTIVE AND SUSTAINABLE FISH CULTURE

Effective, sustainable fish culture requires the economic production of a product that meets consumer expectation, with the minimum of negative impacts on the welfare of the fish and the environment (Tucker & Hargreaves 2008; Le Francois *et al*. 2010). For whatever purpose fish are being cultured there is a set of common requirements for sustainable culture. How fish behave is just one of many factors to be taken into account, but it is an important factor.

### 1.7.1 Production criteria

First, for effective and economically-viable culture the fish must survive, which means keeping them free from injury and disease. The fish should grow well and efficiently. When being produced as food for human consumption, fish must also be of an acceptable quality both nutritionally and aesthetically. Fish reared for other reasons must be of an appropriate size, in good health and fulfil the purpose for which they were reared in other respects. Key points that must be considered are responsible use of land and water resources and the cost-effectiveness of the rearing methods. It is also necessary that the end product is affordable and in regular supply, so the sustainability of the farming operation in terms of use of raw materials and energy is also an important consideration (Wedemeyer 2001; Tucker & Hargreaves 2008; Le Francois *et al*. 2010).

### 1.7.2 Environmental criteria

Concern over the environmental impacts of aquaculture is relatively recent, increasing in step with the industrialization of fish farming, and it has attracted attention from environmentalists and conservationists, as well as regulatory authorities and the general public. Criticism has been directed against fish farming because of perceived environmental impacts that involve destruction of wetland habitats, excessive use of water resources, pollution by farm effluents and the potential impacts of farm escapees on native faunas. Potential environmental effects depend upon the species being farmed, the type of culture system and production intensity and the extent to which the farming operation directly impacts the landscape (Naylor *et al*. 2005; Tucker & Hargreaves 2008; Le Francois *et al*. 2010).

#### *Land resources*

Land resources are under pressure from many different human activities. As far as aquaculture is concerned, sites that are suitable for land-based fish farming are limited by desirable combinations of climate, topography, water availability and access to other resources such as a labour force, power supplies and transport facilities (Stickney 2000; Wedemeyer 2001; Tucker & Hargreaves 2008). Most of the problems associated with land use for fish farming relate to the value of alternative uses, leading to potential conflicts. This is especially the case in coastal regions, where land area is limited, where sensitive and environmentally valuable habitats exist and where land is used for a wide variety of other purposes. For example, the clearing of mangrove forests to provide space for the construction of ponds for fish and shrimp farming has been a contentious land use issue in several tropical and sub-tropical countries in recent years. Mangrove forests protect coastlines from erosion and flooding, provide habitats for a wide variety of species, including acting as nursery grounds for commercially important fish, and act as an important interface between marine and freshwater environments.

#### *Water resources*

Both fresh waters and coastal ecosystems are under pressure from many different human activities. Fresh water is a scarce resource, but it is an obvious and essential resource for the farming of fish and no single factor influences success or failure more than access to adequate supplies of good quality water (Tucker & Hargreaves 2008; Le Francois *et al.* 2010). Fish farms must compete with other users for finite water supplies, especially in arid regions or where most of the fresh water comes from groundwater resources. Some water sources that receive agricultural, industrial or domestic discharges may not be suitable for use in fish farming or must be subjected to prior treatment to remove physical, chemical and biological hazards. Fish production systems produce wastes to an extent depending upon the type of production and the degree to which the units are open to surrounding waters. Well-managed ponds will generally release very little waste to nearby waters and when fish are reared in land-based tanks or raceways, the effluent can be treated to remove solids, some dissolved nutrients and wastes and to destroy pathogens (Wedemeyer 2001; Tucker & Hargreaves 2008). On the other hand, when there is direct contact between the rearing units and surrounding waters, as is the

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case with cage systems, the control of effluent release is extremely difficult. The major sources of fish farm wastes are uneaten food and the excreta produced by the fish; effluent release from open systems can be reduced by a combination of good feeding routines and use of the correct types of feed (Le Francois *et al*. 2010. Chapters 5–7).

***Feed resources***

Fish meals and oils extracted from marine fish have been important feed ingredients throughout the years of expansion of intensive fish culture. These ingredients have been major components in the pellets fed to high-value carnivorous species such as salmonids, sea basses and sea breams and marine flatfishes, because both fish meals and marine fish oils are excellent sources of several essential nutrients (Chapter 6) and they have been available on the international market at reasonable price (Dabrowski & Hardy 2010; Le Francois *et al*. 2010). Fish meals are rich in protein, have a good balance of amino acids, are a good source of certain vitamins and essential minerals and have taste properties that make them attractive feed ingredients for many species of farmed fish. Marine fish oils are esteemed as feed ingredients because they are a good source of essential fatty acids and some fat-soluble vitamins. Both fish meals and marine fish oils have increased in price and are in shorter supply than previously, so are being increasingly replaced by alternative ingredients. In particular, there is increased replacement of fish meals with terrestrial plant proteins and there is also an increase in the use of plant oils to partially replace marine fish oils in the pellet feeds given to farmed fish (Le Francois *et al*. 2010. Chapter 6).

***Living resources***

A major cause for public concern about the environmental impact of fish culture and an important aspect of the management of fish in aquaculture systems centres on potential threats to wild fish populations. Such threats might be removal of natural prey through capture of fish for the manufacture of fish meals and fish oils, or might relate to transmission of parasites and diseases. In addition, major environmental concern is centred on the threats to wild populations through release of cultured fish, which can occur either deliberately or unintentionally. Intentional releases are usually carried out in an attempt to mitigate the effects of over-exploitation, habitat alteration and destruction on wild populations, but these attempts at restoration have met with mixed success (Stouder *et al*. 1997; Araki *et al*. 2008). Fish are also released in supplementation and sea ranching programmes to increase the resources that can be harvested. The fish may be released at all life stages, but the release of captive-bred, hatchery-reared juveniles is most usual. Unintentional releases occur when juvenile and adult fish escape from hatcheries and fish farms, or when fish held in cages mature, reproduce and release fertilized eggs and larvae into surrounding waters. For example, many farmed Atlantic cod (*Gadus morhua)* mature before they reach harvest size and some spawn in sea cages and produce fertilized eggs. In some cases 20–25% of larval and juvenile cod in the vicinity of a farm may derive from fish that spawn in nearby sea cages (Kah *et al*. 2010).

Irrespective of whether releases are intentional or unintentional, the fish of cultivated origin will generally intermingle with naturally-occurring populations of the same species, exploiting the same feeding areas and possibly interbreeding with wild fish (Araki *et al*. 2008; Tucker & Hargreaves 2008; Le Curieux-Belfond *et al*. 2009; Nielsen & Pavey 2010; Chapter 10). Interbreeding between cultured and wild fish could alter the genetic structure of wild populations through outbreeding depression, homogenization or a reduction in effective population size. For example, interbreeding between wild and cultured fish could result in changes in allele frequencies in wild populations and the genetic profiles of wild populations could be altered by the introduction of rare alleles selected for in the cultured fish on the basis of performance criteria. As discussed above, fish that have been held in captivity for several generations generally differ markedly in several characteristics from fish of wild local stocks. Population sizes could decrease if cultured fish replace wild fish and then have low reproductive success. The effects of cultured fish on the genetic profiles of wild populations are expected to be least when local, wild fish are used as broodstock in restoration, enhancement and sea ranching programmes (Araki *et al*. 2008; Nielsen & Pavey 2010).

Many fish species have been transplanted to areas outside of their natural distributional range for farming and other purposes and several of these have established self-sustaining populations in the wild, following either intentional release or escape from captivity (Lever 1996; Shelton & Rothbard 2006). This can be illustrated by the rather curious case of the establishment of populations of some tropical aquarium species in a number of localities within the British Isles. For example, following the discard of pet-shop stock into a canal in north-west England a breeding population of the guppy (*Poecilia reticulata*) established itself; this was possible because the reach of the canal into which the fish were released received warm-water effluent from a nearby factory (Lever 1996). A number of the species that have been naturalized into

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non-native areas are now considered pests with detrimental effects on native faunas and habitats (Lever 1996; Tucker & Hargreaves 2008).

The only sure way to prevent the establishment of feral populations and to hinder interbreeding between cultured and wild fish is to ensure that any fish released into the wild are infertile. Interspecific hybrids are usually infertile, so the farming or stocking with hybrids is one way to circumvent both the establishment of self-sustaining populations and interbreeding with local wild fish. Sterile fish can also be produced by genetic manipulations involving the induction of polyploidy, particularly triploidy. Triploid fish have three sets of chromosomes, two from the female and one from the male and are produced by application of thermal or pressure treatments shortly after egg fertilization. Because triploid fish have an extra set of chromosomes, the germ cells cannot undergo all the meiotic divisions needed to produce viable eggs or sperm, so the fish are usually functionally sterile (Kah *et al*. 2010; Le Francois *et al*. 2010). Triploid fish are not considered genetically modified organisms according to European regulations (EU, Directive 90/220/CEE), but are perceived negatively by fish farmers, traders and consumers and few efforts have been made to develop the technique for mass use. Triploid rainbow trout are produced when large fish are in demand, such as for smoking, and triploid rainbow trout and other salmonids are raised for the reproductive containment of fish released by angling associations in several European countries. The introduction of exotic fish species such as grass carp (*Ctenopharyngodon idella*) in United States for the purpose of weed control in ponds requires that the fish are sterile triploids to reduce the threat of uncontrolled reproduction in the wild (Piferrer *et al*. 2009).

Although the production of sterile farmed stock might eliminate problems related to genetic impacts of intentionally-released fish or farm escapees on natural populations, it would not serve to eliminate all forms of interaction. Released fish could be members of non-native or introduced species, highly-selected stocks or hybrids with a range of characteristics that could impact wild populations in a number of different ways. The released fish could act as either predators or prey, could be vectors of parasites or disease organisms and could compete for food or other habitat resources resulting in displacement or exclusion of native species and natural populations. In all likelihood several of these interactions would act simultaneously. Given these considerations, and the low success rates of many supplementation programmes, the culture of fish for this purpose is questioned by some environmentalists and fisheries managers (Devlin *et al*. 2006; Jonsson & Jonsson 2006; Tucker & Hargreaves 2008; Le Curieux-Belfond *et al*. 2009; Le Francois *et al*. 2010). This book discusses how the culture of fish for supplementation or reintroduction could be made more effective through consideration of the behavioural traits of cultured fish, in cases where it has been decided that this is appropriate and advisable.

### 1.7.3 Welfare criteria

#### *Why welfare matters in fish culture*

The culture of fish for whatever purpose raises a number of welfare issues, both for fish that are reared in captivity and sometimes for wild fish (Huntingford *et al*. 2006; Ashley 2007; Branson 2008). A wide variety of factors, both biotic and abiotic, have the potential to create welfare problems for cultured fish. Such problems can arise early in life; for example, unfavourable temperatures during larval development may give rise to deformities in the soft tissues, including abnormalities in the heart and swimbladder. Unfavourable temperatures may also interfere with development of skeletal tissues, causing, for example, malformed gill covers and jaws (Branson 2008; Chapter 2). Deformities may also arise if the fish experience unfavourable conditions at a later stage in development; for example, provision of nutrient-deficient live prey and formulated feeds at first feeding can cause spinal deformation (Branson 2008; Dabrowski & Hardy 2010). Abnormal development in both hard and soft tissues interferes with swimming and hence compromises many aspects of behaviour. In addition, malformed gill covers cause breathing problems and may make the fish vulnerable to gill infections, while malformed jaws are likely to interfere with feeding. Such general and specific effects all lead to poor welfare, but they also compromise production, since deformed fish survive and grow less well than normal fish and have a lower market price. In addition to such dramatic effects on physical condition, many unavoidable aspects of routine husbandry can potentially compromise fish welfare; these include confinement, housing at high densities, grading, disease treatment, transport and harvest (Huntingford *et al*. 2006; Ashley 2007; Branson 2008).

Since intensive aquaculture is a relatively new enterprise in which rearing conditions have often not been optimized, good welfare and good production often go hand in hand, with interventions that promote welfare also improving production. For example, when fish are allowed to feed according to their natural appetite rhythms (Chapter 7), their welfare improves, according to various indicators, including reduced fin damage, as does feed conversion

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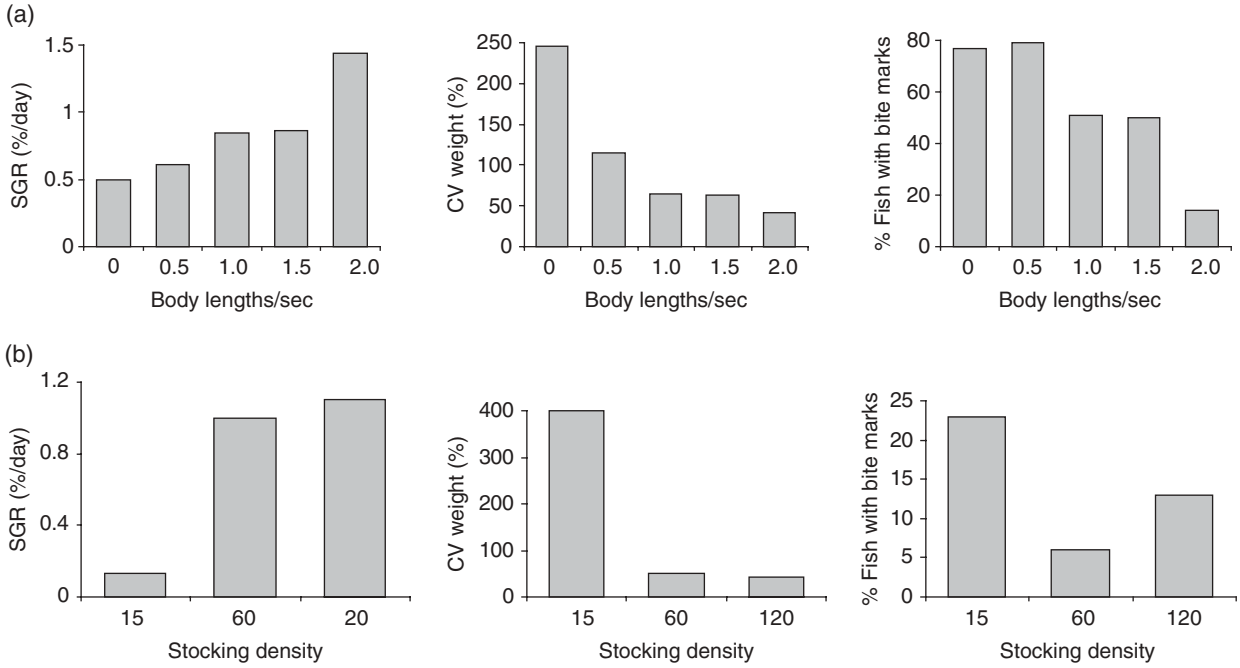


**Figure 1.5.** Detecting and improving the welfare of farmed fish. Specific growth rate (SGR %/day), coefficient of variation in weight (CV weight %) and percentage of fish with bite marks in Arctic charr held (a) at different current speeds (body lengths/sec) and (b) at different stocking densities (Kg/m$^3$). Adapted from Jobling *et al.* 1993; Jobling 1995.

efficiency (Noble *et al*. 2007). This is one reason why, over and above having a responsible attitude to their stock, good fish farmers are concerned about the welfare of the fish in their care. Another reason is that public pressure has resulted in regulations and legislation with which farmers must comply. In addition, there are various schemes through which farmers can charge a premium for fish that have been reared in conditions that promote welfare, the Royal Society for the Protection of Animals (RSPCA)'s freedom food label for farmed salmon being a case in point(http:/www.rspca.or.uk/science group/farm animals/standards/salmon).

The response of Arctic charr (*Salvelinus alpinus*) to early culture efforts illustrates well some of the problems that can arise when fish are being farmed. When trials aimed at commercial development of Arctic charr culture were initiated in the mid 1970s, rainbow trout and Atlantic salmon farming were already well established. Hatchery and husbandry techniques had been developed, tanks and other equipment were readily available and cage culture was well-established (Le Francois *et al.* 2010). When Arctic charr were reared in fresh water at similar stocking densities and with similar feeding routines to those used for farming rainbow trout and salmon, a number of problems arose, with implications for both production and welfare. In the first place, growth was uneven, with some fish growing rapidly and others growing very slowly. Behavioural observations showed that at low stocking densities and in shallow water with low current speed, many of the charr were relatively inactive, remaining close to the bottom and sides of the tank. These fish were often small and dark and tended to feed in midwater and on the tank bottom rather than at the surface. In contrast, a few pale-coloured charr, usually the largest, swam almost continuously in the water column, frequently chased and delivered nips to other fish and fed either in midwater or close to the water surface. The high levels of attacks and fin-nipping delivered by the large charr resulted in many of the smaller fish having bite marks on their fins and bodies (Figure 1.5; Jobling *et al*. 1993; Jobling 1995). A further indication that rearing conditions were suboptimal came from the fact that some of the charr showed a reduced ability to regulate gas within the swim bladder. These fish experienced difficulty in maintaining neutral buoyancy and swam on their sides or belly-up, often at the water

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surface, though they were still able to feed and grow. Thus, many of the early farmed charr showed several indicators of poor welfare, including slow growth, dark colouration, damaged fins, restricted space use and abnormal swimming.

***Strategies for improving the welfare of cultured fish***

Having identified welfare problems, two broad approaches to mitigation are available; these are not mutually exclusive. One possible strategy is to make a careful choice of which fish to culture, since some species and strains of fish are more amenable to being held in captivity than others. For example, some species and strains are less aggressive than others (Chapter 9) and welfare problems arising from aggression among cultured fish could be mitigated by culturing these species or strains. In a number of lakes, two forms of Arctic charr exist, one that feeds selectively on large, benthic invertebrates and one that specializes on zooplankton (Chapter 5). The pelagic form is less aggressive than the benthic form (Chapter 9) and so might be more suitable for culture.

A second mitigation strategy is to design culture facilities, equipment, husbandry practices and management systems that promote welfare. In the early farming of Arctic charr it proved possible to mitigate the adverse effects on welfare by some fairly simple and practicable steps. Increasing the depth of water, subjecting the fish to flowing water and increasing stocking density helped to solve several welfare problems. When charr were exposed to flowing water, they exhibited schooling behaviour, distributed themselves evenly in the water column, fed in midwater or close to the surface and showed reduced levels of aggression; the net result was fewer fish with bite-marks, higher rates of growth and reduced size heterogeneity (Figure 1.5a). In addition, a smaller number of fish showed signs of stress or exhibited problems related to buoyancy regulation. Similar effects, including the induction of schooling, reduced chasing and fin-nipping and improved growth, were achieved by rearing the fish at higher stocking density (Figure 1.5b; Jobling *et al*. 1993, 1998; Jobling 1995). The effects of the two interventions (increased stocking density and exposure to flowing water), which were independent of each other, can be explained in terms of the behavioural biology of aggression (Chapter 9).

### 1.7.4 Behaviour and effective, sustainable aquaculture

Behaviour can influence the effectiveness and sustainability of aquaculture in the period during which fish are being grown to a useable size. For example, how fish feed in culture systems can affect how much food is wasted, as well as whether fish survive and how well they grow (Chapters 5–7) and whether and how much fish fight can affect how fast they grow, their physical condition, their welfare and how efficiently they convert food into flesh (Chapter 9). Thus behaviour during the culture process determines the effectiveness of production and the condition and health status of the fish, regardless of the reason why the fish are being farmed.

Over and above this, the purpose for which the fish are being cultured determines what is required of their behaviour. For example, the attractive traits for which ornamental fish are cultured are best appreciated if they behave in an appropriate way. Fish that emerge from cover and can readily be seen, especially if they display bright colours and elaborate fins, are more rewarding that those that consistently hide. In addition, for many people simply watching the behaviour of their fish is a key part of the rewards of maintaining an aquarium. For all these reasons, the value of cultured ornamental fish depends on their showing many of the behaviour patterns that are normal for their species. Where fish are reared for scientific purposes, how they behave is also important if they are used to study neurobiology or behaviour; if their behaviour and the mechanisms that generate it are abnormal, the generality of any research conclusions may be limited.

The success of programmes in which fish are cultured for release into the wild clearly depends on how well they survive, grow and in some cases reproduce after being released. Their behaviour is important here, because how efficiently fish feed, compete with conspecifics and avoid predators are all determinants of post-release survival and growth. As discussed in later chapters, there is evidence that captive-reared fish differ from wild fish in foraging ability, in predator avoidance and in agonistic behaviour towards conspecifics (Einum & Fleming 2001; Jonsson & Jonsson 2006; Araki *et al*. 2008; Nielsen & Pavey, 2010). It is therefore important that cohorts of cultured fish and individuals within the cohorts show a natural spectrum of species-typical behaviour. Where the aim is simply to generate a population of fish for subsequent angling, the spectrum of behaviour in individuals and populations is important, as the fish need to survive long enough to service an angling use and to behave sufficiently naturally to be an interesting catch. Exactly how such traits develop is not critical. If the aim of a supplementation programme is to generate or augment self-sustaining wild populations for conservation, then clearly both the ability to reproduce and the inherited behavioural profiles of the released fish are important (Fleming & Petersson 2001; Jonsson & Jonsson 2006; Araki *et al*. 2008; Chapter 10).

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## 1.8 STRUCTURE AND CONTENT OF THIS BOOK

The aim of this book is to familiarize the reader with the fundamentals of behavioural biology of fish and to show how this is relevant to fish culture. Understanding fish behaviour requires knowledge of some other aspects of their biology, such as their sensory capabilities and how they process and respond to sensory information. Early developmental processes are also important in governing the physiological and behavioural responses shown by fish later in life and the environment experienced by a fish during the earliest stages of its life can have long-lasting effects on how it will react under a given set of circumstances. A brief overview of these topics is presented in Chapter 2, by way of preparation for the material presented in later chapters.

The behaviour of aquatic animals is difficult to study because the environment in which they live is often inaccessible to human observers. Studying the behaviour of fish in aquaculture systems is additionally challenging because huge numbers of fish are often held together in conditions that are not conducive to direct observation. This has required development of special techniques for collecting scientific data on the behaviour of cultured fish and these are described in Chapter 3.

The remaining chapters take specific aspects of behaviour in turn, first presenting fundamental information about their causes, development and consequences for fitness, illustrated wherever possible using examples from cultured species, and then discussing the implications for aquaculture. This includes an account of how the behaviour concerned is expressed in cultured fish, the problems for production arising from its expression and the effects of domestication and captive rearing on the behaviour concerned. Solutions to these problems are also described, looking at how behavioural knowledge can be used, among other things, to devise husbandry systems that promote production, welfare and environmental protection and to mitigate the effects of captive rearing.

The most studied aspects of behavioural biology that are relevant to fish culture relate to finding, selecting and consuming food, closely followed by studies of reproductive behaviour. More recently the topics of orientation and movement, aggressive interactions and antipredator behaviour have been introduced into the aquaculture literature. All of these are covered in this book, starting with orientation in and movement through space, which could be important given that cultured fish are unable move as freely as they would in nature (Chapter 4). Knowledge about feeding and nutrition is critical for effective fish culture and much is known about the nutritional biochemistry and physiology and the growth biology that underpins effective production of some species. However, behavioural aspects of feeding are also important, including how fish acquire and process food (covered in Chapter 5), their dietary preferences (covered in Chapter 6) and the factors that determine how much fish eat and when (covered in Chapter 7). Farmed fish are usually protected from predators, but they do sometimes experience predatory attack and even when this is not the case anti-predator behaviour may be elicited by husbandry practices. Knowledge about antipredator behaviour is therefore important for effective culture and this is described in Chapter 8. Cultured fish very often live in close proximity to many other individuals of the same species and this can affect social relationships and how frequently fighting occurs, topics covered in Chapter 9. Finally, behavioural traits associated with life history events, including reproduction, are very important in culture; reproduction must be controlled and often prevented during on-growing, but must be promoted in broodstock to produce the next generation to be farmed. The life history patterns and reproductive behaviours of fish and their implications for fish culture are covered in Chapter 10. The final chapter considers common themes relating to the expression and importance of fish behaviour in aquaculture, both as it is currently practiced and in the light of developments that may take place in the future.

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# 2
# Fish in Aquaculture Environments

*Malcolm Jobling*

**Abstract:** This chapter presents background information about finfish and their adaptations to an aquatic environment, needed for a proper understanding of the facts about behaviour presented in later chapters. After a brief description of the characteristic features of finfish, information is given on how fish swim and how body shape and fin structure is adapted to movement in particular habitats. The special features of water as a sensory environment are described, as are the senses that finfish have and how these function. This is followed by an account of the fish nervous and endocrine systems and how these interact to coordinate and control biological processes. Such interactions allow fish to cope with adverse conditions, including those encountered in culture systems, and are central to the stress response. Life histories and patterns of reproduction are complex and variable and this has important implications for many aspects of fish culture. An overview is therefore given of the various reproductive patterns found in finfish. Finally, an account is given of the complex ways in which early environmental effects (including maternal input to the eggs) interact with inherited traits to shape the biology of finfish, including their behaviour.

**Keywords:** endocrine system; life history programming; maternal effects; nervous system; reproduction; sensory systems; stress responses; swimming.

## 2.1 INTRODUCTION

Fish culture can be considered as a specialised, aquatic area of agriculture, and there are some similarities between the rearing of fish and the raising of terrestrial farm animals. There are, however, also numerous differences, mostly relating to the challenges imposed by the rearing of animals in water as opposed to on dry land. Many abiotic and biotic factors contribute to the rearing environment to which farmed fish are exposed; all of these factors will influence the behaviour and culture performance of the fish. The fact that fish are aquatic animals means that all aspects of their life are intimately linked to water quality and quantity, and this has major consequences for husbandry practices (Stickney 2000; Wedemeyer 2001; Tucker & Hargreaves 2008; Le Francois *et al*. 2010). For example, the amount of oxygen that dissolves in water is much lower than the amount present in the same volume of air, so fish must have a very efficient respiratory system to obtain the oxygen that they require not only to survive, but also to feed and grow effectively. Reduced (subsaturation) oxygen concentrations are not uncommon in water, and at times respiration may become difficult for fish, both in the wild and on farms. Water serves not only as the respiratory medium; its high density means that it supports and buoys up the fish, meaning that they require less skeletal support than do terrestrial animals, but the high density of water, and its viscous nature, create problems for effective locomotion. Finally, the water with which fish are surrounded

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dilutes any toxic metabolic waste products the fish excrete, but living in water poses unique problems relating to the regulation of salt and water balance of the blood and other body fluids.

### 2.1.1 Fish and their behaviour

Fish are jawed vertebrates that are adapted to live in water and they possess gills throughout their lives. The gills, which have respiratory, iono-regulatory and excretory functions, open to the exterior via some form of slits or opercular opening. The paired limbs of fish are their pectoral and pelvic fins. Such is the diversity of the fish that no other characters are possessed by all of them. Some features are possessed by so many fish species that they can be considered as being typical for the group; for example, the skin usually has a covering of scales, and the heart is typically two-chambered and pumps only venous blood.

The behaviour of fish depends on many different aspects of their biology. These include the sense organs, the nervous system and the mechanisms that generate and control the resulting movements. Behaviour is also adapted to events taking place inside the body, so the physiological processes that regulate internal state also determine how fish behave. Fish are in continuous receipt of, and respond to, stimuli of various kinds from the environment. These stimuli may elicit immediate responses or may provide information that leads to changes in the longer term; for example, seasonal changes in photoperiod are the most reliable environmental signal for time of year at most latitudes. As such, most fish that show seasonal changes in physiology and behaviour, such as in migration or reproduction, use photoperiodic information for appropriate timing of their activities (see Chapter 10).

In order to make use of environmental information and to generate appropriate behavioural responses, the fish must have detection and receptor systems (sense organs), internal communication systems (nervous and chemical signalling systems), the ability to integrate and co-ordinate the information, and effector systems capable of acting upon the information received. As discussed in Chapter 1, the aquaculture environment is potentially stressful to fish in a variety of ways, so the physiological mechanisms by which fish respond to challenge are particularly important when it comes to understanding how cultured fish behave. Finally, compared to many terrestrial vertebrates, fish have varied and complex life cycles and patterns of reproduction and this fact, as well as being directly relevant to the reproductive behaviour of farmed fish (Chapter 10), has a number of general implications for fish culture and the behaviour of fish in culture systems. This chapter gives an introduction to these topics, providing the background knowledge needed to understand the subsequent chapters.

## 2.2 LOCOMOTION AND SWIMMING ABILITY

Fish move by swimming, but swimming covers several types of locomotion, using different regions of the body and requiring a range of complex adaptive movements. The high density of water allows many fish to be at, or very close to, neutral buoyancy so structures that serve to support the bodies of terrestrial animals can be specialised for swimming in fishes. Along with muscles, the structures that may be used by fish during swimming include the vertebral column, the caudal (tail) fin, the median (dorsal and anal) fins and the paired pectoral and pelvic fins. This gives rise to a range of propulsory systems that can be broadly divided into paired and median fin propulsors, and body and caudal fin propulsors, each of which is specialised for a given locomotory function, including swimming at speed, slow swimming and precision movements (Evans 1993; Jobling 1995; Willmer *et al*. 2005).

### 2.2.1 Body form

The constraints placed upon a fish moving through water are markedly different from those placed on an animal moving on land or through the air. Water is a dense, viscous medium that places a premium on effective propulsion. Propulsion based on the trunk and caudal fin is most efficient for swimming, and several aspects of the external morphology of a fish can lead to good hydrodynamic performance (Evans 1993, 1998; Jobling 1995; Willmer *et al*. 2005; Evans & Claiborne 2006).

Hydrodynamic efficiency is greatest when the body is streamlined, or fusiform. For this purpose, the ideal body length is about 4.5 times the maximum depth, with the body deepest about one-third of the way back from the snout. The caudal fin of the fish should be stiff and sickle-shaped (lunate or deeply forked), being 5–7 times deeper than its maximum breadth. Such a tail form reduces turbulence and gives maximum thrust at high speeds, and a narrow caudal peduncle (narrow necking) can serve to reduce lateral resistance to tail movements. Finally, restriction of lateral movement to the tail region during swimming will further act to reduce turbulence; this is achieved by holding the front of the body stiff when the fish swims and only moving the tail region. These are the adaptations seen in active, pelagic fish species, best exemplified by fish within the tuna and mackerel family (Scombridae, Figure 2.1; Evans 1993, 1998; Jobling 1995; Willmer *et al*. 2005; Evans & Claiborne 2006).

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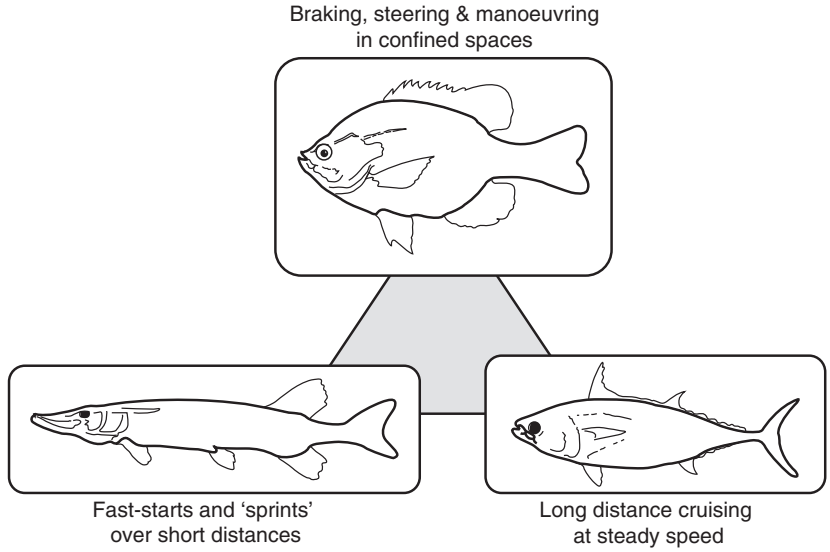


**Figure 2.1.** The 'swimming specialist triangle' illustrating body shapes in fishes and the dispositions of fins that are optimal for different kinds of swimming. Adapted from Webb 1984.

When a fish makes a sudden dart in order to capture prey or to flee from a predator it will usually accelerate from a 'standing start'. The rate of acceleration is high, and acceleration results from large amplitude lateral movements of the tail. It is only rarely that more than a few beats of the tail are involved in producing such accelerations. A relatively long, flexible body enables the fish to coil into a C or S shape, like a sprinter in the starting blocks, for an effective fast-start. Fast acceleration requires rapid and co-ordinated muscular contractions; these are stimulated and controlled by the Mauthner cells (specialised nerve cells in the hindbrain of the fish. Chapter 8), giving a C-start latency of 5–10 ms. In fast-start swimming the propulsive movements occur by large lateral movements of the tail, so a large caudal fin area is advantageous. The area around the caudal region can be increased by the fish having a deep caudal peduncle and dorsal and anal fins placed well back on the body. The large amplitude lateral motions of the caudal region not only generate thrust forces in the direction of motion, but also give rise to substantial side forces. The potentially negative effect of these side forces is reduced if the fish body is deep in the region close to the centre of mass, so fish with good fast-start performance have a cigar-shaped body of similar depth along its entire length. Examples of fast-start, sprint specialists include the pike (*Esox lucius*) and barracudas (*Sphyraenidae*, Figure 2.1; Evans 1993, 1998; Jobling 1995; Willmer *et al*. 2005; Evans & Claiborne 2006).

The fins of teleost fish are supported by spines and rays. The fin rays are flexible and can be moved by muscles inserted at their bases. This means that adjustments can be made to change fin area, orientation and angling relative to the body surface. In combination with the positioning and insertion of the fins, their flexibility enables the fish to brake effectively and to make fine adjustments in orientation. When the pectoral fins are high on the body the forces produced during braking act directly through the centre of gravity. This makes for efficient braking and reduces, or eliminates, the tendency for the body to pitch forward. In addition, pelvic fins that are placed well forward on the body can function as brakes in combination with the pectoral fins. Flexibility of the paired fins, particularly the pectorals, also gives the possibility of improved steering and better control over changes of direction; it is an advantage to have the fulcrum around which the body turns (the pectoral fin) placed as close to the centre of gravity of the body as possible. Further, for effective changes of direction the resistance to turning of the head and tail should be more or less equal. Thus, the caudal region should be relatively short. From this it follows that the best steering and turning abilities are shown by fish that have relatively short bodies, and that have pectoral fins located high on the body close to the centre of

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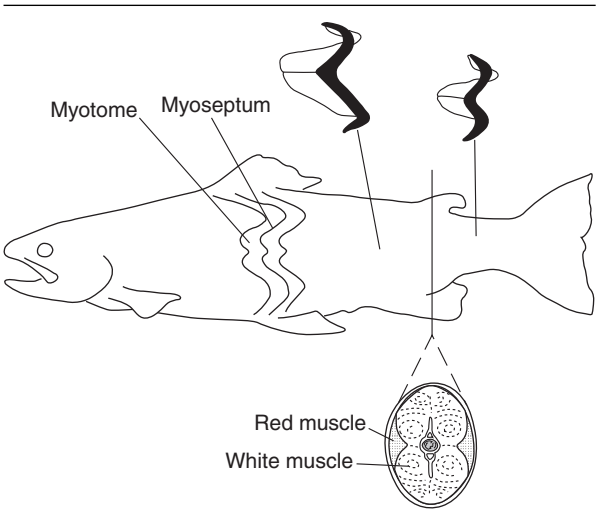


**Figure 2.2.** Schematic side view of a fish showing the arrangement of the myotomes and (inset) a cross section of the trunk showing the position of the white and red muscle. Reproduced from Jobling 1995. With kind permission from Springer Science + Business Media B.V.

gravity, seen, for example, in sunfishes (*Lepomis macrochirus* and *L. gibbosus*) and tilapias (*Oreochromis niloticus* and *O. mossambicus*, Figure 2.1; Evans 1993, 1998; Jobling 1995; Willmer *et al*. 2005; Evans & Claiborne 2006).

### 2.2.2 Swimming muscles

The driving power for swimming most often arises from contractions of the lateral body musculature that lies on either side of the fish's backbone. This lateral musculature is divided into serially arranged muscle blocks or myotomes delimited by collagenous connective tissue myosepta (Figure 2.2; Jobling 1995; Willmer *et al*. 2005; Evans & Claiborne 2006). The myotomal muscle fibres are attached to the myosepta, and the myotomes have different contraction patterns depending upon whether the fish is swimming steadily or is engaged in burst activity. When the fish is swimming at a steady, moderate speed, the muscles contract relatively slowly and they perform these contractions over long periods of time. In burst performance, the muscle contractions are rapid, but the bouts of contraction are of short duration. There are several types of muscle fibres in the lateral muscles of fish, and the myotomes can be separated into anatomically distinct regions. The bulk of the muscle is composed of fast contracting twitch fibres, the white fibres. A superficial band of slow contracting, aerobic muscle fibres, the red fibres, lies outside the white fibres (Figure 2.2).

As a generalisation it can be said that the white fibres are the fast-start muscles, whereas the red fibres are used during steady swimming at low to moderate speed (Evans 1993, 1998; Jobling 1995; Willmer *et al*. 2005; Evans & Claiborne 2006). The proportions of red fibres in the muscle mass are greater in pelagic, cruising fish such as mackerel (*Scomber scombrus*), herring (*Clupea harengus*) and salmonids than in benthic, more sedentary species, such as plaice (*Pleuronectes platessa*) and other marine flatfish and gurnards (Triglidae). In addition, the relative size of the lateral musculature will reflect the life-style of the fish, with active, pelagic species having a greater muscle mass than sedentary, bottom-living species; the lateral muscle can range from about 25–30% of the body mass in sedentary species to over 60% of the body mass in the most active, pelagic cruising species.

## 2.3 SENSING ENVIRONMENTAL STIMULI

### 2.3.1 Sensory cues in the aquatic environment

In order to be able to respond appropriately to events that occur in their local milieu, fish must be able to detect environmental signals. These signals may relate to abiotic factors such as oxygen concentrations or temperature, or can be generated by other animals, such as potential prey, predators, competitors or possible mates. The environmental stimuli that fish experience include light, mechanical disturbances, electrical stimuli and myriad chemicals. Fish have sensory systems capable of photoreception, mechanoreception and chemoreception, and some fish are also capable of detecting electrical stimuli. The sense organs and sensory systems transmit information to central sites, primarily via nervous connections, where interpretation and co-ordination is carried out (Evans 1993, 1998; Jobling 1995; Willmer *et al.* 2005; Evans & Claiborne 2006). The properties of water mean that signal transmission may differ between water and air; in speed of transmission and in rate of attenuation of the signal, for example. This means that although the sensory systems of fish and terrestrial animals have much in common, there may also be differences, for example in sensitivity and the relative importance of the various senses in governing responses, activities and the day-to-day functioning of the animals concerned (Evans 1993, 1998; Jobling 1995; Willmer *et al*. 2005; Evans & Claiborne 2006).

### 2.3.2 Vision

Visual cues are undoubtedly important in many aspects of the lives of fishes. There are three characteristics of light that may influence the behaviour of fish and their ability to locate objects in the environment. These characteristics are

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light quality (the spectral characteristics of the light with respect to wavelength), light quantity (illuminance or light intensity) and light duration (photoperiod, defined as the ratio of hours of light to hours of darkness during a 24 h period). The light:dark cycle, based upon the 24 h solar day, also helps define the annual cycle of the seasons.

### *Underwater visibility*

The visibility of an underwater object is determined by the characteristics of the object and of the animal observing it. The determinants of visibility of an object include its shape, size, colour, degree of transparency and whether it is moving or stationary. As light intensities increase the distance at which a fish is able to detect an object (the reaction distance) increases rapidly up to a threshold (the saturation intensity threshold). Above the saturation intensity threshold reaction distance remains relatively constant (Mazur & Beauchamp 2003; Holzman & Genin 2005). Reaction distance is also influenced by the size of the object (Holzman & Genin 2005) and water characteristics, such as its turbidity (Utne-Palm 2002; Mazur & Beauchamp 2003; Sweka & Hartman 2003; Stoner 2004). At any given light intensity fish will generally be able to detect larger objects at greater distances than small (Holzman & Genin 2005). Also, fish are able to locate moving targets more easily than motionless ones, so increased prey activity may increase predation risk by increasing the likelihood of detection by predators. In addition to light (intensity and spectral properties) and the characteristics of an object, the visual acuity of the fish will also be an important determinant of whether or not an object, such as a prey item or a predator, is detected.

Turbidity refers to the degree to which the penetration of light in water is limited by the presence of suspended and dissolved substances. Suspended material is made up of small inorganic particles of silt, clay or fine sand, and organic detritus comprising plant and animal remains. Phytoplankton suspended in the water column also contribute to turbidity. There are, however, differences in light absorbing and scattering properties of phytoplankton and suspended inorganic material. Chlorophyll and other pigments present in phytoplankton absorb large quantities of visible light, whereas inorganic particles induce turbidity by the scattering of light. This means that the visual abilities of fish often differ when water contains high concentrations of phytoplankton and when turbidity is the result of suspended inorganic material (Radke & Gaupisch 2005). As water becomes more turbid there is a reduction in the transmittance of light, and the distance at which fish are able to detect an object is reduced; in other words, reaction distance declines with increasing water turbidity (Utne-Palm 2002). Turbidity scatters light and reduces transmittance, and can reduce the apparent contrast of an object, leading to reductions in reactive distances that can impair the ability of the fish to detect it. This means that there are interactions between light intensity and turbidity in governing the reaction distances of fish to prey, predators, competitors and potential mates (Utne-Palm 2002; Sweka & Hartman 2003).

### *Properties of light*

Solar radiation is made up of photons within the visible spectrum (from violet at 400 nm to red at 700 nm) together with infrared (IR) and ultraviolet (UV). The intensity of light at the water surface varies with time of day and season, and is also influenced by environmental conditions, light being filtered during its passage through the atmosphere and photons reflected and refracted at the water surface. Light intensity experienced below the water surface is a function of surface illumination, wave action, water clarity and depth. More light will enter through a still water surface than a rough one, and conditions also vary with time of day. Around dusk and dawn the sunlight arrives at the water surface at a low angle and via a long atmospheric path, resulting in reduced intensities and with a spectrum shifted towards short wavelengths. On the other hand, moonlight is richer in longer wavelengths, and starlight has a greater proportion of photons towards the red end of the spectrum. Twilight, the periods around dusk and dawn, is accompanied by rapid changes in light intensity, and also in the spectral and polarisation properties of the light.

When light passes through water its intensity decreases, and the loss of intensity varies with colour, different wavelengths being absorbed to different degrees. This means that both intensity and spectral characteristics of the light change with depth. Light at wavelengths within the IR, red, violet and UV ranges is absorbed more strongly than is light of intermediate wavelengths. Both light intensity and light spectral characteristics affect the visibility of underwater objects (Douglas & Djamgoz 1990; Guthrie & Muntz 1993; Hawryshyn 1998; Utne-Palm 2002). In order for an underwater object to be visible it must differ sufficiently from the background. Absorption and scattering of photons account for the bulk of the attenuation of the light that is reflected off underwater objects, and these are the two main factors that make visual detection of such objects difficult. Visual thresholds vary markedly among fish species. In general, fish that live in turbid water or at depth have lower visual thresholds than those that live in clear, shallow waters, or close to the water surface (Kestemont & Baras 2001; Stoner 2004).

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**Table 2.1.** Comparison of the properties of rods and cones, the major photoreceptors present in the fish retina.

| | Rods | Cones |
|---|---|---|
| Photopigment | High concentration | Low concentration |
| Photoreceptor | Single type | Several types with different sensitivity |
| Colour vision | Absent | Present |
| Sensitivity | High. Saturated at low light intensity | Low. Saturation requires high light intensity |
| Speed of response to stimuli | Slow. Low temporal resolution | Fast. High temporal resolution |
| Most sensitive to: | Scattered light | Direct light |
| Acuity/discriminative ability | Low | High |
| Conditions for good detection | Dim, low intensity. Scotopic or nocturnal vision | Bright, high intensity. Photopic or diurnal vision |

Adapted from Hawryshyn 1998.

***Photoreceptors and visual sensitivity***

Photoreceptors are sense organs that respond to stimulation by the light (photons) that impinges upon them (Douglas & Djamgoz 1990; Guthrie & Muntz 1993; Yokoyama & Yokoyama 1996; Hawryshyn 1998). There are two principal types of photoreceptors in the fish retina, the rods and cones, which differ in both structure and function (Table 2.1). The rods are responsible for the detection of light under dim conditions (scotopic vision), whereas the cones function under bright light conditions (photopic vision). Cones are common in the retinas of animals that are active by day, whereas rods occur in greater numbers in the retinas of night-active animals. Fish of different species are active at different times during the light:dark cycle; they can be broadly divided into diurnal, nocturnal and crepuscular species. Diurnal species are active during the hours of daylight, nocturnal species are active during the hours of darkness, and crepuscular species are most active during twilight hours, around dusk and dawn. Species that are active at different times of the day often use different sensory modalities for detecting and locating objects in their environment. For example, amongst the percids, the perch (*Perca fluviatilis*) and ruffe (*Gymnocephalus cernuus*) often co-occur in lakes and ponds, but differ in their foraging habits and the senses used for prey detection. The perch is a mobile, visually-orientated, day-active predator whereas the ruffe has a visual system better adapted to function at low light intensities, and also has a well-developed mechanosensory lateral line system. The perch is effective at capturing prey in clear, well-lit waters, but is far less successful at finding and consuming prey in the dark. The ruffe, on the other hand, is far more successful than the perch at feeding at night and is a superior competitor under such conditions (Schleuter & Eckmann 2006).

The wavelengths of light to which fish are most sensitive vary with species and developmental stage (Douglas & Djamgoz 1990; Evans & Fernald 1990; Guthrie & Muntz 1993; Losey *et al*. 2003; Marshall *et al*. 2003; Temple *et al*. 2006). The visual pigments are composed of a protein, an opsin, coupled to a chromophore, which is a derivative of vitamin A. The spectral properties of the visual pigments are determined by the amino acid sequences of the opsins and whether the chromatophore is vitamin A1- or A2-based (Yokoyama & Yokoyama 1996; Hawryshyn 1998; Flamarique 2005). The proportions of different opsins and the nature of the chromatophores in the retina may change with seasonal and with developmental changes of the fish (Temple *et al*. 2006). Visual pigments may also differ between individuals of a given species when they occur in habitats that differ in lighting conditions. These differences may, in part, be genetic but there is also considerable intraspecific plasticity in the development of visual pigments. Other components of the visual system may also change in relation to the environmental light conditions experienced by the fish (Wagner & Kröger 2005). This developmental plasticity in the visual system in response to alterations in the spectral conditions to which the fish is exposed provides a mechanism that ensures functional vision in different light environments. Fish experience both short-term and long-term changes in their spectral environments. The complement of visual pigments and the cellular organisation of the retina may change during the life cycle of the fish (Douglas & Djamgoz 1990; Evans & Fernald 1990; Hawryshyn 1998). Sometimes the changes are not

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induced by a change in the visual environment, but precede a change in habitat. One such change is the loss of the UV-sensitive cones that occurs in salmonids that are undergoing the parr–smolt transformation (Hawryshyn 1998; Flamarique 2005).

The visual pigments of surface-dwelling, pelagic and coastal zone marine fish often have peak sensitivities at around 490–510 nm, while freshwater species tend to have visual pigments with peak sensitivities within the 500–550 nm range (Douglas & Djamgoz 1990; Guthrie & Muntz 1993; Losey *et al*. 2003; Marshall *et al*. 2003). Although light within both the IR and UV wavelengths is rapidly attenuated as it passes through the water column, light within these wavelengths penetrates to sufficient depth to be used for fish vision. Some freshwater fish are sensitive to wavelengths within the IR, and the ability to detect IR may enhance the visual abilities of the fish under twilight conditions and at night; in other words, the possession of IR-sensitive photopigments is an adaptation for scotopic vision (Matsumoto & Kawamura 2005). The detection of UV light may be important for a number of behaviours, including prey detection and feeding, mate choice, schooling, spatial orientation and navigation (Toveé 1995; Yokoyama & Yokoyama 1996; Hawryshyn 1998; Losey *et al*. 1999, 2003; Utne-Palm 2002; Jordan *et al*. 2004; Flamarique 2005; Modarressie *et al*. 2006).

### 2.3.3 Mechanosensory systems

#### *Underwater mechanical signals*

Mechanoreceptors can be used to detect gravitational forces, pressure (depth perception), water currents, vibrations resulting from particle oscillations, and sound (far-field particle vibrations). Acoustic energy is transmitted efficiently through water, and sound persists without any major attenuation of the signal over long distances (Popper & Fay 1984, 1993; Hawkins 1993; Schellart & Wubbels 1998; Wahlberg & Westerberg 2005). This allows aquatic animals to use sound as an effective form of communication, and sounds from other sources may also provide important information required for survival. The natural environment is, however, characterised by noise of abiotic and biotic origins, and relevant sounds must be detected against this background. Thus, the detection of one sound signal can be impaired by the presence of another (noise), a phenomenon termed masking.

#### *Hearing underwater*

Auditory perception varies widely among fish species, although a broad classification can be made into those species that are auditory specialists and those that are generalists. The majority of bony fish have a gas bladder, often called the swimbladder, that functions to control buoyancy and develops as an outgrowth from the pharyngeal-oesophageal region at the larval stage. Fish that have a gas bladder usually have better hearing abilities than fish that lack a gas bladder, because the gas bladder can amplify underwater sounds and transmit the vibrations to the inner ear. Furthermore, auditory specialists such as herrings, carps, minnows and freshwater catfishes have a connection between the gas bladder and inner ear making them very sensitive to the sound pressure component of an acoustic signal. The volume of the gas bladder changes in relation to changes in sound pressure, and this motion is transmitted to the inner ear. Auditory generalists mostly rely upon the motion of water particles in a sound field to stimulate the sensory cells of the inner ear and usually lack a direct connection between the gas bladder and inner ear. Consequently, auditory specialists detect a wider bandwidth of frequency with greater sensitivity than do the generalists. Sounds become more difficult to detect as background noise levels increase, and the discriminatory abilities of auditory specialists, such as carps and freshwater catfishes, are affected to a greater extent than are those of generalists (Popper 2003; Wysocki & Ladich 2005; Wysocki *et al*. 2006). As such, masking is a greater problem for auditory specialists than for the generalist species, and auditory specialists are at greater risk of suffering temporary hearing loss than are the generalists.

#### *The lateral line*

Fish also use the lateral line system to detect mechanical vibrations, and the ear and lateral line have some functional overlap (Sand 1984; Bleckmann 1993; Hawkins 1993; Popper & Carlson 1998; van Netten 2006). The fish ear may be able to detect sound frequencies within the range 50–2000 Hz, and it is also used to monitor the position and acceleration of the body. The lateral line, which consists of two subsystems, responds to differences between the motion of the fish and movements of the surrounding water. The two subsystems of the lateral line are the superficial neuromast and the canal neuromast systems. The superficial neuromasts are velocity detectors, whereas the canal neuromasts are pressure gradient detectors. The lateral line subsystems may detect frequencies from less than 1 to several hundred Hz. Together the lateral line subsystems are sensitive enough to permit monitoring of the movements of nearby individuals, such as neighbouring fish within a shoal or school, and may also be used in prey detection and in object localisation and recognition (Sand 1984; Bleckmann 1993; Montgomery *et al*. 1995;

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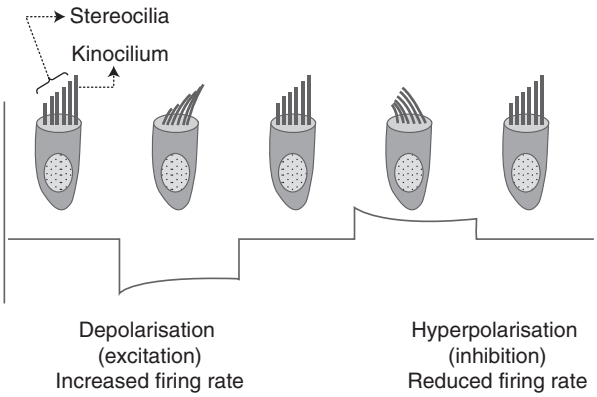


**Figure 2.3.** The structure and function of hair cells. The upper section shows in schematic form various possible positions of the klinocilium and stereocilia (see text). The lower section shows the associated pattern of excitation and inhibition in the sensory neuron. Reproduced with permission from Willmer *et al.* 2005, courtesy of Wiley-Blackwell.

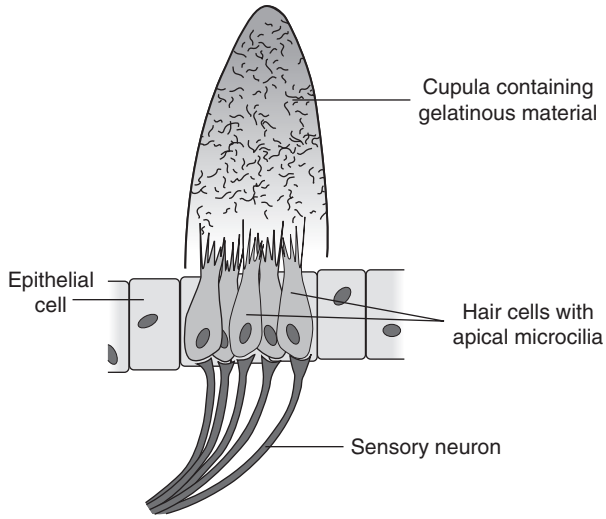


**Figure 2.4.** The structure of a neuromast. Reproduced with permission from Willmer *et al.* 2005, courtesy of Wiley-Blackwell.

Janssen 1997; Schellart & Wubbels 1998; van Netten 2006). The main difference between the ear and the lateral line system is the distance over which they operate. The lateral line detects signals that originate close to the fish, whereas the ear detects signals that may arise from sources at a considerable distance from the fish. Near-field signals can stimulate both the ear and the lateral line, whereas far-field stimuli are detected only by the ear.

### *Mechanoreceptor structure and function*

The auditory and lateral line systems rely upon mechanoreceptors for their function. Mechanoreceptors work by detecting physical deformation of a rigid or semi-rigid structure. The transduction of a mechanical stimulus is mediated by receptor membrane ion channels that are sensitive to stretch, and are either activated ('opened') or inhibited ('closed') by mechanical deformation. The mechanoreceptors in the ear and lateral line are hair cells (Sand 1984; Popper & Fay 1984, 1993; Bleckmann 1993; Hawkins 1993; Popper & Carlson 1998; Schellart & Wubbels 1998; Willmer *et al*. 2005; van Netten 2006). Hair cells are neuroepithelial cells that have sensory hairs, stereocilia, on the apical surface that increase in length from one side of the hair cell to the other (Figure 2.3; Willmer *et al.* 2005). The stereocilia are interlinked and move as a unit; when the tip of the largest stereocilium is deflected there is movement of the whole array. In addition to the bundle of stereocilia, hair cells also have a single true cilium, the kinocilium, linked to the tallest stereocilium, and the orientation of the kinocilium gives the hair cells directional sensitivity (Figure 2.3; Sand 1984; Ashmore 1988; Bleckmann 1993; Hawkins 1993; Popper & Fay 1993; Willmer *et al*. 2005).

Hair cells rarely occur in isolation, but are most often found in groups within specialised structures, the neuromasts (Figure 2.4; Willmer *et al*. 2005). Neuromasts are found on the body surface and within the lateral line system. The neuromasts contain groups (10–100) of hair cells, the cilia of which project into a small overlying cap of gelatinous material, the cupula. Disturbance of water around the fish displaces the cupula and results in a bending of the cilia and stimulation of the hair cells (Sand 1984; Bleckmann 1993; Montgomery *et al*. 1995; Popper & Carlson 1998; van Netten 2006). Thus, the neuromasts can signal the to-and-fro movements of water around the fish. This allows the fish to localise the source of a disturbance, such as that produced by a potential prey item, a conspecific within a school, or an approaching predator. Some of the neuromasts, the canal neuromasts, lie within the lateral line canals that run along the side of the fish's body whereas others, often termed free or superficial neuromasts, are either located in pits or occur directly on the body surface. The functional characteristics of the canal and free neuromasts often differ, with the canal neuromasts responding to higher frequencies than the free neuromasts. In addition, the extent of the lateral line system differs widely across

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fish species, both in the number of body canals and the extent of the canal system on the head. The differences in lateral line patterns on the body and head indicate that fish use their lateral line systems in different ways, such as for orientation and maintaining contact with conspecifics within a school or for locating and striking at potential prey (Bleckmann 1993; Janssen 1997; van Netten 2006).

An important factor for efficient functioning of the lateral line system is the ability to distinguish between a signal and interfering noise. Environmental noise could arise from water currents and turbulence, and movements made by the fish may also represent a significant source of noise. Self-generated noise could mask signals that come from external sources, and fish may employ a number of behavioural strategies to reduce, or overcome, this problem. For example, the fish can employ periods of move-and-stop in which it reduces self-generated noise by ceasing to swim, or the fish may adopt slow gliding movements rather than active propulsion that involves side-to-side displacement along much of the body length (Montgomery *et al*. 1995).

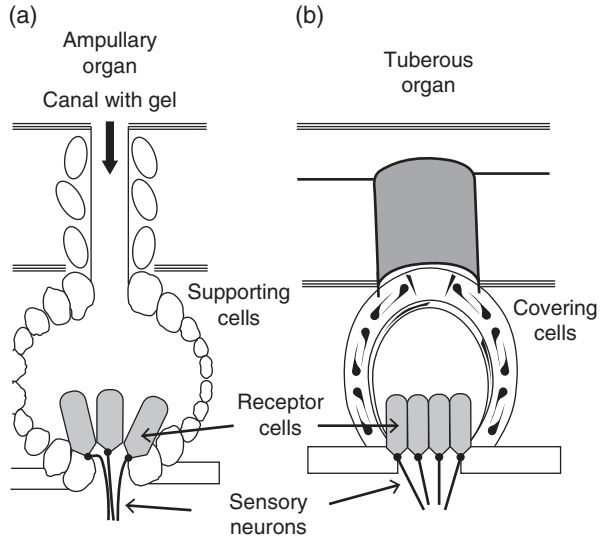


**Figure 2.5.** The structure of the two kinds of electroreceptive organs of fish. (a) Ampullary organ. (b) Tuberous organ.

### 2.3.4 Thermoreception

Most fish are ectothermic poikilotherms and regulate their body temperature by behavioural means; they have distinct species, or life-stage, specific thermal preferenda and move away from water that is excessively hot or cold (Evans 1993, 1998; Jobling 1995; Willmer *et al*. 2005; Evans & Claiborne 2006). This behavioural thermoregulation is initiated in response to detection of external and internal temperatures by thermoreceptors and signal integration by the central nervous system (CNS). It is effected by motor actions that result in the fish changing its position, either vertically, horizontally or both, within the water body. Fish have thermoreceptors in the skin and in the hypothalamus (a region of the brain, see below). These receptors are sensory neurons (nerve cells) that respond to a change in temperature, so monitor relative, rather than absolute, conditions. They are simple free nerve endings, without any clearly defined special morphological features. Some thermoreceptors appear to be multi-functional; those in the skin may act as both thermal and mechanoreceptors, whereas those within the hypothalamus may respond to both temperature and chemical stimuli (Willmer *et al*. 2005).

### 2.3.5 Electroreception

The receptor cells that are responsible for the detection of electricity are derived from hair cells, so the electroreceptive organs of fish are similar in structure to neuromasts. There are two types of electroreceptor organs found in fishes (Evans 1993, 1998; Jobling 1995; Willmer *et al*. 2005; Evans & Claiborne 2006). One type, the ampullary receptor organs, is possessed by a wide variety of fishes from several taxonomic groups. These include sharks, skates, rays and chimaeras (Chondrichthyes), lungfishes and coelacanths (Sarcopterygi) and a range of ray-finned, bony fishes (Actinopterygii) that occur in both freshwater habitats and the sea, reedfishes (Polypteri), sturgeons and paddlefishes (Chondrostei) and some teleosts. Ampullary receptor organs are located in pits or recesses in the skin, and are connected to the skin surface by a canal that is filled with a gel that can conduct electric currents (Figure 2.5a). These electroreceptor organs are sensitive to low frequency (0.1–25 Hz) electric fields. Most of the fish that have ampullary receptor organs are marine; the high ionic concentration of seawater makes it a good conductor of electricity, and enhances the ease of detection of electrical currents. For example, most elasmobranchs and chimaeras are highly sensitive to weak electric fields. The electric sense is associated with structures called ampullae of Lorenzini, which open to the body surface in series of small pits. The electroreceptors are concentrated around the head in sharks and chimaeras, and over the upper and lower surface of the enlarged pectoral fins of skates and rays.

The ampullary receptor organs are used for passive electroreception, the detection of electric fields that originate from sources external to the fish that is receiving the signal. Several physiological functions of animals, such as the

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transmission of nerve impulses and muscle contraction, result in the generation of bioelectricity, so animals are surrounded by very weak electric fields. Fish that have ampullary receptor organs are able to sense these electric fields, and use electroreception for detecting prey (Evans 1993, 1998; Jobling 1995; Willmer *et al*. 2005; Evans & Claiborne 2006). Electroreception has much to recommend it as a sensory system for prey detection, because the conduction of electrical stimuli is rapid, and electrical signals have the advantage over visual stimuli that they are not diminished in turbid water. Electrical signals have advantages over chemical ones, both with respect to speed of transmission and also in being transient, because they give accurate information about the immediate presence of nearby animals.

The second type of electroreceptor organ is the tuberous receptor organ (Figure 2.5b). Tuberous receptor organs detect higher frequency electric fields (50 Hz to >2 kHz) than do ampullary receptor organs, and they are found on fishes that have an active electro-location system (Evans 1993, 1998; Jobling 1995; Willmer *et al*. 2005; Evans & Claiborne 2006). These fish generate electricity using specialised electric organs and then detect the electric fields produced using their tuberous receptor organs. The electric organs are most often highly-modified muscles, but in some species the electric organs are modified nerve cells. All the species that use active electrolocation occur in fresh water, mostly in Africa or South America, and the system is used in a variety of ways. It is used to detect prey, to assist with navigation and spatial orientation in turbid, murky water or at night, and also as a means to communicate with other fish. By modifying the amplitude, frequency and pulse length of the electric signals it produces, a fish can disseminate information about its species, sex and reproductive status, size and social status.

### 2.3.6 Chemoreception

#### *Taste and smell*

Chemoreception involves two major sensory systems, the sense of taste (gustation) and the sense of smell or olfaction (Caprio 1984; Lindemann 1996, 2001; Herness & Gilbertson 1999; Katz *et al*. 2000; Firestein 2001; Rust 2002; Wyatt 2003; Hara 2006). Olfactory input has an important influence upon many aspects of fish behaviour; food search and feeding, antipredator behaviour, reproduction, migration, individual recognition and social behaviours (Hara 1992, 2006; Smith 1992; Chivers & Smith 1998; Kats & Dill 1998; Wyatt 2003).

The sensory cells that make up the two chemosensory systems differ; olfactory cells have axons that go to the brain, whereas taste cells are secondary sensory cells that do not communicate directly with the brain (Caprio 1984; Hara 1992, 1994). The taste cells pass their sensory information to a nerve fibre, which, in turn, transmits the information to the brain. Taste cells, which are grouped in taste buds, can occur anywhere on the body surface, but are most concentrated within the oral cavity (Figure 2.6; Willmer *et al*. 2005). Irrespective of their location on the body, the taste buds connect to nerves that lead to different areas of the brain than do the nervous connections of the olfactory system. Further, the connections of the gustatory system do not have the complex level of integration and coding seen in the olfactory system. The numbers of sensory cells, ranges of substances that stimulate them, and the qualities of stimulatory substances that can be distinguished are all smaller for the sense of taste than for olfaction (Hildebrand 1995).

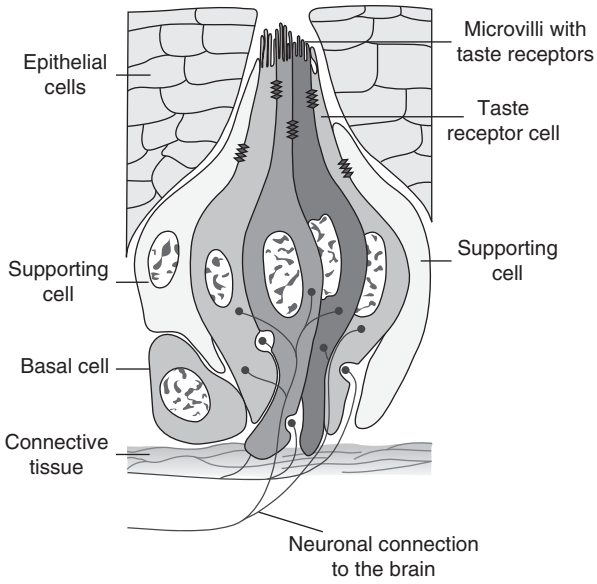


**Figure 2.6.** Structure of the taste bud in fish. Reproduced with permission from Willmer *et al*. 2005, courtesy of Wiley-Blackwell.

#### *Olfactory system*

The olfactory epithelium, localised within the nasal cavity, is made up of several cell types. Only one of the cell types, the olfactory receptor cell, has a chemosensory function (Figure 2.7). The other cell types have supportive or secretory functions. The olfactory receptor cells are bipolar sensory neurons that end in ciliated knob-like swellings that are exposed to the surface of the epithelium (Hara 1975, 1992, 1994; Caprio 1984; Hildebrand 1995; Firestein 2001). These

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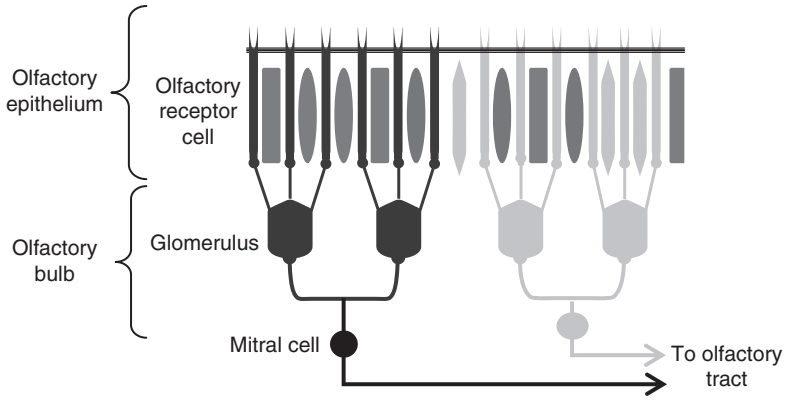


**Figure 2.7.** Schematic diagram of the organisation of the olfactory epithelium in fish.

cilia contain transmembrane olfactory receptors that interact with the odorants, binding to specific chemical features of the molecules concerned (Hildebrand 1995; Firestein 2001; Wyatt 2003; Stockhorst & Pietrowsky 2004; Alioto & Ngai 2005). Most odorants can bind to more than one olfactory receptor and most olfactory receptors can recognise several odorants. Thus, the recognition of an odorant depends upon which receptors are activated and to what extent, and this forms the basis of a 'coding' system that can be used by the nervous system for odour recognition. Olfactory receptor cells that express the same types of olfactory receptors occur in the same regions of the olfactory epithelium, leading to a concentration of the generation of molecular images in the olfactory sensory pathway (Figure 2.7).

Once an olfactory receptor has bound to an odorant, a series of events is initiated that leads to the generation of an electrical neural signal that is transmitted to the olfactory bulb along the olfactory nerve fibres. The olfactory bulb is a relay station; it receives the primary olfactory nerve inputs and sends its output signals to areas within the brain (Hara 1975, 1992, 1994; Caprio 1984; Hildebrand 1995; Stockhorst & Pietrowsky 2004). On entering the olfactory bulb, the olfactory receptor cell fibres intermingle and then terminate in glomeruli, where they form connections with other neurons (mitral cells. Figure 2.7), which convey the olfactory information to the brain (Hara 1992, 1994; Hildebrand 1995; Firestein 2001; Friedrich 2006). Olfactory receptor cells that express particular receptors tend to converge on a single target glomerulus within the olfactory bulb (Hara 1992; Firestein 2001). There are far more olfactory receptor cells and glomeruli than mitral cells, and the mitral cells interact with several receptor cells and usually connect to several glomeruli (Hara 1992; Friedrich 2006). This combination of multiple connections gives a high probability that the mitral cells will respond to the incoming olfactory signals.

Fish olfaction takes place in aquatic environments, so it is water-soluble compounds that most often stimulate the olfactory system (Caprio 1984). Several types of chemical compounds have been identified as potent odorants for fishes. These include amino acids, metabolites of sex steroid hormones, prostaglandins and bile acids (Hara 1975, 1992, 1994, 2006). The amino acids are likely to be the stimuli that play the major role in the olfactory detection of potential prey (see Chapters 5 and 6), whereas the other stimuli convey intraspecific communication information, such as that associated with reproduction (see Chapter 10) or predation risk (see Chapter 8; Hara 1992; Smith 1992; Wisenden 2000; Wyatt 2003; Andersson *et al*. 2006).

### *Gustatory system*

The sensory unit of the gustatory system is the taste bud (Figure 2.6). In fish, taste buds may be located both within the mouth and pharynx (intraoral gustatory system) and on the lips, barbels, fin rays and on the skin, particularly in the head region close to the mouth (extraoral gustatory system. Caprio 1984; Hara 1992, 1994 2006; Lamb 2001; Kasumyan & Døving 2003; Ishimaru *et al*. 2005). The possession of both an intraoral and extraoral gustatory system is rare amongst vertebrates. The high abundance of taste buds is another peculiarity of the fish gustatory system; densities of taste buds appear to be higher in fish than in any other animals. Input from the extraoral gustatory system reaches the brain via the trigeminal and facial nerves (cranial nerves V and VII), gustatory information from the anterior part of the oral cavity reaches it via the glossopharyngeal nerve (cranial nerve IX) and information from within the mouth and pharynx is transmitted by the vagus nerve (cranial nerve X).

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The taste buds are barrel- or onion-shaped structures that contain numerous taste receptor cells, perhaps 50–100 in number (Figure 2.6). The taste receptor cells are bipolar cells that have microvilli bearing the taste receptors in contact with the external environment (Caprio 1984; Hara 1992). When the taste receptors bind to an active chemical (or tastant), the receptor cell is activated and, through complex messenger systems, various transmitter substances, for example, norepinephrine (noradrenaline), serotonin and glutamate, are released from the taste receptor cell (Lindemann 1996, 2001; Herness & Gilbertson 1999; Katz *et al*. 2000; Ishimaru *et al*. 2005). The taste receptor cells connect with sensory neurons, and the release of the transmitter substances from the cells causes excitation of these neurons; these carry the gustatory signals to central sites, where taste processing occurs.

The fact that responses are shown to the presence of nutrients and other chemicals in the gastrointestinal (GI) tract means that there must be gustatory sensors, or a sense of 'taste', within the tract. Sensors of various types are found in the intestinal epithelium, including chemoreceptors, mechanoreceptors and receptors that are sensitive to changes in pH (Buchan 1999; Raybould 1999, 2002; Katz *et al*. 2000; Shanahan 2000; Guilmeau *et al*. 2004; Strader & Woods 2005). Once the stimulatory input has been detected and encoded by the sensory cells, messages of neural, endocrine or immune nature are disseminated from the GI tract to several different target organs and tissues.

Overall, the fish gustatory system is able to detect what humans experience as the four classical taste stimuli (sweet, sour, bitter and salty), as well as a wide variety of amino acids, amines, sugars, organic acids and other compounds (Caprio 1984; Hara 1992, 1994; Lamb 2001; Kasumyan & Døving 2003; Härlin 2005; Yamashita *et al*. 2006). This means that, in combination, the extraoral and intraoral components of the fish gustatory system are ideally suited for the role of distinguishing nutritive, beneficial compounds and foods from those that are potentially harmful or toxic (see Chapters 5 and 6). The gustatory and other receptors in the GI tract and the neural and chemical signalling systems that link them to the CNS and other systems are ideally suited to control appetite and feeding in fish and how they do so is described in Chapter 7.

## 2.4 INTERNAL COMMUNICATION SYSTEMS

### 2.4.1 Role of the neural and endocrine systems

Transmission, integration and co-ordination of sensory input is achieved by the nervous and endocrine systems, each of which transmits signals to a variety of effector organs. The nervous system transmits signals via electric-nervous pathways, whereas the pathways of signal transmission of the endocrine system are hormonal–humoral. These neural and hormonal–humoral signals serve to regulate a variety of body functions, and the regulation is also dependent upon a two-way exchange of information between a control centre and an effector organ (Evans 1993, 1998; Jobling 1995; Willmer *et al*. 2005; Evans & Claiborne 2006). A major difference between the nervous and endocrine systems is concerned with the speed at which they transmit information from the control centre to the effector organs. The nervous system is specialised for the rapid transmission of signals from one point to another, whereas the endocrine system is better suited for the slow transmission of signals. The endocrine system employs the circulatory system for distributing its hormonal messengers, so the signals become widely distributed throughout the body.

### 2.4.2 The nervous system

#### *Components of the nervous system*

The neuronal networks of the nervous system consist of afferent and efferent neurons, with interneurons as linking units. Afferent neurons carry information from peripheral receptors to sites within the CNS and efferent neurons convey information from the CNS to the effector organs. The nervous system can be broadly divided into somatic and autonomic compartments. The somatic nervous system mediates the information from the sensory systems via afferent nervous inputs running from the sense organs to the CNS, and most of the processing of sensory information takes place in the CNS. There are efferent nervous connections between the CNS and skeletal muscles via the somatic nervous system, and much of the somatic nervous activity is under voluntary control. The nervous supply that serves to regulate the functions of most of the internal organs, for example, the heart and blood vessels and GI tract, comprises the autonomic nervous system (ANS). In the periphery the ANS and somatic nervous systems are functionally and anatomically almost entirely separate. Within the CNS the two systems come into intimate contact and connections exist between the two for information exchange and co-ordination of overall function (Evans 1993, 1998; Jobling 1995; Willmer *et al*. 2005; Evans & Claiborne 2006).

#### *Autonomic nervous system*

The ANS is essentially an efferent system that transmits information to the internal organs, but it does have an afferent component that carries information from receptors in the inner organs. Unlike the somatic nervous system the ANS is, for the most part, not subject to voluntary control. The ANS is primarily involved in controlling bodily functions via reflex

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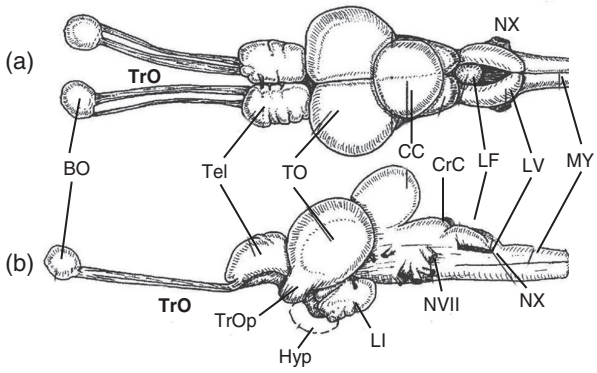


**Figure 2.8.** Structure of the brain of a roach (*Rutilus rutilus*). (a) Dorsal view (b) Lateral view. BO = olfactory bulbs. TrO = olfactory tract. Tel = telencephalon. TO = optic tectum. TrOpt = optic tract. Hyp = hypophysis. LI = inferior lobe. CC = cerebellum. CrC = cerebellar crest. LF = facial lobe. LV = vagal lobe. MY = myelencephalon. NVII = facial nerve. NX = vagus nerve. Reproduced from Kotrschal *et al.* (1998), courtesy of Springer.

arcs. Visceral or somatic afferent fibres convey information from the receptors, and the ANS provides the efferent fibres that transmit the reflex response. Such responses include contraction or relaxation of smooth muscles and the functioning of the heart and endocrine organs. Simple reflexes can be completed within one organ, but more complex activities, involving several organ systems, are controlled by higher centres within the CNS. The major site of integration of ANS activity is the hypothalamus (see below). Within the hypothalamus the functions of the ANS are co-ordinated with those of the somatic nervous system. The hypothalamus also plays a major role in the integration of the activities of the nervous and endocrine systems (Evans 1993, 1998; Jobling 1995; Willmer *et al.* 2005; Evans & Claiborne 2006).

### *Brain and CNS*

The brain, which is within the skull that protects it from damage, has a series of lobes (Figure 2.8), each of which has a well-defined functional role, but with some brain areas being implicated in the integration and co-ordination of inputs from several sensory systems. Sensory signals are conveyed to the brain via the cranial nerves and their branches. Olfactory stimuli give rise to signals that pass along the olfactory nerves (cranial nerve I) to the olfactory tracts. The nerve fibres from the olfactory system ultimately reach the telencephalon where there is integration of the olfactory signals. The terminal nerve (cranial nerve 0), associated with the olfactory system, may have sensory functions related to the detection of sexual pheromones. Depending upon species, the olfactory bulbs may be either located close to the olfactory organ, or may be situated in close contact with the telencephalon. In the former case the olfactory nerves are short and the olfactory bulbs are separated from the telencephalon by long olfactory tracts.

The diencephalon is divided into three regions; the epithalamus, the thalamus and the hypothalamus. The epithalamus is mainly made up of the pineal organ, which lies on the uppermost surface of the brain. The pineal organ is light-sensitive and is involved in the regulation of the physiological activities that vary in relation to changes in the light:dark cycle, on a daily and seasonal basis. The photoperiod-dependent influences of the pineal organ are mediated via the production and release of an endocrine factor, melatonin, production and release of which is highest at night. Large numbers of nerve fibres run through the thalamus to the hypothalamus, the major integrative centre of the brain. Afferent fibres from the sensory systems converge in the hypothalamus, and efferent pathways from the hypothalamus lead to other regions of the brain, for example the telencephalon, medulla, thalamus and cerebellum, the pituitary gland and several internal organs.

The mesencephalon, or mid-brain region, is commonly known as the optic lobes. Sensory impulses from the eye reach the brain via the optic nerves (cranial nerve II), passing along the optic tracts to the optic lobes, which are primarily concerned with the processing of visual information. Integration of the sensory inputs that lead to changes in swimming activity and positional changes occurs in the cerebellum, and this region of the brain receives inputs, either directly or indirectly, from all the sensory systems. The medulla oblongata is the region of the brain most closely allied to the spinal cord, and it is often difficult to distinguish a clear boundary between the two. There is a close association between the medulla oblongata and the cranial nerves that carry impulses to and from the skin and lateral line, gustatory system and viscera. As such, the medulla oblongata both receives a range of sensory inputs, and transmits efferent motor impulses.

The sensory cells of the gustatory system are concentrated in the mouth, but there are also components of the gustatory system on the anterior part of the body and its appendages. Sensory inputs from the gustatory system are conveyed to the brain by branches of cranial nerves V, VII, IX and X. Impulses from the inner ear reach the brain via the auditory nerve (cranial nerve VIII), but this nerve does not have branches to the lateral line. The lateral line in the head region is innervated by branches of cranial nerves V

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and VII, whereas the lateral line canal that runs along the body has connections via the vagus (cranial nerve X) and glossopharyngeal (cranial nerve IX) nerves. The vagus nerve (cranial nerve X) contains both afferent (sensory) and efferent (motor) neurons, and is the most important conveyer of information to and from the CNS to the internal organs (Evans 1993, 1998; Jobling 1995; Willmer *et al*. 2005; Evans & Claiborne 2006).

### 2.4.3 The endocrine system

#### *Chemical messengers*

Chemical messengers operate in a variety ways. Neurotransmitters operate over very short distances, conveying information from one neuron to another or from a neuron to an effector cell. When chemical messengers are secreted from neurons and enter the blood they are termed neurohormones or neuroendocrines. Chemical messengers may just affect the cell from which they were secreted, may diffuse over short distances to affect nearby cells, or may be secreted into the blood and affect cells that are some distance from the site of release, in which case they are called endocrine messengers, or hormones. Thus, hormones are synthesised in specific hormone-producing cells and, following release into the blood, act on targets that may be other hormone-producing glands or non-endocrine effector organs. Many hormones circulate simultaneously, so there must be ways in which the hormone and its specific target organ(s) recognise each other; the target has receptors for the hormone, and recognition is achieved when the hormone binds to the receptor. In addition, chemical messengers can be used to pass information between animals of the same or different species, in which case they are known as semiochemicals (Evans 1993, 1998; Jobling 1995; Willmer *et al*. 2005; Evans & Claiborne 2006).

#### *Brain, hypothalamus and pituitary*

The release of hormones often occurs on receipt of signals from the peripheral sense organs by the brain. Within the brain such signals are integrated within the hypothalamus; stimulation of the hypothalamus initiates the synthesis and release of hypothalamic messengers, releasing hormones and inhibitory factors. Synthesis of such messengers occurs in nerve cells within the hypothalamus, and the releasing hormones or inhibitory factors are released following stimulation of these cells. Hypothalamic-releasing hormones and inhibitory factors are neuropeptides that have effects upon the production and release of hormones from the pituitary gland (or the hypophysis), located directly below the hypothalamus, to which it is connected by a stalk. The pituitary gland consists of two lobes; the adenohypophysis and the neurohypophysis. The hypophysial stalk contains nerve fibres that run from the hypothalamus to both lobes of the pituitary gland (Figure 2.9; Jobling 1995). The adenohypophysis is the site of synthesis, storage and release of several peptide hormones. The hormones that are released from the neurohypophysis are not produced there, but are transported from their site of production in the hypothalamus.

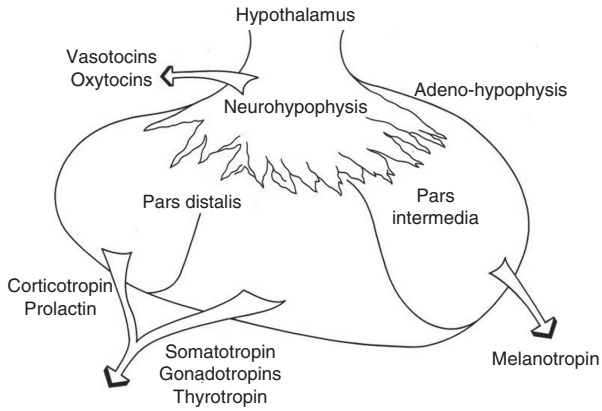


**Figure 2.9.** The pituitary gland and its link to the hypothalamus in fish. The adenohypothesis of the pituitary is made up of the *pars distalis*, site of secretion of most hormones, and the *pars intermedia*. Reproduced from Jobling 1995. With kind permission from Springer Science + Business Media B.V.

In addition to links between the hypothalamus and the pituitary gland, there are also neuronal connections from the hypothalamus to some other endocrine tissues (Figure 2.10; Jobling 1995). Connections of this type include those associated with the GI tract and the chromaffin tissue of the head kidney. The chromaffin tissue is located close to the posterior cardinal veins, large blood vessels that carry the venous blood returning from the body direct to the heart. Catecholamines released from the chromaffin tissue are, therefore, dispersed rapidly throughout the body in the blood. Catecholamine concentrations in the blood are usually low, but they increase in response to emergency conditions. The neuronal links between the hypothalamus and the chromaffin tissue ensure that there is a rapid release of catecholamines following detection of an acute emergency, and the fact that the catecholamines are liberated into blood that drains into the heart ensures that they are rapidly distributed to all parts of the body. This means that the time between the detection of an emergency situation and point when the catecholamines come into contact with their targets is

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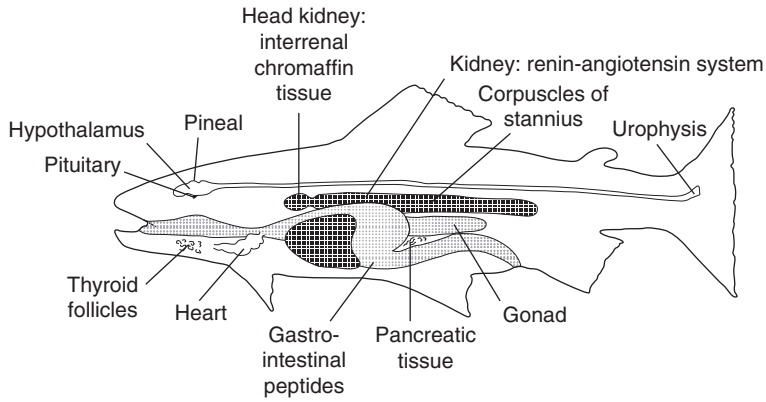


**Figure 2.10.** The location of the main endocrine organs in fish. Reproduced from Jobling 1995. With kind permission from Springer Science + Business Media B.V.

short. As such, this combination of neuronal and hormonal transmission of signals is well-suited to bringing about rapid responses in widely dispersed target tissues.

### *Fish hormones*

The endocrine system of fish, which is similar to that of mammals, is highly complex and involves many different chemical messengers; this section describes some of these, concentrating on those that are of most relevance to how fish behave. The role of hormones in the control of specific aspects of behaviour is discussed in the relevant chapters. Three main groups of hormones are recognised on the basis of chemical structure; peptides and glycopeptides, hormones derived from specific amino acids and the steroid hormones (Evans 1993, 1998; Jobling 1995; Willmer *et al*. 2005; Evans & Claiborne 2006).

Peptide hormones are produced in the hypothalamus and pituitary, the heart, the GI tract and associated organs, the corpuscles of Stannius and the urophysis (Figure 2.10). The hormones of the pituitary neurohypophysis are the vasotocins and oxytocins, involved in salt and water balance, and in the co-ordination of reproductive functions. The hormones of the adenohypophysis are the gonadotropins (GTHs), growth hormone (GH or somatotropin), adrenocorticotropic hormone (ACTH or corticotropin), thyroid-stimulating hormone (TSH or thyrotropin), prolactin and melanocyte-stimulating hormone (MSH or melanotropin). The majority of these hormones are synthesised by cells within the *pars distalis*, but MSH derives from cells located within the *pars intermedia*. The GI tract is the site of production of many peptide hormones, most of which act on the gut and its associated organs. The majority of the gut peptides play a role in the control of digestion, by influencing gastrointestinal motility, enzyme secretion or nutrient absorption. For example, cholecystokinin (CCK) has an effect on gut motility, the secretion of enzymes from the pancreas and the release of bile from the gall bladder. In addition, CCK has an influence upon feed intake (see Chapter 7).

Osmoregulation is a major problem for fish, and a large number of hormones are involved in this process. Atrial natriuretic peptide (ANP), released from the heart, is a peptide involved in blood volume regulation, and in salt and water balance. Glycopeptide hormones produced by the corpuscles of Stannius, small spherical bodies that lie on, or embedded within, the kidney, are also involved in the control of the ions present in body fluids. The urophysis is a neurosecretory area at the caudal tip of the spinal cord that produces vasoactive peptides (urotensins) that are released into the blood in response to an excessive loading of body salts. These hormones are critical for effective body function in fish, but do not influence fish behaviour directly, so are not considered further in this book.

The steroid hormones are usually bound to proteins for transport in the blood; for example, the sex steroid hormones bind to globulin and cortisol is transported bound to transcortin. The steroid hormones differ from the peptide hormones in that they are have an affinity for lipid (or are lipophilic), and can cross cell membranes and enter the target cells to exert their effects. This is the usual mode of action of the steroid hormones, but there are also cell membrane receptors for some of the steroid hormones. Once they have entered the target cell, the steroid hormones bind to specific receptor proteins in the

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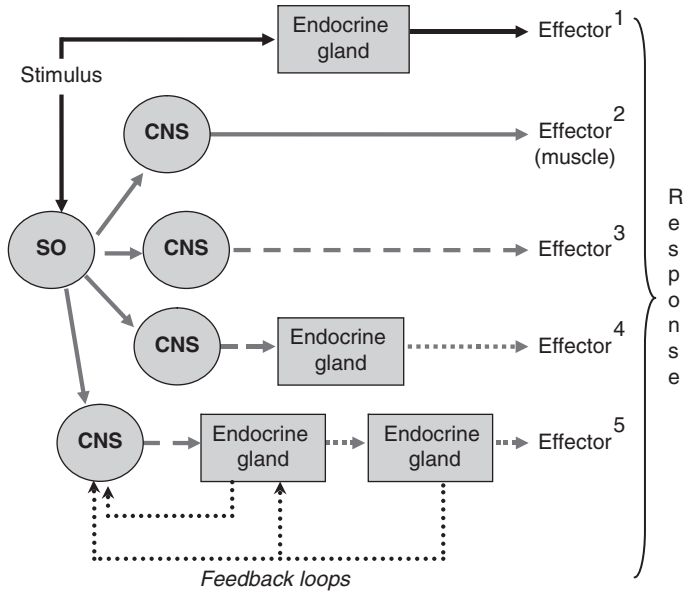


**Figure 2.11.** Schematic representation of the interaction between chemical messengers (local and humoral) and the nervous system in the control of biological processes. SO: sense organ. Black arrows: positive or negative feedback: Solid grey arrow: nerve. Dashed grey arrow: Dotted grey arrow: hormone. 1: Direct endocrine link. 2: Neural reflex arc. 3: First-order neuroendocrine link. 4. Second order neuroendocrine link. 5. Third order neuroendocrine link. Reproduced with permission from Willmer *et al.* 2005, courtesy of Wiley-Blackwell.

cytoplasm. The hormone-receptor complex then attaches to sites within the cell nucleus where it induces changes in protein synthesis.

Steroid hormones are stored in very limited quantities at their sites of production (the gonads and interrenal tissue), and are synthesised as needed. Cholesterol is the precursor for all the steroid hormones and it is converted to pregnenolone, from which all the steroid hormones can be derived via a series of chemical steps involving removal or addition of carbon atoms. Progesterone is a female sex hormone and can also be converted into other steroids. The corticosteroids are produced in the interrenal tissue, cortisol being the the main corticosteroid in fish, acting both as a stress hormone, and in the regulation of salt and water balance. Both the male and female sex hormones are also steroids. The male sex hormones, or androgens, include testosterone and 11-ketotestosterone, whereas the female sex hormones are oestrogens, such as oestradiol.

The thyroid hormones and catecholamines are derived from the amino acid tyrosine. The catecholamines epinephrine (adrenaline) and norepinephrine (noradrenaline) are produced in the chromaffin tissue and are secreted into the blood under stress conditions. Melatonin, secreted from the pineal gland, has tryptophan as its precursor. This hormone is secreted in response to changes in the light:dark cycle with synthesis and secretion being greatest during the hours of darkness. The precisely regulated circadian melatonin rhythm imparts important time-of-day information, providing information about both day (low melatonin) and night (high melatonin), and also about seasonal changes. In other words, melatonin levels vary directly with the variations in the light:dark cycle, and seasonal changes in daylength, which are most exaggerated at high latitudes. Changes in daylength have important influences upon biological systems. For example, many species use changes in the light:dark cycle as the major cue for the timing of their reproductive cycles and breeding (see Chapter 10). The existence and control of daily rhythms of biological activity has implications for all aspects of behaviour.

### 2.4.4 Cross-talk between the nervous and endocrine system

In complex animals such as fish, co-ordination and control of biological processes can be achieved by chemical messengers that act locally, by the release of regulatory chemicals (hormones) into the blood, or via nervous mechanisms (Figure 2.11; Evans 1993, 1998; Jobling

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1995; Willmer *et al*. 2005; Evans & Claiborne 2006). The chemical and nervous control systems have been viewed as being distinct, but the systems are closely allied within the hypothalamus where there is much exchange and integration of information. There are also links between the endocrine and nervous systems through use of common chemical messenger substances, such as catecholamines that may act as both neurotransmitters and endocrine factors. Several of the regulatory peptides are also multifunctional. In other words, regulatory peptides can occur in both endocrine cells and neurons and, depending on location in the body, can act in different ways. For example, CCK may act as a neurotransmitter, local chemical messenger or as a hormone. In addition, individual neurons may produce and release 4 or more neurotransmitters, and the differential release of transmitter substances allows for the chemical encoding of a wide range of messages.

Some physiological processes are regulated by relatively simple endocrine, neural or neuroendocrine links, but many aspects of fish physiology and the control of behavioural responses involve regulation by more complex links that include cross-talk between the nervous and endocrine systems (Figure 2.11; Willmer *et al*. 2005). These links will often incorporate a considerable degree of feedback control. Feedback control may, for example, involve direct effects of hormonal release on the hypothalamus, but there are also several other types of feedback mechanisms. For example, one hormone may stimulate release of a second hormone from a target organ, and the second hormone can provide the feedback signal to either the hypothalamus and/or the endocrine organ that was the source of the first hormone. In addition, hormones released from endocrine target organs may produce metabolic changes in their own targets, and the end-products of these metabolic reactions can also function as feedback signals to the hypothalamus and endocrine organs. Finally, feedback may occur via neuronal routes, with certain neurons being stimulated by the chemical messengers released from endocrine glands (Figure 2.11; Evans 1993, 1998; Jobling 1995; Willmer *et al*. 2005; Evans & Claiborne 2006). The end result of such complex feedback systems is that the functioning of biological systems, including those related to behaviour, is finely tuned to both external events and internal state.

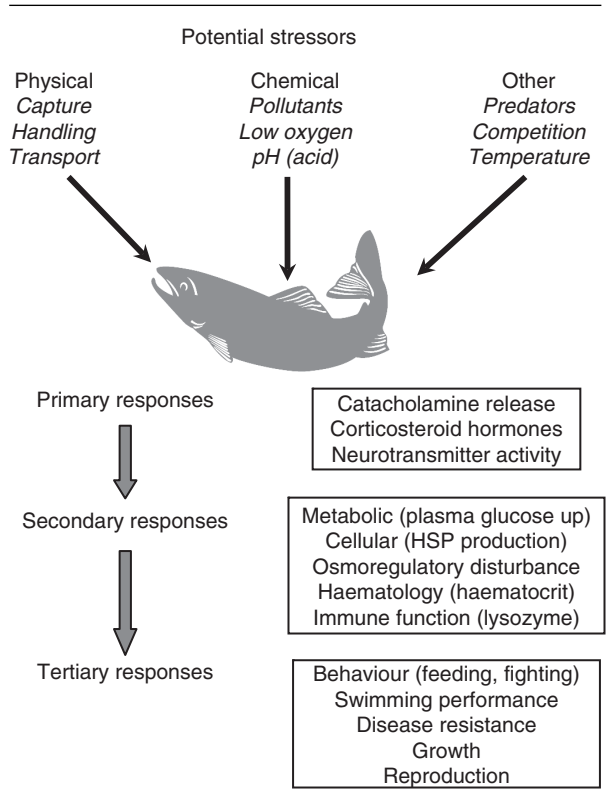


**Figure 2.12.** Schematic representation of environmental stressors and the hierarchy of the stress response in fish.

## 2.5 COPING WITH ADVERSE CONDITIONS

### 2.5.1 Unpredictable environments

Fish use environmental cues such as changing day length (photoperiod) and temperature to 'predict' the future, and they adjust their lives in accordance with the predictable seasonal cycles. Superimposed upon these predictable environmental cycles are unpredictable environmental perturbations that have the potential to disrupt the normal progression of life. Such unpredictable disturbances are usually of short duration, and are often referred to as environmental stressors. Many changes in abiotic factors could be stressors; these might be habitat deterioration resulting from natural events such as storms or man-made events such as industrial and sewage effluents. Biotic changes that could be stressors include increased numbers of predators, decreased food resources, outbreaks of disease, increased infestation with parasites, changes in numbers of competitors, or changes in status within a social group. Cultured fish will be exposed to many such abiotic and biotic stressors (Figure 2.12).

The fish must be able to make rapid, short term adjustments to their physiology and behaviour to accommodate such stressors, even though these adjustments will be disruptive to normal life in the short term. Once the emergency passes, the fish can resume normal life. The

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short term adjustments made upon being exposed to an environmental disturbance serve to direct the individual into survival mode, and such adjustments are usually categorised as stress responses**.** The stress responses may involve dramatic changes in behaviour and physiology that can occur within minutes to hours of exposure to the environmental stressor (Figure 2.12; Evans 1993, 1998; Jobling 1995; Iwama *et al*. 1997; Adams 2002; Willmer *et al*. 2005; Evans & Claiborne 2006).

These physiological and behavioural changes usually enable the fish to avoid the potentially deleterious effects that might accrue if exposure to the stressor were prolonged for days or weeks, in other words, if they experienced chronic stress. The acute responses to perturbations in the environment may therefore reduce the risk of damage that would occur under chronic stress, and thereby serve as an effective means for coping with a short-term emergency. Nevertheless, when fish experience disturbances that lie outside the normal range, the effects may be dramatic. In the case of a severe disturbance the fish may die almost immediately, and long-term exposure to less severe disturbances can also result in death of certain individuals within the population. In addition, the exposure to stressors may result in changes that, whilst not being lethal, impair the ability of the fish to function normally.

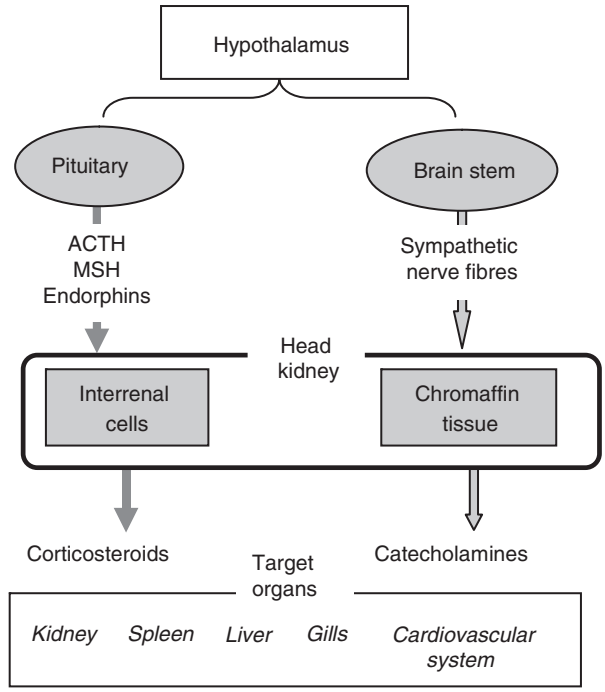


**Figure 2.13.** Schematic representation of the communication pathways and processes involved in the primary stress response.

### 2.5.2 The stress response

Exposure of fish to environmental stressors induces a characteristic series of endocrine, and other, responses. These are termed primary, secondary or tertiary depending upon the level of biological organisation being monitored. Primary stress responses describe changes at the endocrine level, whereas tertiary responses refer to those changes that involve the whole animal (Figure 2.12; Evans, 1993, 1998; Jobling 1995; Iwama *et al*. 1997; Adams 2002; Willmer *et al*. 2005; Evans & Claiborne 2006).

#### *Primary stress responses*

Detection of adverse stimuli leads to the activation of afferent neural pathways that run in sympathetic nerve fibres of the autonomic nervous system from the hypothalamus to the chromaffin tissue (Figure 2.13). Direct stimulation of cholinergic receptors in the chromaffin tissue leads to the rapid release of catecholamines, and plasma levels of catecholamines may increase several-fold within a few minutes. The catecholamines are then widely distributed throughout the body in the blood, and they initiate effects in other organ systems, such as the cardiovascular and respiratory systems. Exposure to stressors may also have profound effects on brain monoaminergic systems, specifically those involving the neurotransmitter catecholamines (dopamine and its derivatives) and indoleamines (serotonin and its derivatives). The brain monoamines change following exposure to stressors such as ammonia, heavy metals and handling, but it is the responses to social stressors that have been most studied. These neurotransmitters are involved in behavioural changes associated with feeding, swimming activity and aggressive interactions.

Neurons that run from the hypothalamus to the pituitary gland stimulate production and secretion of ACTH (Figure 2.13). The ACTH is transported to the head kidney in the blood, where it stimulates interrenal cells to produce and release corticosteroid hormones, particularly cortisol (Figure 2.13). ACTH is the most important tropic hormone for corticosteroid hormones in fish, but cortisol secretion is also influenced by other substances, including MSH. Since there are close links between the hypothalamus, the release of ACTH and cortisol secretion, acting as a cascade, it has become usual to refer to this series of interactions as being governed by the hypothalamic–pituitary–inter-renal axis

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(HPI axis; Evans 1993, 1998; Jobling 1995; Iwama *et al*. 1997; Adams 2002; Evans & Claiborne 2006).

In addition to having cells that produce and secrete catecholamines and corticosteroids, the head kidney also contains tissue of the immune system. Cellular components of the immune system, such as leucocytes, produce a range of protein signalling molecules or cytokines, such as interleukins and tumour necrosis factor, that may have modulatory influences upon other endocrine signals. Immune tissues also produce ACTH and MSH and through these can have a direct influence on the HPI axis. Information exchange between the immune and endocrine systems is bidirectional; leucocytes and the tissues of the spleen have receptors for corticosteroids and catecholamines, implying that the immune system can respond directly to endocrine signals from the HPI axis. In addition, there is a direct innervation of the spleen via sympathetic fibres of the autonomic nervous system; contraction of the spleen under nervous stimulation leads to release of red blood cells (erythrocytes) into the circulation when fish are subjected to certain environmental stressors such as hypoxia or exhaustive swimming activity. The liver, gills and kidneys are target organs for corticosteroids, and catecholamines and corticosteroids have a major impact on the cardiovascular system to influence rates and patterns of blood flow to the body organs (Figure 2.13).

### *Secondary stress responses*

Coping with stress is energy-demanding, and the physiological adjustments are directed towards increased delivery of oxygen to the tissues, and increased substrate mobilisation and utilisation to meet the increased energy demand. The primary stress responses, release of catecholamines and cortisol, trigger a broad suite of biochemical and physiological changes that lead to changes in mobilisation and metabolism of respiratory substrates, cardiovascular and respiratory functions, status of the blood (the number of blood cells and concentration of haemoglobin) and immune functions (Evans 1993, 1998; Jobling 1995; Iwama *et al*. 1997; Adams 2002; Evans & Claiborne 2006).

A major role of the catecholamines is to modulate cardiovascular and respiratory functions, thereby maintaining oxygen supply to the tissues. The effects include increased blood flow to the gills, and changes in gill permeability and in the rate of movement of water across the respiratory surfaces to enhance oxygen uptake. These changes lead to increased salt and water fluxes across the gill membranes, and this can create ionic and osmotic imbalances. In freshwater fishes, there may be a loss of ions, such as sodium and chloride, and increased influx of water leading to reduced plasma osmolality. The increased water influx results in an increase in urine production. Marine fishes may experience an increase in ion influx, and increased water loss over the gills, leading to an increase in the osmotic concentration of the blood.

The catecholamines also play a central role in the mobilisation of respiratory substrates via the rapid stimulation of the breakdown of tissue glycogen to glucose, primarily in the liver. The cortisol released into the blood from the inter-renal cells also has metabolic effects, contributing to the increase in plasma glucose concentrations via enhanced conversion of amino acids into glucose in the liver. In other words, the immediate elevation in plasma glucose concentration following exposure to a stressor is due to glycogen breakdown stimulated via catecholamines, whereas the longer-term maintenance of glucose is mediated by cortisol-induced production of glucose from amino acids.

Fish cells respond to a rapid elevation in temperature by synthesising heat-shock proteins (HSPs). There are several proteins that belong to the HSP family, some of which have regulatory transport functions within the cell. Others accumulate around, and bind to, various structures within the cell and hinder the initiation of deleterious changes to the structural proteins. The synthesis of HSPs increases thermotolerance, so one role of HSPs is to protect cells against the pathological effects of heat. HSPs are synthesised following exposure to a range of stressors, including heavy metals and other chemical agents, radiation and viral infections, so they are probably best considered as generalised stress proteins produced as a cellular response to exposure to adverse environmental conditions. The HSPs start to accumulate within an hour after exposure to stressors, and concentrations remain elevated under conditions of long-term, or chronic, exposure to the stressor. Cortisol mediates the expression of HSPs, suggesting that there are important links between the endocrine stress axis and cellular stress responses.

### *Tertiary stress responses*

The secondary stress responses, which lead to rapid mobilisation of energy reserves, are adaptive mechanisms that typically persist for only a few hours or days following exposure to the stressor and they do not result in any serious deleterious effects. In contrast, chronic exposure to stressors can induce a number of pathological changes, and can lead to reductions in reproductive success, depression of growth rates, and decreased disease resistance (Evans 1993, 1998; Jobling 1995; Iwama *et al*. 1997; Adams 2002; Evans & Claiborne 2006). Nonetheless, some of these tertiary responses can be adaptive, such as

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when wild fish fail to breed under conditions that would compromise the survival of their eggs and larvae.

Exposure of fish to many types of environmental stressor may result in increased susceptibility to a wide range of pathogens, including viruses, bacteria, fungi and protozoans. The susceptibility to disease seems to be the result of associations between cortisol and the immune system; increased plasma concentrations of cortisol can lead to immunosuppression. Corticosteroids may exert their influences upon the cells of the immune system in three main ways; by inducing programmed cell death (apoptosis) of lymphocytes, by reducing the numbers of circulating leucocytes, and by inhibiting cytokine production. The end results of these actions are reduced proliferation of leucocytes, which are white blood cells, changes in phagocytic (pathogen-engulfing) activity of immune cells, reductions in numbers of antibody-producing cells, and reductions in levels of virus-neutralising, and other, antibodies.

Exposure to stressors also leads to reductions in feeding. Reductions in feeding, accompanied by the catabolic effects of other endocrine changes, results in reduced rates of protein synthesis and growth. Inhibition of development and growth in stressed fish may be mediated by the effects of elevated concentrations of cortisol on production of myostatin, a messenger that influences muscle cell formation and development, as well as cell proliferation and differentiation in a range of tissues.

Reproductive performance is also affected by stress, adverse effects being related to interference with the functioning of the hypothalamic–pituitary–gonadal (HPG) axis. Cortisol is implicated in mediating the suppressive effects of stress on reproduction. Chronically elevated plasma cortisol concentrations have been linked to reductions in hypothalamic gonadotropin-releasing hormone (GnRH), and decreases in circulating concentrations of gonadotropins and sex steroid hormones. Thus, it seems that cortisol has the potential to exert an influence at several points in the endocrine cascade that makes up the HPG axis. The end results of the disturbances in the endocrine cascade may be inhibition of egg production, maturation and release in females, reduced fecundity as a result of increased atresia of developing eggs, reduced egg size as a result of interference with production of yolk components, lower sperm counts in males, reduced fertilisation rates of eggs and poorer survival of eggs, and increased mortality of developing embryos and larvae (Evans 1993, 1998; Jobling 1995; Iwama *et al*. 1997; Adams 2002; Evans & Claiborne 2006; Kah *et al*. 2010).

Thus, when fish are exposed to environmental stressors a hierarchy of responses is initiated, and if the stress is severe or long-lasting, successively higher levels of biological organisation become affected. The cumulative effects of prolonged exposure to environmental stressors at sublethal levels may affect disease resistance, growth and reproductive success, which, in turn, may reduce recruitment to successive life stages and, eventually, cause population numbers to decline (Evans 1993, 1998; Jobling 1995; Iwama *et al*. 1997; Adams 2002; Evans & Claiborne 2006; Kah *et al*. 2010).

## 2.6 CONTRASTS IN LIFE HISTORY PATTERNS AND REPRODUCTIVE BIOLOGY

The ultimate goal in the life of individuals is to breed and produce viable offspring. There are many ways in which this goal can be achieved, and the array of reproductive arrangements found in fish is extraordinarily diverse (Chapter 10). For example, several species of fish are hermaphroditic, some being male and female at the same time and others undergoing a sex change during the course of their lives; the sex change can be from male to female, or vice versa. In most fish species the sexes are distinct and there is not normally a sex change, but even here sex may not be irrevocably fixed by genetic constitution. It is possible to induce sex change by manipulating the environment to which the fish is exposed during early development (Hoar & Randall 1988a, b; Jobling 1995; Devlin & Nagahama 2002; Kah *et al*. 2010). While such variability is particularly relevant to reproductive behaviour, and so is discussed further in Chapter 10, it has implications for many aspects of fish behaviour so is considered briefly here.

### 2.6.1 Reproductive options

Most of the teleost species that are farmed (Chapter 1) have their sexes separate and do not undergo sex-change, but some are hermaphrodites that change sex during the course of their lifetime; these include sea basses (Serranidae), barramundi and snooks (Latidae and Centropomidae), and sea breams and porgies (Sparidae; Le Francois *et al*. 2010). In addition, most teleosts are egg-layers (oviparous), but about 500 species (about 2% of teleosts) are live-bearers, in which fertilisation is internal and the females give birth to live offspring. Several live-bearers have attained popularity as aquarium fishes, including the guppy (*Poecilia reticulata*), a range of mollies (*Poecilia* spp.), platyfishes and swordtails (*Xiphophorus* spp.), and mosquitofishes (*Gambusia* spp.) that are reared both for display in aquaria and as pest control agents. In these species the males have the anterior rays of the anal fin elongated to form the gonopodium that is used to transfer sperm to the female.

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***Live-bearers***

In all live-bearing teleosts gestation of the fertilised eggs and developing embryos occurs within the ovary, so the ovary is both the site of egg production and the place where fertilisation and early development occur. In many live-bearing species the embryos are wholly dependent upon the nutrients present in the egg yolk, leading to a condition known as ovoviviparity; the developing embryos are gestated within the body of the mother, but are not provided with additional nutrients over and above those already present in the egg. In truly viviparous species the developing embryos derive some nutrients from their mother and this usually requires special adaptations of both maternal and embryonic tissues. The developing embryos may, for example, take up nutrients from ovarian secretions via the gut, gills, enlarged fin-folds or the yolk-sac membrane, or there may be establishment of more intimate contact between the maternal and embryonic tissues with the formation of a placental connection; adaptations of these types are seen in surf-perches (Embiotocidae), klipfishes (Clinidae) and the four-eyed fishes (Anaplepidae; Hoar & Randall 1988a, b).

***Egg-layers***

The vast majority of teleosts are oviparous, but within this framework there are large interspecific differences with respect to the numbers of offspring produced, and the degree of protection and care given to the developing eggs and young by the parents. Nevertheless, common characteristics that define the oviparous species are the development of the fertilised egg outside of the body of the female, derivation of the nutrients for the developing embryo from the egg yolk and the occurrence of hatching when the eggshell or capsule is broken. In most oviparous teleosts the eggs are released prior to fertilisation, but in a few species, including wolf-fishes (*Anarhichas* spp.), there is thought to be internal fertilisation and then release of the eggs (Hoar & Randall 1988a, b; Jobling 1995; Moksness *et al*. 2004; Kah *et al*. 2010).

Oviparous species display variation that ranges from the production of large numbers of freely-floating pelagic eggs at one extreme to parental care of few eggs and offspring at the other. Many marine species produce large numbers of small pelagic eggs, whereas other species produce smaller numbers of larger, demersal eggs that may be guarded by one or both of the parents. For example, the ling (*Molva molva*) is a highly fecund member of the codfish family (Gadidae); it produces 20–30 million small (approximately 1 mm diameter) freely-floating eggs that hatch after about 10 days, and the newly-hatched larvae (3–3.5 mm in length) are pelagic. By contrast a large female lumpsucker (*Cyclopterus lumpus*) will produce *ca.* 200 000 demersal eggs (2–2.5 mm in diameter); these are formed into large, sticky 'clumps' (egg-balls) that are then guarded and tended by the male. The eggs hatch after several weeks to give larvae 5–7 mm in length.

***Summary of reproductive options***

It is possible to make a number of generalisations about the reproductive patterns seen in the teleosts. First, the numbers of eggs produced (fecundity) tends to be high when the eggs and sperm are liberated freely into the water, is lower in those species that hide their eggs, and is lowest in species that show parental care. Second, fecundity and egg size are inversely related, with fish producing either many small eggs or a few large ones. In addition, the production of small, pelagic eggs is largely restricted to marine species, whereas freshwater species usually have larger, non-buoyant, sticky eggs that are deposited on a substrate, or placed in some type of nest. Some reasons for these links should be obvious. If a fish produces a few large eggs that give rise to well-developed offspring and also exhibits parental care, the chances of the offspring surviving are high; in contrast, eggs that are not protected are more susceptible to predation, so more must be produced if survival of some offspring is to be ensured. In addition, given that a fish has limited resources that can be invested in reproduction, there must be some form of trade-off, with the resources being divided amongst either few large eggs or many small (Hoar & Randall 1988a, b; Jobling 1995). Such striking contrasts in egg production and early development have implications for many aspects of fish behaviour, from how soon and on what the larvae need to feed (see Chapters 5–7) to patterns of kinship, competition and aggression (see Chapter 9).

### 2.6.2 Rates of development

In broad terms, the rate at which the embryo develops within the egg and the time taken from egg fertilisation to the hatching of the larva can be considered a species-specific characteristic, but environmental factors, particularly water temperature, have a major modifying influence on rates of development. Rates of development usually increase, and incubation times are shorter, in warm water than in cold. Incubation of eggs at high temperature may, however, result in increased incidence of malformations and abnormalities in the embryo, or the death of the eggs. Temperature can also influence several other aspects of early development, including size at hatching, efficiency of yolk utilisation, time to first-feeding and time to metamorphosis (Hoar & Randall 1988a, b; Jobling 1995; Wood & McDonald 1997; Moksness *et al*. 2004; Le Francois *et al*. 2010).

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**Table 2.2.** Comparison of egg characteristics and early life history traits in four species of cold-water, farmed fish.

| | Approximate egg number (n/kg female) | Egg type | Egg diameter (mm) | Incubation | Approximate time to hatch (degree days) | Approximate size at hatch (mm) | Time from hatch to first feeding (degree days) |
|---|---|---|---|---|---|---|---|
| Atlantic salmon *Salmo salar* | 1200 | Demersal | 5–6 | Eggs buried in coarse gravel in river bed | 500 | 15–25 | 300 |
| Spotted wolf-fish *Anarhichas minor* | 2000 | Demersal | 5–6 | Eggs guarded by male | 900 | 23 | 0–30 |
| Atlantic cod *Gadus morhua* | $5 \times 10^5$ | Pelagic | 1.1–1.9 | Eggs free-floating No parental care | 90 | 3.5–4.5 | 30 |
| Turbot *Scophthalmus maximus* | $3.5 \times 10^5$ | Pelagic | 0.9–1.2 | Eggs free-floating. No parental care | 75–100 | 2.5–3 | 35 |

Degree days = days × mean water temperature. Demersal = egg remains on, near or buried in the substrate. Pelagic = egg floats in the water column.

The relationship between incubation temperature and the early development of fish is often summarised by the concept of 'degree-days'. Implicit in this concept is the assumption that the product of temperature and the time in days needed to reach a given stage of development is constant and this often holds true. It is also commonly observed that large eggs take longer to develop than small eggs, and the time to hatch at any given temperature might be almost ten times longer for large eggs than small. An equation that combines these two sets of observations, describing the inter-relationships between egg size, temperature and time to hatch (incubation time) for freshwater and marine fish species allows fish farmers to predict when eggs of a given species of fish, and hence a given size, will hatch when incubated at different temperatures, or under conditions of fluctuating water temperature (Jobling 1995; Wood & McDonald 1997; Moksness *et al*. 2004).

### 2.6.3 Developmental contrasts in farmed species

The general principles underpinning developmental relationships can be illustrated using four commercially important, farmed, cool-water species as examples. Atlantic salmon (*Salmo salar*) and spotted wolf-fish (*Anarhichas minor*) produce relatively small numbers of large eggs that are laid onto the substrate (demersal) and the embryos spend several weeks developing within the egg membranes prior to hatching (Table 2.2). The newly hatched fish are relatively large and in an advanced state of development. There are, however, some differences between the spotted wolf-fish and the salmon. Salmon eggs are buried in a series of nests (redd) in coarse substrate at the bottom of a relatively-swift flowing river, and egg incubation and the earliest part of post-hatch development occurs within the redd. The spotted wolf-fish is an egg-guarder that lays its eggs on the seabed at depths of 110–250 m; the female then forms the eggs into spherical 'clumps' (egg-balls) that are guarded by the male. At hatch the young spotted wolf-fish have almost exhausted their egg yolk reserves, and begin to feed almost immediately. On the other hand, the newly-hatched salmon has a large yolk sac that can nourish it for several weeks before there is a need for external food. In contrast to its close relative, the common wolf-fish (*Anarhichas lupus*) has characteristics that are similar to those of the salmon; the newly-hatched larvae of the common wolf-fish have large yolk sacs that can provide them with nutrients for several weeks before they need to search for food and start to feed on various types of prey organisms. The fact that salmon and wolf-fish are large at hatch, and are at a relatively advanced stage of development before they start to take external food is advantageous when viewed from the point of view of the fish farmer. Young fish of these species can be start-fed on artificial dry feeds without any need for an initial phase of feeding on small, live

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prey organisms followed by a period of weaning on to dry feeds (Moksness *et al*. 2004; Le Francois *et al*. 2010).

Atlantic cod (*Gadus morhua*) and turbot (*Scophthalmus maximus*) produce large numbers of small, pelagic eggs that hatch after a few days of incubation (Table 2.2). The newly-hatched larvae are small and not particularly well developed at the time of hatching. Although recently-hatched larvae have a large yolk sac, this is rapidly absorbed over a period of a few days, and the fish start to consume external food within a relatively short time after hatching. In the cod and turbot, only a relatively small proportion of the developmental time from egg fertilisation to the juvenile stage is spent within the egg and as a yolk-sac larva, with 65–80% of the developmental duration of the young fish being spent as a free-swimming, feeding larva. By way of contrast, over half of the early development of the salmon and wolf-fishes takes place prior to the young fish hatching from the egg. The small (a few mm in length) larvae of turbot and cod quickly deplete their limited yolk reserves, and they start to feed a few days after hatching. The larvae initially feed on protozoans and other micro-organisms (the 'infusoria' of aquarists), small (80–200 µm) planktonic organisms, such as tintinnids (Oligotrichida), rotifers and the young stages (nauplii) of copepods. As the larvae grow they are able to pursue, capture and consume larger prey items. Their range of prey is first expanded to include small copepods, and then larger planktonic organisms, such as harpacticid copepods and amphipods, are also eaten. When cod and turbot are farmed, they first undergo a period of feeding upon live-feeds and are then weaned onto dry feeds in the form of flakes or crumbles, and are finally fed on pellets of larger size (Moksness *et al*. 2004; Dabrowski & Hardy 2010; Le Francois *et al*. 2010).

## 2.7 LIFE HISTORY PROGRAMMING

### 2.7.1 Genotype–environmental interactions

Although some aspects of development are genetically hard-wired, the environment experienced during early life has numerous influences upon phenotype and the attributes of individuals at different life history stages depend upon a series of intricate interactions between genotype and the environment (Hoar & Randall 1988a, b; Jobling 1995; Wood & McDonald 1997; Moksness *et al*. 2004; Rijnsdorp *et al*. 2009). The concept of life history programming seeks to provide a link between environmental influences on gene expression and organ and tissue differentiation during early development and the morphology and physiological functioning of individuals at later stages in their life. According to this view, development involves a synchronised series of events that are under genetic control, but during some critical stages individuals respond to environmental stimuli via adaptations at cellular, molecular and biochemical level, some of which result in changes at the physiological and behavioural levels (Via *et al*. 1995; Rossiter 1996). Such early adaptations may permanently change physiological and behavioural repertoires, remaining apparent even when the stimulus that initiated them has abated. The programming that occurs during early life may improve subsequent fitness if it provides a realistic prediction of the environment experienced later in life. This means that developmental plasticity may tune gene expression to produce a phenotype that is well-suited to survival in the anticipated future environment. On the other hand, in cases of mismatch, the individual's ability to respond to environmental challenges may be inadequate, with increased risk of compromised performance and reduced survival (Gluckman & Hanson 2004).

Among environmental factors, temperature has a major influence on physiological and biochemical processes in fish, including metabolic rate, enzyme activity, protein synthesis, food intake, growth and reproductive development (Jobling 1995; Iwama *et al*. 1997; Wood & McDonald 1997; Adams 2002; Willmer *et al*. 2005; Evans & Claiborne 2006; Rijnsdorp *et al*. 2009). An abrupt temperature change will lead to short-term changes in the rates of physiological processes, but if the temperature is then held constant for an extended time there will usually be a gradual change in the physiological rates, as acclimation occurs on a longer time scale. A wide range of physiological activities at the tissue, cellular and subcellular level are subject to change during acclimation. The long-term programming effects should not be confused with these shorter-term acclimations. The life history adaptive responses to environmental conditions such as temperature, salinity, dissolved oxygen and various stressors, involve directed gene expression that is regulated at transcriptional and post-transcriptional levels and has the potential to influence a multitude of early developmental processes (Johansen *et al*. 2009). Both short-term acclimation effects and life history programming are likely to be involved in the problem areas identified as limiting factors, or so-called bottlenecks, in fish culture (Brooks *et al*. 1997; Moksness *et al*. 2004; Dabrowski & Hardy 2010; Kah *et al*. 2010).

### 2.7.2 Maternal contributions

A strong environmental influence on early development, and hence an important source of input to life history programming, comes from the environment provided by the eggs, and this is dependent on the female that produces them. Reproduction is a phase in the fish life cycle with narrow tolerance to environmental perturbation, so this is

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an important source of variability in the phenotype of fish. In addition to genetic material, the maternal contribution to the developing embryo comes in the form of maternally-derived messenger RNAs, hormones, immune factors and nutrients transferred from the mother to the egg.

### *Transfer of maternal hormones*

The endocrine status of a female fish correlates with that of the eggs she produces. The hormones that regulate the earliest phases of embryonic growth and development come from the yolk, where they are accumulated during oogenesis. Thyroid hormones enter the oocytes at yolk formation, and these hormones play a role in the regulation of rates of morphogenesis in the developing embryos. Thyroid hormones also play important roles in governing rates of larval development and in metamorphosis (Hoar & Randall 1988a, b; Wood & McDonald 1997; Moksness *et al*. 2004). The females may also transfer steroid hormones to the eggs, which may have detrimental effects on egg fertilisation and embryonic development (Iwama *et al*. 1997; Adams 2002). Females exposed to environmental stressors during the latter stages of the reproductive cycle may transfer cortisol to the developing oocytes, and batches of eggs with elevated cortisol concentrations tend to have reduced fertilisation percentage and reduced survival of the embryos to hatch. The female also transfers a number of immunological factors to her eggs, including immunoglobulins and lysozymes (Swain & Nayak 2009; Kah *et al*. 2010).

### *Transfer of egg nutrients*

Additional maternal contributions to the egg include a wide range of macro- and micronutrients; a detailed account of such substances and their importance in fish nutrition is given in Chapter 6. Eggs are mostly made up of water and protein, with one or a few oil globules (lipid droplets). The proteins and lipids are used as building blocks for tissue synthesis and as metabolic fuels. The eggs of different fish species vary in the proportions of proteins and lipids they contain. In general, lipid content tends to be highest in eggs that have long incubation times, whereas free amino acid concentration is usually higher in the pelagic eggs of marine species than in demersal eggs (Hoar & Randall 1988a, b; Jobling 1995; Moksness *et al*. 2004; Dabrowski & Hardy 2010).

Egg lipid content is usually within the range 2–10% egg wet weight, and lipid-rich eggs often have oil globules that contain high proportions of neutral lipids that provide metabolic fuel for the fish during development. The egg phospholipids provide the essential fatty acids needed for incorporation into cell membranes as tissues become differentiated. Lipid-rich eggs generally contain lower proportions of phospholipids (less than 50% of the lipids) than do lipid-poor eggs (60–80% of the total lipid content). Whilst the fatty acid compositions of the egg phospholipids vary to some extent, certain long-chain highly unsaturated fatty acids that are required for the normal development of the brain, neural tissues and the retina of the eye tend to be present in quite large amounts. Deficiencies of these essential fatty acids lead to the development and survival of the embryo and newly-hatched larva being compromised (Moksness *et al*. 2004; Dabrowski & Hardy 2010; Le Francois *et al*. 2010).

The concentrations of free amino acids (FAAs) present in the pelagic eggs of marine species are usually much higher than those in either demersal marine fish eggs or in the eggs of freshwater fish species. The FAA pool may account for 20–50% of the amino acid content in pelagic fish eggs, whereas FAAs rarely exceed 5% of the total in eggs of other types. The FAAs, derived from the breakdown of yolk proteins, begin to accumulate during oocyte maturation, and the increase in FAAs leads to an osmotic influx of water, or hydration of the oocyte, just prior to ovulation. Where hydration is marked the previously opaque oocyte becomes a transparent and buoyant egg. The osmotic influx of water into the oocytes of marine fish species may be an adaptation to enable the embryo to survive in an hyperosmotic environment, because the embryo appears to be largely dependent upon endogenous water sources during the course of development. Consequently, FAAs play an important role in osmoregulation in pelagic marine fish eggs. The FAAs also appear be the major source of metabolic fuel for developing marine fish embryos and larvae and 50%, or more, of the energy requirements of the developing embryo may be met by amino acid catabolism (Jobling 1995; Moksness *et al*. 2004; Dabrowski & Hardy 2010). The egg also contains micronutrients, in the form of vitamins and minerals that are required in small doses if the egg is to develop correctly and the young fish to grow normally. For example, eggs contain vitamin C (ascorbic acid), a vitamin with several biological functions; it acts as a cofactor in collagen synthesis, it is an antioxidant, and also plays a role in steroid hormone synthesis. Eggs also contain carotenoids; these are antioxidants and precursors of vitamin A (Jobling 1995; Moksness *et al*. 2004; Dabrowski & Hardy 2010).

### *Maternal influences on embryonic and larval development*

Following fertilisation of the egg there are delays in the activation of the zygote genome, and during this time there is reliance upon gene products introduced into the egg by

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the female (Pelegri 2003; Aegerter *et al*. 2004, 2005; Kah *et al*. 2010). There is thus a potential for environmental challenges to influence the endocrine, nutritional and immunological status of maturing females, modify the composition of the egg and thereby have a knock-on effect on the development of the offspring. Maternally derived egg components, in the form of RNAs or biologically active proteins, support a range of cellular events and developmental processes, and maternally derived mitochondrial DNA may make a major metabolic contribution to ensure that the energy demands for embryogenesis are met (Wolff & Gemmell 2008). The maternally derived immunoglobulins persist for a limited period during embryogenesis and early larval development, and may not be detectable by the time the yolk is completely absorbed (Swain & Nayak 2009).

Abnormal concentrations of, or disturbances to activity or processing of, maternal factors may lead to abnormal cell cleavage, developmental anomalies and ultimately death of the embryo or larva. For example, when females have disrupted sex steroid profiles during oogenesis and oocyte maturation these can be reflected in increases in abnormal cell cleavage in early embryonic stages, and lead to reduced survival. Thus, the environmental conditions experienced by a female during her reproductive cycle have the potential to impact egg and larval size, embryonic survival and the frequency with which developmental anomalies occur (Iwama *et al*. 1997; Adams 2002; Moksness *et al*. 2004; Kah *et al*. 2010; Le Francois *et al*. 2010).

### 2.7.3 Environmental factors and the development of motor systems in fish

Environmental temperature has important influences upon rates of development and differentiation in embryonic and larval fish (Hoar & Randall 1988a, b; Jobling 1995; Wood & McDonald, 1997; Hall & Johnston 2003; Hall *et al*. 2003; Moksness *et al*. 2004; Johnston *et al*. 2009). These, in turn, influence performance and behaviour and affect the ability of the fish to cope with challenges during later life. For example, serially repeated structures such as vertebrae, myomeres and fin rays can be modified by the environment experienced during early development. Thus the numbers of vertebrae and other serially repeated characters differ between fish exposed to different thermal regimes; such differences are a reflection both of direct effects of habitat temperature, and also of genetic differences between local populations that occur within the geographic range of the species. For fish of a given population, incubating the eggs and rearing the larvae at low temperature tends to result in a higher number of vertebrae, indicating an effect of habitat temperature on phenotypic expression. However, when fish of different populations are held under the same conditions, those that naturally occur in warmer waters usually have lower vertebral counts than fish that are offspring of parents from colder waters. Such differences, which may well have implications for swimming ability, may persist over several generations of rearing under identical conditions, indicating that they have a genetic basis.

Temperature experienced during early development is a cause of significant variation in muscle phenotypes of larval fish. This is because temperature has an influence upon the timing of myogenesis relative to other developmental events, the expression of muscle-specific protein genes and the expression patterns of different forms of muscle (Hall & Johnston 2003; Hall *et al*. 2003). Small differences in temperature may be sufficient to influence growth phenotype, and incubation temperature can have long-term consequences for the growth and recruitment of fibres in skeletal muscle (Johnston *et al*. 2009). There may, for example, be a more sustained period of muscle growth at low than at high temperatures (Johnston 2006). Differences in muscle structure and function will also have implications for swimming ability and hence for fish behaviour.

### 2.7.4 Long-term consequences of early developmental events

Fish larvae, particularly those of marine species with small pelagic eggs, hatch at an earlier developmental stage than many other vertebrates. This means that environmental factors may play an important role in shaping their rates of development and differentiation. Early hatching makes marine fish larvae vulnerable to adverse external stimuli; a mismatch between physiological capacity and the environment, leading to the exceeding of tolerance limits, can have serious negative consequences for development and survival (Wood & McDonald 1997; Moksness *et al*. 2004; Rijnsdorp *et al*. 2009). Some effects of the environment in which young fish develop, for example, organ dysfunction and skeletal deformations, will influence how they behave, through general effects on body functioning. Other effects will have have more specific relevance for particular aspects of behaviour; for example, fat-storing cells (adipocytes) may fail to develop in non-feeding larvae and juveniles (Flynn *et al*. 2009), and environmental factors can have an influence on sexual development, affecting phenotypic sex and gonad differentiation, which will clearly influence how the fish behave when they start to reproduce (Devlin &

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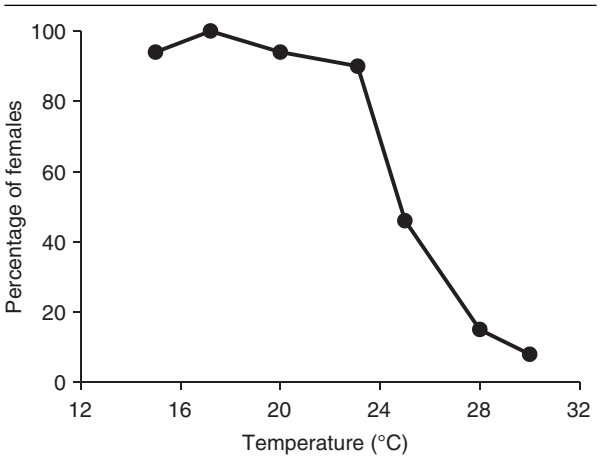


**Figure 2.14.** Effects of temperature on percentages of female fish that develop in genotypic female populations of goldfish, *Carassius auratus*, held at different temperatures during early development (from day 12 after fertilisation until an age of 3 months). Reproduced with permission from Le Francois *et al.* 2010.

Nagahama 2002; Evans & Claiborne 2006; Kah *et al.* 2010; Figure 2.14; Chapter 10).

## 2.8 SYNOPSIS

The previous sections have shown that the sense organs of finfish are broadly similar to those of terrestrial vertebrates, but with a number of special adaptations to the aquatic environment; these include highly sensitive mechanosensory systems and, in some cases, the ability to detect electric fields. Sensory information from the external environment and from the fishes own body passes to the CNS where it is processed and appropriate actions initiated. These may take the form of movements, or behaviour. A fish body, with serial muscle blocks, streamlined form and flexible fins, is ideally suited for effective movement through water and the finer details of body shape and fin position are tuned to the fishes' lifestyle and habitat.

Through the close link between the hypothalamus and the endocrine system, sensory information arriving at the CNS mediates various physiological responses. These include the physiological stress response, a complex of rapid, reversible changes that, in nature, enable the fish to respond to a variety of challenges. In addition environmental information, for example relating to photoperiod and temperature, can initiate longer-term changes, as when fish come into reproductive condition. These complex, interacting systems together form the machinery that generates behaviour and are revisited in the context of specific aspects of behaviour in later chapters.

Fish have highly variable life history patterns, in terms of the number and size of eggs produced and whether development is direct or involves abrupt changes in body form and life style (metamorphosis). These variable traits have many implications for fish culture; for example, the size and stage of development at which larvae hatch, which depend in part on egg size, determines how easy it is to raise them in culture systems. The occurrence of metamorphosis, with many associated morphological and behavioural changes, places severe demands on the tuning of aquaculture conditions to meet the requirements of the fish. The fact that females of many fish species transfer significant amounts of both nutrients and hormones to their eggs means that maternal effects are likely to influence many traits in their offspring, including their behaviour. There is thus considerable scope not just for genetic and direct environmental effects on how young fish develop and behave, but also for complex interactions between these two kinds of influence. This is a common, interlinking theme in the chapters that follow.

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# 3
# Tools for Studying the Behaviour of Farmed Fish

*Marie Laure Bégout, Sunil Kadri, Felicity Huntingford and Børge Damsgård*

**Abstract:** This chapter initially describes the difficulties encountered when studying animal behaviour and some methods used to overcome these difficulties. It also spells out what farmers need to know about the behaviour of fish within culture systems; this includes space use, feeding, responses to signs of danger and interactions with other fish. The main tools available for collecting this information are then considered. Several indirect methods for reconstructing the behavioural history of fish are described, such as using stable isotope analysis to reconstruct diets and scars to reconstruct previous encounters with predators or rivals. Studying the behaviour of fish in culture systems may require fish to be identified, either individually or by category, and some methods for achieving this are described. Direct methods for collecting behavioural data for fish in culture systems are then reviewed; these include behavioural observation using video monitoring, tracking of individual fish using electronic tags, tracking fish *en masse* using echo integration and using demand feeding systems to monitor feed intake. For each tool, advantages and limitations are highlighted and examples are given of their use in studies of the behaviour of fish in culture systems.

**Keywords:** brain biochemistry; echo integration; electronic tagging; marking fish; measuring behaviour; PIT tags; self-feeding systems; stomach analysis; stable isotopes; video systems.

## 3.1 INTRODUCTION

Studying animal behaviour is challenging in a number of ways and the study of the behaviour of aquatic animals such as fish is particularly difficult, because they move in a three-dimensional world that is difficult for humans to access. The aim of this chapter is to describe and illustrate some of the methods available for studying behaviour in general and the behaviour of fish in culture systems in particular. First, there is a brief account of some of the problems posed by the study of behaviour and the methods that biologists use to quantify the behaviour of animals. Consideration is then given to the information that is needed about the behaviour of cultured fish, both at the individual and at the group level, and the main tools currently available for gathering this information are described. These include indirect reconstruction of behavioural history and direct data collection for monitoring of what fish do in culture systems. Many direct data collection methods require fish to be identified, either individually or by category, and some methods for achieving this are described. Methods for collecting behavioural data for fish in culture systems include behavioural observation using

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video monitoring, tracking of individual fish using electronic tags, tracking fish *en masse* using echo integration and various methods for measuring feeding. For each tool, advantages and limitations are highlighted and exemplified.

## 3.2 DESCRIBING AND MEASURING BEHAVIOUR

Anyone who has watched a fish moving about, whether in the wild, on a fish farm or in an aquarium, will be aware of at least three reasons why behaviour is difficult to study. First of all, it is ephemeral, in the sense that it does not usually leave any permanent record. A rare exception is provided by the breeding male three-spined stickleback (*Gasterosteus aculeatus*), which sometimes bites into the sandy substrate during territorial disputes, leaving marks from which territorial boundaries can be reconstructed (Tinbergen & Van Iersel 1947). Biologists who study fish morphology can return to specimens many times, checking previous measurements and taking new ones; those who study behaviour do not have this luxury, although the development of video recording has gone some way to addressing this problem. Prior to the video-era the procedure was to carry out detailed preliminary observations and then to focus on a few key actions and behaviours for detailed measurement.

This leads on to a second problem, namely that behaviour tends to be continuous in nature. Morphological features usually have clear edges and can be measured and, in the case of teeth or scales for example, can be counted. In contrast, behaviour often seems to consist of a seamless series of events, which makes measurement difficult. Consider the breeding male stickleback patrolling his territory; for most of the time, he swims around, collecting nest material, tending his nest, looking out for potential mates and rivals and much more besides. The daunting task of turning this continuous stream of movement into something that can be counted is made possible because some movements or postures are repeated in a more-or-less identical manner on different occasions. Such behaviour patterns, or 'units of behaviour', can be defined objectively and quantified. As an example, when one fish bites another during a fight, it often does so in a consistent fashion, so counting numbers of bites can be a reliable way of assessing how vigorously one fish attacks another, even though fights may go on for different lengths of time. Where movements are truly continuous and cannot be broken up into discrete units, there are still techniques for measuring how much of them an animal does. For example, space use in territorial sticklebacks can be quantified by laying a grid over the fish's home range and noting in sequence each square of the grid the fish enters. From this, an estimate can be derived of how active the fish is by counting the number of times it moves between grid squares and of where the fish concentrates its activity by identifying grid squares that are statistically under- or over-utilised.

A third problem for behavioural biologists is that they are interested in something that can be very complex. For example during fights cichlid fish flash their fins at each other, beat their tails, circle round each other, wrestle with locked mouths and bite. When undisturbed, the members of a school of minnows (*Phoxinus phoxinus*) move around in synchrony; when threatened or attacked by a pike (*Esox lucius*), they perform many complicated group manoeuvres, streaming rapidly away from the predator and creating what are called 'fountains'. Such complexity adds an additional level of difficulty when it comes to describing and measuring what animals do and where and when they perform particular actions. Added to all this, behaviour is highly plastic in nature. Morphological traits are not immutable, but they usually remain reasonably constant over time, but behaviour is modified rapidly and continually by many internal and external variables. For example, how vigorously male sticklebacks respond to a territorial rival may be influenced by the temperature of the water, by light intensity, by his current energy reserves, by whether or not there are receptive females or potential predators around, by what happened in any previous encounters with a rival, on what the intruding rivals are doing and so on.

Because behaviour is plastic, if it is to be studied scientifically, great care has to be taken to control the circumstances in which it is measured. This means standardising influential variables where possible and using statistical analyses to allow for those that cannot be controlled. Staying with the stickleback example, to get a reliable measure of how vigorously males attack intruders requires standardising the previous experience of the fish concerned, including how long they have been in their tank, what happened in their last fight and when they last ate. It also requires standardisation of their current circumstances, including light levels, temperature, the presence or absence of potential predators and the distance of the intruder from the nest. It is usually impossible to control how intruders behave, but this can be allowed for statistically. For example, if attack rate of a territorial fish is related to activity levels of the intruder, the score for each fish can be expressed as a residual from the regression between owner attack and intruder activity. When all these things are done, the attack rate of a given fish at a given time can be measured with sufficient accuracy to allow hypotheses about behaviour to be rigorously tested.

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Behavioural biologists have developed a number of procedures and methods for overcoming these and other problems so that they can generate the reliable and accurate measurements of animal behaviour that are essential if this is to be studied scientifically. These have been described by Martin & Bateson (1993), Barnard (2007) and Stamp-Dawkins (2007).

## 3.3 WHAT WE NEED TO KNOW ABOUT THE BEHAVIOUR OF FARMED FISH

In the context of aquaculture, assessment of fish behaviour is especially challenging due to difficulties in making sure that design and sampling are adequate and appropriate. In addition, there may be differences in fish responses under experimental and commercial culture conditions and potential methodological bias arising from repeated fish handling. Commercial production involves rearing fish in a variable environment with large populations and water volumes and this creates conditions in which behaviour is particularly difficult to observe and measure accurately. In addition, farm conditions differ markedly from those in controlled laboratory environments and this will influence fish behaviour. The extent to which results from laboratory studies can be extrapolated and directly applied to commercial conditions is thus open to debate. However, behavioural studies conducted under experimental conditions provide a pool of knowledge about the behaviour of fish that are cultured. In addition, a number of techniques have been developed especially for collecting information about the behaviour of fish held on commercial farms.

The general features of fish behaviour that farmers need to know about are how they move, how they feed, what diets they choose and how much they eat, how they respond to disturbance and potential danger and how they interact with conspecifics. In addition, it is important to know about the occurrence of abnormal behaviour, which may be displayed in response to a wide range of abiotic or biotic factors and so may be indicative of acute or chronic stress, or impaired welfare (see Chapters 1 and 2).

Many behavioural responses are species-specific, so each species of farmed fish should be studied independently. Additionally, even when fish are held in similar conditions, individuals of a given species do not always show the same response. This may for example be the consequence of differences in gender, age or disease status. It may also be a consequence of genetic differences in responsiveness between individual fish, or coping strategies (see Chapter 8), and individuals may behave in different ways on different occasions as environmental conditions change. Thus, a complete description of the behaviour of farmed fish often requires tracking individuals within farmed populations over time, in parallel with longitudinal assessments of environmental conditions, such as temperature, water quality characteristics and other abiotic factors.

## 3.4 INDIRECT RECONSTRUCTION OF THE BEHAVIOUR OF CULTURED FISH

As discussed later in this chapter, a variety of techniques have been developed for visualising and measuring the behaviour of farmed fish directly. These can be highly effective, but are often expensive, are not always completely appropriate and may not provide information on the behaviour of individual fish. In some cases it is possible to use cheaper, indirect approaches, reconstructing aspects of the behaviour of farmed fish based upon relatively simple observations.

### 3.4.1 Reconstructing fish diets

The stomach contents of a fish provide information about its recent feeding history (Murphy & Willis 1996; Jobling *et al*. 2001), but the information is not perfect; for example, variable rates of digestion of different types of prey complicate interpretation. Nevertheless, stomach content analysis is widely used by fish biologists. To give just one example, stomach content analysis of wild Atlantic cod (*Gadus morhua*; Mello & Rose 2005) revealed that the cod feed on amphipods, decapods and crustaceans for most of the year, but that consumption of fish peaks in the summer.

Bony structures such as otoliths, vertebrae and opercula have ring patterns that can be used to reconstruct growth rates (Murphy & Willis 1996) and possibly also to provide an indirect indicator of feeding rates. In addition, such hard parts may be used to identify and reconstruct the sizes of fish prey consumed by piscivores, although care is needed when employing this method (Jobling & Breiby 1986). Moreover, different types of food differ in the ratio of stable carbon isotopes they contain and traces of these isotopes are deposited in fish otoliths. As such, studies of the stable isotope signatures of material from different regions of otoliths can provide an integrated record of fish diets over time. For example, the stable isotopes in the otoliths of catfish (*Hypostomus* sp) differ detectably in fish fed on diets with different stable isotope contents, for example, maize as opposed to freshwater algae (Nonogaki *et al*. 2007). This approach has been used to compare diets of farmed and wild Atlantic cod of different ages at different times of year (Figure 3.1; Gao *et al*. 2001). The extent to which tissues are enriched with the heavier form of carbon

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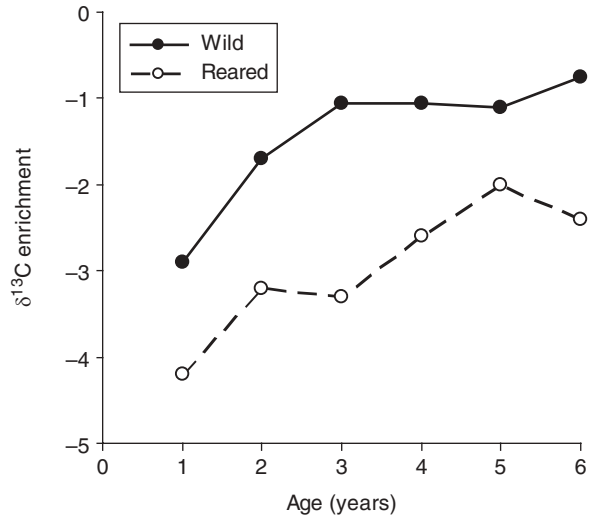


**Figure 3.1.** Degree of enrichment of the tissue of farmed and wild cod of different ages with a specific carbon isotope ($\delta^{13}$C) in winter. Wild cod (filled circles) show stronger $\delta^{13}$C-enrichment than do reared cod (open circles) at all ages. Adapted with permission from Gao *et al.* 2001.

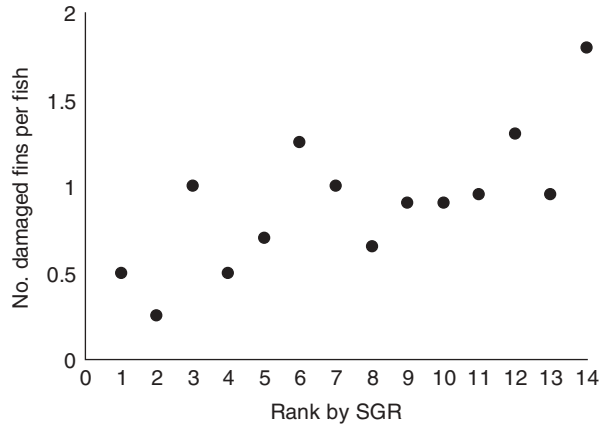


**Figure 3.2.** The number of damaged fins per fish in relation to growth rates over 1 month in 250 g Atlantic cod. Fish that grew faster (indicated by a low rank in terms of their specific growth rate or SGR) had the least damage. Adapted from Hatlen *et al.* 2006.

($\delta^{13}$C values) increases with age in both wild and farmed cod up to an age of 4 years, but are consistently higher in wild fish. In addition, the youngest wild fish show marked differences between summer and winter, something that is not seen in farmed cod that are fed artificial pellets of similar composition throughout the year.

### 3.4.2 Reconstructing interactions with predators and rivals

Fish may have external signs that can be used to assess their previous experience. For example, scars may indicate encounters with predators (Chapter 8) or attacks by conspecifics (Chapter 9). In sticklebacks, scars can be used to identify fish that have escaped attack by piscivorous birds or fish (Reimchen 1994). This approach has been used to evaluate the extent to which cormorants (*Phalacrocorax carbo sinensis*) cause damage to farmed common carp (*Cyprinus carpio*), using computer-assisted analysis of images of fish with wounds. The degree of scarring of the body surface was 27% in one year old and 4% in 2-year-old fish and body condition (assessed from the relationship of fish weight to length) of the 2-year-old carp was significantly lower in scarred than in undamaged fish. This study demonstrates that scars on fish can be used to assess encounters with predators and also shows that cormorants can cause production loss through unsuccessful as well as successful attacks (Adámek *et al.* 2007).

Fish may bear scars arising from aggressive encounters with other fish of the same species. For example, in male cichlids, *Tilapia zilli*, scale loss is an indicator that a fish has taken part in a fight and is particularly prevalent in fish that lose fights (Neat *et al.* 1997). Attacks by conspecifics are a common cause of fin damage in salmonids (Christiansen & Jobling 1990; Turnbull *et al.* 1998), so the incidence of fin damage within a population can be used as an indicator of aggressive interactions. For example, in juvenile farmed Atlantic cod wounds on the dorsal fin are common, especially when feed supply is restricted. The incidence of fin damage is highest in slow-growing fish (Figure 3.2), suggesting that such fish may be prevented from feeding by aggressive attacks (Hatlen *et al.* 2006).

Other indirect ways of reconstructing experience of aggression and fighting depend on knowledge of the consequences of victory and defeat (see Chapter 9). For example, socially dominant fish often get preferential access to food and, as a consequence, feed regularly, whereas socially subordinate fish tend to feed irregularly. Therefore, when the food intake of identified individual fish in a group is monitored over time it is possible to deduce their social status from their food intake and the regularity with which they feed (Christiansen & Jobling 1990; McCarthy *et al.* 1992; Jobling & Baardvik 1994; Jobling *et al.* 2001). Fish with stable feed intake may be classified as dominant and those with variable feed intake

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as subordinate (McCarthy *et al*. 1992). Using this approach, Kristiansen (1999) showed that dominance interactions are strongly polarised in brown trout (*Salmo trutta*), with larger individuals suppressing feeding by small fish.

Subordinate fish have characteristic brain biochemistry, with the rate of turnover of the neurotransmitter serotonin being higher than in dominant fish (Winberg *et al*. 1992; Chapter 9). Analysis of serotonin metabolism of farmed Atlantic salmon (*Salmo salar*) show that fish that fail to grow over extended periods have the high serotonin turnover rates typical of subordinate fish (Cubitt *et al*. 2008). The conclusion that such fish are excluded from feeding by more dominant companions was confirmed by direct observation; the fish that fail to grow well avoid areas where large fish are scrambling for access to food (Cubitt 2002). In sea bass (*Dicentrarchus labrax*) there are differences in brain serotonergic activity within groups that are fed using on-demand, self-feeders (see below); bass that activate the trigger mechanism of the feeder have lower serotonergic turnover than do fish that show little or no trigger activation. It is suggested that fish with low or null-triggering activity could be stressed by the high activity of possibly-dominant high-triggering individuals (Di Poï *et al*. 2007).

### 3.4.3 Indirect assessment of stress

Production and welfare are both compromised when cultured fish are stressed, so it is important to be able to measure stress in fish in culture systems. Measurement of plasma concentrations of the hormone cortisol is commonly used in this context (Chapters 1 and 2), but capturing fish for blood sampling is a stressful procedure that can lead to increases in plasma cortisol levels within a short space of time. This potentially compromises interpretation of such data, as well as raising welfare problems. Recently, cortisol has been measured non-invasively in groups of fish held in tanks by monitoring cortisol in the water. This has been applied to both freshwater fish such as, rainbow trout (*Oncorhynchus mykiss*. Ellis *et al*. 2004) and marine fish (Ellis *et al*. 2007; Fanouraki *et al*. 2008) held under controlled conditions in tanks. Extending the method to commercial farms is challenging, because account must be taken of fish biomass and rate of water exchange and possibly other interfering factors that are hard to measure (Ellis *et al*. 2007). An alternative approach is suggested by the fact that the density of melanophores in the skin of Atlantic salmon and rainbow trout is variable and correlates with cortisol release in response to exposure to a stressor. This potentially provides a tool for the non-invasive assessment of stress responsiveness and coping strategy in individual salmonids (Kittilsen *et al*. 2009).

## 3.5 METHODS OF MARKING AND TAGGING FISH

Indirect methods for reconstructing the behaviour of fish are not ideal for many purposes and direct monitoring is preferable whenever possible. Prior to conducting direct behavioural observation, there is often a need to identify fish within a population. Identification is useful not only when recording immediate behaviour, but also for long term monitoring of individual or group performance. Tagging and marking are used for identification purposes, both at the individual and group level (Murphy & Willis 1996). Tagging or marking fish involves treatment and handling, which may disturb and possibly stress the fish, so careful handling is most important when undertaking such procedures (Baras 1991; Murphy & Willis 1996; Thorstad *et al.* 2000, 2001; Bridger & Booth 2003; Sulikowski *et al*. 2005, Brown *et al*. 2011).

External tags and marks can be used for visual identification, whereas internal tags or marks usually require specialised equipment or intrusive methods for detection and identification. An advantage of internal marks, such as chemical marking of bony structures, is that they can enable large numbers of fish to be marked at an early age (Murphy & Willis 1996). In some cases an external tag or mark is used to signify the presence of an internal tag or mark.

### 3.5.1 External marks and tags

An external mark may be defined as a visible mark on the outside of the fish that is used to identify individual fish or to distinguish between groups of fish, but without any additional information or specialised reporting format. External marks may be natural, based on variation in colour patterns and morphological traits such as scale numbers, number of fin rays and distribution of melanophores (Garcia de Leaniz *et al*. 1994). Additionally, differences in overall body shape (morphometrics) may allow fish from different populations to be distinguished (Bergek & Björklund 2009). External marks may also be artificially applied, as when fish are marked with dye, stains or brands (Murphy & Willis 1996). External marking techniques are suitable for behavioural studies in relatively confined areas, such as aquaria, tanks or small cages, where direct observation is possible or recovery of marked individuals is feasible, but are also used by fish biologists in a range of field applications (Murphy & Willis 1996). Such marks are often simple, cheap and quick to apply, but carry limited information. External marks such as fin clipping have often been used as a means of calling attention to the presence of internal tags, but fin clipping may be stressful and affect swimming behaviour, so should be used with caution.

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External tags are visible structures that are usually attached to the fish by piercing tissues (Murphy & Willis 1996). Such tags, which may carry an individual code, batch code or visible instructions, can be easily detectable without specialised equipment and can sometimes be used for recognition during behavioural observations. External tags include ribbons, threads, wires, plates, discs, dangling tags, straps (McFarlane *et al*. 1990), T-bar Anchor Tags (Harden Jones 1979; Morgan & Walsch 1993), Carlin tags (Carlin 1955) and coloured beads (Jadot *et al*. 2003).

Ideally the behaviour, growth and survival of tagged and untagged fish should be similar. While this may be true for many types of tags and marks, some tags may well affect behaviour and influence growth and survival (Murphy & Willis 1996; Bridger & Booth 2003). For example, fish with external tags may be more vulnerable to predation and their growth may also be affected. By permanently penetrating the skin the tag may provide an access route for infection. Additionally, tags may become overgrown with algae and other organisms, adding weight to the tag and increasing drag, as well as preventing tag detection or reading. The need to identify fish, individually or by group, with minimal influence on behaviour, health or survival has thus led to the development of internal tags.

### 3.5.2 Internal tags

Internal tags are defined as tags inserted or injected into tissues and carried in the body cavity, muscle or cartilage, and can be used to identify individuals or groups of fish. Most types have to be removed from the fish to be identified, but some, such as passive integrated transponder tags (PIT tags), can be read by an external antenna, so, once implanted, they provide a non-invasive and non-destructive means of identification. PIT tags are transponder tags that transmit information by acoustic waves when an electrical current is induced. They consist of a small glass-encapsulated electromagnetic coil and microchip that is inserted into the body cavity or muscle of a fish using a veterinary syringe. PIT tags are made in three sizes, ranging from 11 to 32 mm in length and 2.1 to 3.1 mm in diameter. In large fish they may be injected into any part of the fish where the flesh is thick enough to retain the tag, but are most often positioned loosely in the abdomen. The tag is inert until it is activated inductively by a tag reader, which provides the power for the tag to transmit a unique alpha-numeric code. The system offers 34 billion codes and operates at 125, 134 or 400 kHz. However, the detection range is limited, tags usually being decoded with a portable hand-held reader that has a range of 10–15 cm. Automatic readers are also available with either a tunnel detector up to 30 cm in diameter or detector plates, which can be placed on the floor of a tank or a designated area of a cage, raceway or stream. PIT tags may last throughout the life of the fish and the tagging system allows rapid retrieval of transmitted information from large numbers of tagged individuals. They can be detected and decoded in living fish in fresh and salt water and eliminate the need to anaesthetise, handle, restrain or kill the fish during data retrieval. Used with computer stations, they allow repeated identification and measurement of individuals within a population.

An example of the use of PIT tagging to study fish behaviour is provided by Brännäs (1998), who studied movements and distribution of groups of Arctic charr (*Salvelinus alpinus*) offered a choice between tanks. PIT tag detection antennae were positioned at the entrances to the tanks and the passages of individual fish monitored continuously. The use of PIT tags has limitations at high rearing densities, because the detection range of PIT tags is limited to a few cm and the presence of several fish within detector range may interfere with tag detection. Additionally, code identification may fail when the antenna is at an oblique angle to the tag (Brännäs & Alanärä 1993; Covès *et al*. 2006). PIT tags have been used in studies of social interactions, such as the formation of dominance hierarchies, learning capabilities and memory (Millot *et al*. 2009) and of feeding rhythms and macronutrient selection (Houlihan *et al*. 2001; Rubio *et al*. 2003a). An example of the use of PIT tags together with video analysis is given in Section 3.6.6.

Other types of internal tags include plastic or glass tubes, metal plates and small pieces (size 0.5–2.0 mm × 0.25 mm) of magnetised stainless steel that may have a binary code of Arabic numbers engraved or laser etched on their surface. The latter, known as coded wire tags, are normally injected into the snout of a fish, often in combination with an external mark to aid recovery (Schurman & Thompson 1990). Such tags are extensively used for identifying large numbers of fish and due to their small size can be used on fish of a large range of sizes. Magnetic body cavity tags (MCTs) are steel plates inserted into the body cavity of the fish and detected during fish processing by magnets placed in strategic positions within the processing line. Radio frequency identification tags (RFID, NONATEC®) are a new generation of tags that operate at a high frequency (13.56 MHz) and allow the identification of very small individuals using a laboratory bench reader while fish are under anaesthesia; NONATEC® tags are 1 mm in diameter, 6 mm in length and weigh 7.15 mg.

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### 3.5.3 Internal tags that are visible externally

Some tags are placed subcutaneously, but are visible by eye. One example is the visible implant tag (VIT), or the newer visible implant alphanumeric (VIalpha) tag. Such tags were developed to combine the advantages of external tags with those of internal tags and are used where minimal disturbance of the fish is important. VIT are made of plastic strips and VIalpha are made of medical-grade silicone rubber, often with the addition of fluorescent material. These tags come with printed information and are often placed in transparent tissue just behind the eye.

## 3.6 DIRECT BEHAVIOURAL OBSERVATION VIA VIDEO MONITORING

Video technology offers a cheap, user-friendly and reliable method for monitoring fish behaviour and many studies are now based on video recording and analysis. The easiest approach is to film behaviour as it occurs, analysing and quantifying it later. Behavioural studies also incorporate advanced surveillance equipment and video analysing tools to quantify events or complex behavioural patterns as they happen. Deployment of video technology thus ranges from manually recording and counting events to automatically measuring behavioural variables such as group cohesion, conspecific interactions, inter-individual distance or individual movement pattern. In some cases behaviour is monitored at the group level, but in most cases the behaviour of individuals is quantified.

### 3.6.1 Video technology

The technical platforms used in video studies of fish behaviour are generally based upon either standard consumer video systems or more specialised surveillance equipment made for security in banks and shops, for example. Such equipment is often inexpensive, mass produced using state-of-the-art technology and may easily be adapted to monitoring of fish from above the water surface. For example, a single camera with a recorder unit (a 'CamCorder') can be suspended over a fish tank, enabling easy monitoring of behavioural events. Another option is to mount the camera over the tank and transfer the video signal to a remote monitoring system, thereby minimising disturbance to the fish and allowing safer recording. As with most technically advanced equipment, video systems are vulnerable to damage by water and humid conditions, so it is advantageous to have as much equipment as possible in remote positions away from the risk of contact with water. Underwater cameras are specialised pieces of equipment that are often custom-made, because they have to be waterproof and in some cases to be tolerant of rough conditions. Underwater cameras are often used together with over-water recorders and monitors. Video monitoring is sometimes carried out as part of husbandry practice in sea cages, for example when used by fish farmers to assess feed intake and feeding behaviour.

The quality of the video footage is dependent on a number of technical factors that have been gradually developed and improved over time. Video was initially based upon tapes, but now uses digital formats, recorded directly on digital versatile disc (DVD) or stored as files on the recorder or a computer. The quality of the digital pictures depends on the format and size of the file. While the capacity of older video formats was mainly related to numbers of pictures per second, digital format capacity is dependent upon the numbers of pixels in each video frame. Some surveillance systems are not based upon film, but take pictures in digital photographic format, with the number of pictures per second depending on the sampling rate of the computer. However, most video analysing tools are limited to a video format and cannot analyse fast sequences in a picture format. Inexpensive web cameras can produce a file that may be linked to an internet web page and thus transferred in real-time to any computer. However, the quality of such equipment is currently poor, limiting this method to very basic behavioural observations of fish.

Video monitoring equipment often consists of a number of cameras that may be used over extended time periods and there are several technical means by which the amount of data collected can be edited or condensed. A 'time-lapse' system involves a reduction of the numbers of frames per second, such that on a 12 frames per second time-lapse for example, a film normally allowing 3 hours of recording at 24 frames per second would last for 6 hours. Using such systems, several hundred hours of filming may be stored economically. Playback speed can then be reduced to simulate normal timing, but this may distort movements, making them difficult to interpret. Multiple arenas can be observed simultaneously via one or several video cameras connected to, for example, a 4-channel mixer that compresses the four video signals into a single video output. The signals are then processed by a frame grabber and used as input to an analysing tool (Ylieff & Poncin 2003). Such a set-up can simultaneously track several fish in a single tank; for example, with three fish monitored in each of four aquaria, up to 12 fish can be tracked in the same session.

### 3.6.2 Limitations

Video recording has both possibilities and limitations; the constraints imposed by the method must be taken into

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account when planning a study and during sampling and analysis. Video monitoring is limited to clear water, a background that contrasts with the fish and adequate illumination of the arena. Most modern video cameras are very light-sensitive and function under poor light conditions, but each set-up must be pretested in order to ensure a good balance between ambient light and the light sensitivity of the equipment. Black-and-white cameras are generally more light-sensitive than colour cameras and may be used in situations where colour is not important. Using infrared (IR) light also allows filming in darkness, but image quality may not be adequate for monitoring movements unless appropriate IR filters are used. Where fish are moving rapidly, it may be difficult to observe behaviour in detail or to identify the fish involved. In addition, a tank or a sea cage is a three-dimensional (3D) space, while a video system is two-dimensional (2D) and any behaviour that involves movements in 3D will be projected into 2D, either in the horizontal or vertical plane.

Although mostly developed for laboratory experiments and very time consuming in manual mode, video recording has sometimes been used to study fish behaviour in larger arenas, such as sea cages. Some systems have been developed to allow automated tracking of fish from video sequences, although the aquatic environment does not lend itself easily to image processing, because of reflection and refraction of light. These difficulties are compounded by the limitations of using 2D input images to measure animals swimming in a 3D environment.

### 3.6.3 Preparation before sampling

A key challenge of using video for assessing fish behaviour is to develop good, validated procedures, including pre-tests of relevant technological limitations. Pre-testing could include validation of the various parameters, determining, for example, whether the light conditions are appropriate, whether the behavioural events of interest can be observed under the prevailing conditions and whether external tags or identification marks are visible in recorded footage. To track several fish in a tank, coloured plastic pearls have been attached under the dorsal fin (Jadot *et al*. 2003) and natural colour patterns have also been used (Ylieff & Poncin 2003); in such cases, pre-testing is also needed to ensure that these are visible in recorded footage. A pre-test should also include an estimation of the length of recording necessary to answer the question at issue, which to a large extent depends on the frequency of the behaviour under study and the sample sizes required.

### 3.6.4 Sampling

Once the system has been established it is necessary to develop a sampling protocol that provides sufficient data to answer the questions at issue, without excessive use of time. As an example, in a study of exploration behaviour and flight responses of sea bass (Millot *et al*. 2009), video recordings were collected (Figure 3.3a) and analysed using spatial and temporal sampling: the tank was divided into four virtual zones of equal surface area (Z1, Z2, Z3 and Z4 in Figure 3.3b) and each video recording was analysed in three sequences of 20 min around a stimulus event. This showed up marked differences in space use before the stimulation, just after the stimulation and 40 min after the stimulation (Figure 3.3c).

### 3.6.5 Analysis

Some video analysis tools work in real time, simultaneously with the recording, while others use stored films or data files. Programmes that are used to track movement do not necessarily store a complete record, but may store only the *XY*-coordinates of the tracked objects. There are two broad strategies for monitoring such variables: either the video recording is encoded afterwards (offline) in a computer-aided manual mode or the variables are extracted online in a semi- or fully-automatic mode. Where videos are not saved during the observations, it is not possible to review the behaviour retrospectively, for example, in order to look at tracking sequences that deviate from normal.

Individual observation is often based upon recognition of specific fish. An algorithm to discriminate fish can use differences in characteristics such as size, contrast or colour. For example, Jadot (2003) studied the behaviour of salema (*Sarpa salpa)* when tagged with two different ratios of tag mass to body mass (2% or 6%). The study used a computerized video tracking system based on a digital imaging technique that is capable of discriminating objects from the background (Noldus *et al*. 2001, 2002). Once an object or animal can be identified as an entity, its path, speed and space utilization can be tracked continuously for a period of time (Noldus *et al*. 2001). Ylieff & Poncin (2003) used such a system to estimate distance moved, velocity and social interactions as reflected by the mean distance between fish and the time spent in defined zones for individually identified carp (*Carassius auratus*) and damselfish (*Chromis chromis*).

Behavioural analyses may also be based upon group data without any recognition of individual fish. An automated video monitoring system developed by Stien *et al*. (2007) offers an economic and efficient procedure for registering vertical distribution of fish and the system is particularly appropriate for use in large tanks. A digital underwater camera is used to film a section of a tank wall which is marked with vertical black lines. Automatic image analysis is used to identify the parts of the lines that are not

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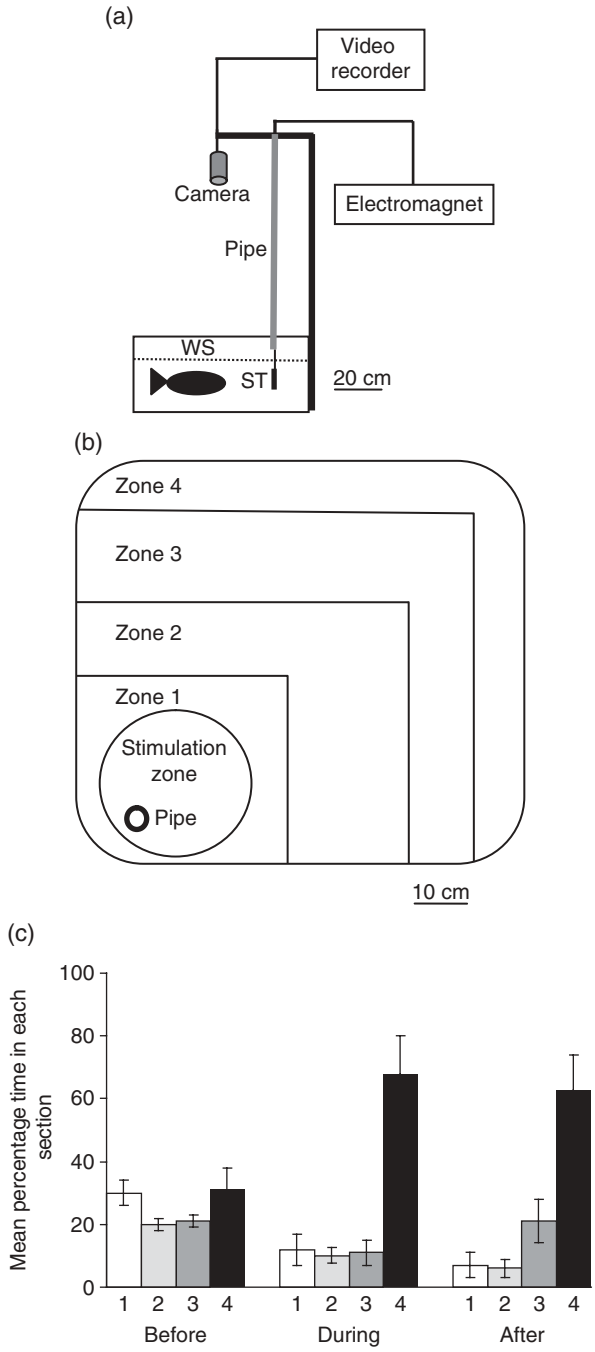


**Figure 3.3.** Video monitoring of the behaviour of seabass exposed to a stimulation event. (a) Schematic representation of the experimental setup. WS: water surface. ST: stimulus. (b) Zone delimitation on the tank floor. (c) Proportion of time spent (mean ± SE, %) by a domesticated fish in each tank zone (1–4) before, during and after imposition of a stimulus. Reproduced with permission from Millot *et al.* 2009.

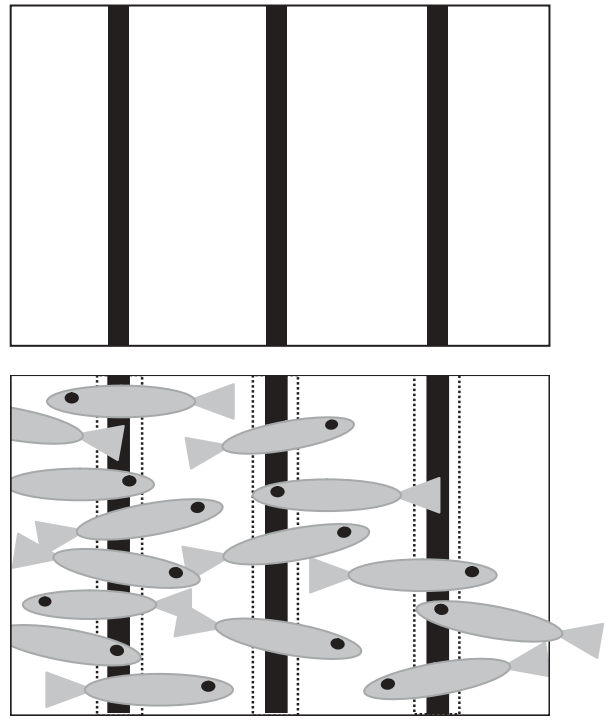

**Figure 3.4.** Schematic representation of the deployment of a simple video-based system for quantifying the vertical distribution of fish at high densities in large tanks, based on the subtraction of a live image from a background reference image. The top figure depicts the reference image and the bottom figure depicts fish in front of the reference background. The coverage of the areas indicated by dotted lines is measured as a proxy for the distribution of the fish. Adapted with permission from Stien *et al.* 2007.

obstructed by fish and the lengths of the visible parts are compared with their known lengths to give an index of the density of fish in the relevant section of the tank. The procedure does not require uniform or stable lighting conditions, only that the vertical black lines are clearly visible (Figure 3.4; Stien *et al*. 2007).

### 3.6.6 An example of the use of video analysis to study the behaviour of PIT tagged fish

Kristiansen *et al*. (2004) combined video monitoring of swimming and feeding behaviour with PIT tagging to identify individual fish at the water surface; the data were eventually used to relate behaviour to growth performance in Atlantic halibut (*Hippoglossus hippoglossus*). A video camera pointing downwards at an angle of between 15

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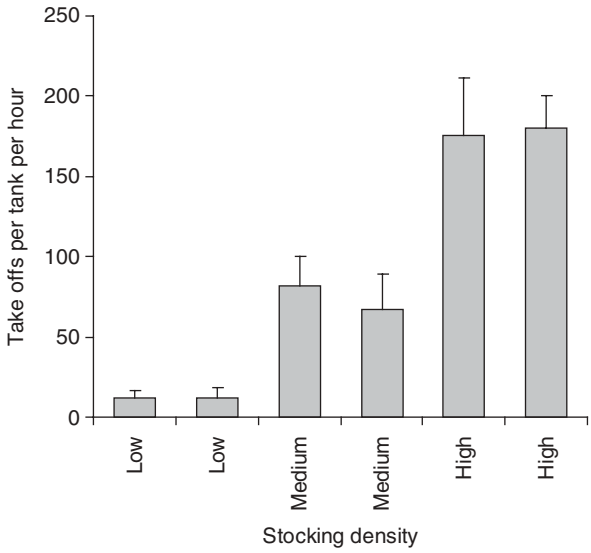


**Figure 3.5.** Using a combination of video monitoring and PIT tagging to quantify behaviour in farmed halibut. Mean numbers of take-offs per tank per hour in fish classified in relation to rearing density (low: 6 kg $m^{-2}$, medium: 18 kg $m^2$ and high: 40 kg $m^2$) in two tanks. The error bars show 95% confidence interval for the mean of each tank. Reproduced with permission from Kristiansen *et al.* 2004.

and 20° was placed just under the water surface and a wide-angle lens offered coverage of about 70% of the tank bottom and the water column. All fish were individually tagged with PIT tags and a PIT tag detection antenna was placed just below the water surface close to the feeding area. Records were made of the number of halibut that swam to the area where food was delivered and trials were carried out at different stocking densities. The number of fish rising to the surface per tank increased with stocking density (Figure 3.5).

## 3.7 DIRECT BEHAVIOURAL MONITORING USING ELECTRONIC TAGS

### 3.7.1 Electronic tagging

An important advance in the study of fish behaviour has been the development of electronic tags that can be attached to fish and send information of various sorts to strategically placed receivers. The range and versatility of such tags is such that novel applications are continuously being discovered. Apart from providing information on fish location and position in the water column in real time and over long time periods, electronic tags can also provide information about environmental variables and can be used to make physiological measurements, thus allowing the factors that most influence behaviour to be studied.

Sea cages are generally characterized by poor visibility and large water volumes and electronic tags have been used to provide information about fish position and movements within these systems. For example, fixed omni-directional hydrophone arrays have been used to determine the position of fish within or around fish farm cages and to relate activity to factors such as fish density and environmental conditions, including wind, rain and temperature regimes (Juell & Westerberg 1993; Bégout Anras *et al.* 2000; Cubitt *et al.* 2005). There are, however some constraints on, and limitations to, the use of electronic tags on farmed fish. For example, particular attention must be paid to attachment methods (see recent review in Brown *et al.* 2011), especially with regard to possible modification of the behaviour of the fish. In addition, regulatory restrictions with respect to the use of tags on fish destined for human consumption may present additional obstacles to the use of any tagging technology in production systems, so use of tags is currently limited to experimental applications or broodstock populations. Finally, species and size-related limitations can act as constraints on use of such technology, because some electronic tags tend to be relatively large, although miniaturisation has recently been achieved. Nevertheless, there is considerable scope for using electronic tags to study the behaviour of farmed fish, especially in combination with biotelemetric measurement of physiological variables such as heart rate and muscular activity. Such combinations offer the possibility of monitoring activity, physiology and environmental conditions in free-swimming fish simultaneously and over long periods (Figure 3.6; Baras and Lagardère 1995).

Potential applications include monitoring fish activity and linking this to feeding systems, which permits more rapid adjustment of feeding times to activity rhythms (Chapter 7). In addition, relating alterations in fish activity and physiology to changes in environmental variables allows objective identification of fish preferences or tolerance margins and rapid assessment of the impact of environmental stressors. The information can also be used to study the responses of fish to predators and to husbandry procedures, such as handling and transfer from fresh to seawater; this is relevant to both fish welfare and production (Chapter 1). Fish health has high priority in the fish farming industry and techniques for long-term monitoring of fish condition have considerable potential in health

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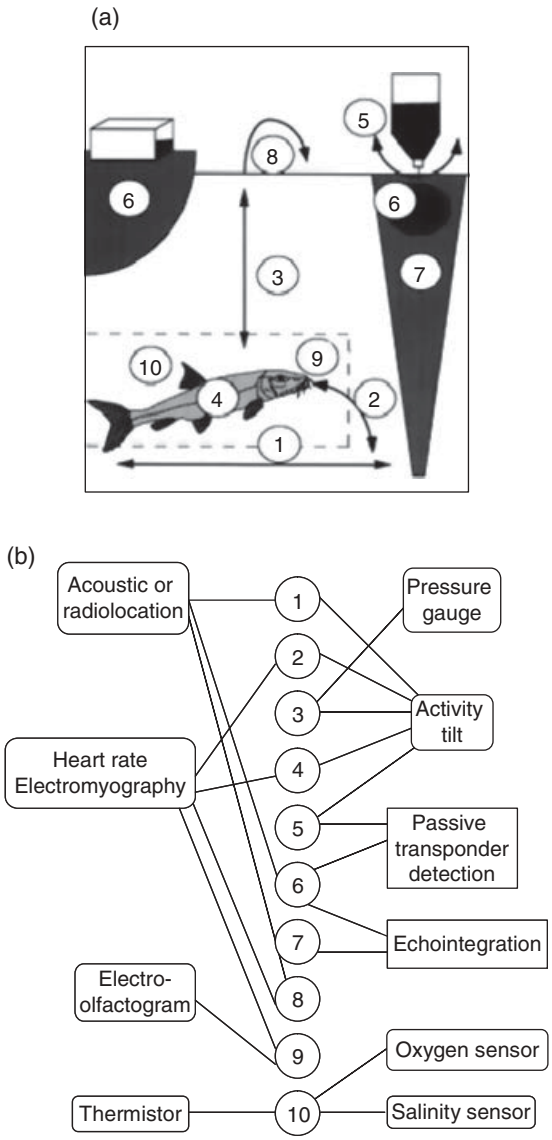


**Figure 3.6.** Schematic representation of the possible applications of telemetry in aquaculture (a) Possible variables for monitoring. 1. Fish position in horizontal plan. 2. Activity. 3. Position in water column. 4. Metabolism. 5. Food distribution. 6. Access to feeding zones and site monitoring (shaded areas). 7. Food wastage. 8. Surfacing activity (leaping). 9. Pollutant detection. 10. Environmental variables (rectangle delimited by dashed lines). (b) Monitoring methods and techniques that can potentially be used for each variable. Reproduced with permission from Baras & Lagardère (1995).

management, in particular if data could be recovered regularly without removing the tag from the fish (see below for DST and Chat tags). The focus of electronic tagging studies has mostly been on the monitoring of feeding, swimming activity and energetics (McFarlane *et al*. 2002; Cooke *et al*. 2004).

### 3.7.2 Types of electronic tag

A large and growing array of electronic transmitter tags are available. Apart from pulsed and coded signals that identify the position of the fish, some tags carry sensors that collect additional data, such as depth, swimming direction and speed, heart or respiration rate or information about muscle contraction. Such electronic tags are larger than PIT tags and require an internal battery to power the transmitter and microchip. The lifetime of the tag, which must be considered in telemetry studies, depends on transmitter size, power supply, range and rate of signal transmission. Telemetry studies on free swimming fish can range over periods of hours to months, but are generally of relatively short duration. Tag detection range can be up to a kilometre in some instances, but is generally less than 100 m, which is compatible with the use of such tags in aquaculture studies. Microchip technology allows for specific instructions to be placed onto a tag, allowing it to be switched on or off under a given set of conditions. For example, tags may transmit only under certain conditions of water chemistry or light intensity and such selective use can increase the longevity of the tags.

#### *Radio and acoustic transmitting tags*

Radio and acoustic transmitting tags transmit a pulsed signal at a selected pulse rate. Theoretically, large numbers of fish can be monitored simultaneously using multiple frequencies or pulse rates, but in practice it is very difficult to distinguish more than four or five pulse rates on an individual frequency. Radio tags, which can only be used in water of very low salinity, are useful because radio waves are less affected by physical obstacles, turbidity, turbulence and thermal stratification than acoustic, non-electromagnetic waves. Radio signals also radiate through the water surface and can be detected at great distances, because there is little loss of signal strength in air. Receivers can be placed in boats, aircraft or at land-based listening stations. Radio tags operate at high frequencies (20–250 MHz), so there is little signal drift. Acoustic tags are mostly used in seawater because sound is transmitted over long distances in salt water, whereas radio waves are attenuated very rapidly. Frequencies of 30–300 kHz are used. Signals from pulsed

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acoustic tags can be detected using a simple receiving system comprising a hand-held directional hydrophone, a portable receiver and headphones. This provides only a rough indication of the position of the fish and accurate position fixing requires triangulation using an array of fixed hydrophones (Bégout Anras & Lagardère 2004).

Non-programmable pulsed transmitter tags transmit a simple radio or acoustic pulse at pre-set time intervals, whereas programmable microprocessor tags transmit radio or acoustic pulsed signals at intervals defined by the user. Specific on/off sequences can be set that are useful for preserving the battery life of the transmitter. New developments include the ability to include sensors that can collect information about the electromyogram, tail beat frequency and heart or respiration rate.

Coded tags are a special type of transmitter tag that operates by emitting a digitally encoded pulse signal at user-defined intervals on specific radio or acoustic frequencies. This allows up to 100 individual signals to be distinguished at a given frequency. This technology has the advantage that many fish can be tracked separately on a single frequency, the information being automatically recorded and downloaded to a computer. Coding can increase data acquisition rates and increase sample sizes in telemetry experiments (Cubitt *et al*. 2005).

In experiments where simple transmitting tags are used, fish depth can be deduced from time of arrival of acoustic signals at the hydrophones (Anon. 1968) and algorithms for the calculation of 3D coordinates from an array of four hydrophones are provided by Hardman & Woodward (1984). Signal strength from a radio source at a known location may also be used to estimate fish depth (Velle *et al*. 1979), although the use of pressure-sensing transmitters (Luke *et al*. 1973; Williams 1990) gives more reliable estimates, independent of signal attenuation.

***Data storage tags (DST)***

DST or archival tags, range from simple dataloggers that record depth or temperature, to sophisticated programmable devices capable of providing a direct estimate of geographical position at regular intervals over periods of many months. Several types of DST have been developed and used to record from free-ranging fish in the open sea (Rikardsen *et al*. 2007) and for monitoring fish in cages (Johansson *et al.* 2007). DSTs that can be programmed to record details of temperature, depth, salinity, pressure, light, chemical and physiological indicators at set intervals have considerable potential for use in behavioural studies and future developments may include tags that can monitor body tilt, heading and position fixing. Some DSTs can record data for up to 5 years and store the information for up to 20 years. In order to retrieve the information stored on DST, the tags must be recovered and this may involve establishing an intensive fish recapture operation. Such operations often rely on careful harvesting, so an external mark or tag is usually applied to facilitate identification of fish carrying DST. Due to the high cost of DST only relatively small numbers of fish are usually tagged, but tag costs are offset by the large amounts of data that can be recorded by and stored on such tags.

***Satellite pop-up or chat tags***

These are tags that send stored data to remote receiving stations. Such tags have been used for oceanic tracking of large fish (Weng *et al*. 2009), but have not been applied to aquaculture systems. Pop-up tags detach from the fish at a predetermined time and float to the surface from where they transmit to the Argos satellite. These tags could be used on large species such as tuna (*Thunnus* sp.) to study depth, temperature preferences or feeding events via dedicated electromyogram sensors. Chat tags are data storage tags that can communicate via a radio or acoustic link to a receiving station. A station could be moored close to a remote sea cage site and data collected without frequent visits to the site or retrieval of the tags from the fish. Due to their size, these tags can only be used on large fish.

### 3.7.3 Scanning stations

The tags described above can provide information about fish position and can be used to monitor key sites such as feeding areas (Juell & Westerberg 1993; Bégout & Lagardère 1995). In such cases, radio or acoustic tags can be detected by antennae or hydrophones connected via a switching box to a programmable datalogging receiving station. The receiver can scan a programmed frequency range at fixed or variable intervals, depending on a programmed algorithm defining a priority scan of frequencies detected on a master antenna. This concept is similar to that of the sono-buoy automatic listening stations developed by Solomon & Potter (1988). The latest developments in automatic stations allow the presence/absence of up to 2000 fish at eight sites to be monitored within 5 seconds using a single receiver and digitally encoded signals (Lotek Engineering Inc. 1992) or datalogging receivers that can be deployed for underwater positioning (Espinoza *et al*. 2011). Cubitt *et al*. (2005) provide an example based on a commercial salmon sea cage farm.

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### 3.7.4 Examples of the use of electronic tags to study the behaviour of farmed fish

Bégout Anras & Lagardère (2004) used acoustic tags to track the position of rainbow trout held in tanks at different stocking densities. The fish were fitted with external electronic acoustic pulsed tags and their positions monitored every 5 seconds for 48 hours; from these data, activity and swimming trajectories, including holding position, chaotic trajectories (equal use of all turning angles) and circular swimming (average turning angle of 60°) could be reconstructed. These were influenced by day-night alternation; for example, at low densities (25 kg $m^{-3}$) the fish showed chaotic trajectories during the day, but remained in a restricted location at night. They also depended on fish density; for example, the chaotic trajectories shown during the day by fish at low densities were replaced by circular swimming when fish are held at medium densities (75 kg $m^{-3}$). This study showed the feasibility of monitoring fish swimming activity under high densities and provided insights into fish activity in relation to constraints imposed by culture conditions.

In addition to fish location in the horizontal plane, knowledge of the vertical distribution of fish may be needed to define the optimal depth of culture systems, feeding regime or timing of food distribution. Fish in production systems may be faced with a conflict between light-induced surface avoidance and food attraction and electronic tags can be used to monitor swimming and participation in feeding events, as carried out for Atlantic salmon held in sea cages (Juell & Westerberg 1993; Bégout Anras *et al*. 2000; Cubitt *et al*. 2005). Transmitter tags have also been used to monitor rainbow trout held under different conditions, for example feeding and fasting, with signals being transmitted in proportion to muscle activity (Chandroo *et al*. 1999; Cooke *et al*. 2000; McFarlane *et al*. 2004). DST can be used to record environmental variables along with fish swimming depth and body temperature; an example is the recording of the activities of Atlantic salmon held in a sea cage subject to thermal stratification (Johansson *et al*. 2009; Figure 3.7).

## 3.8 DIRECT BEHAVIOURAL MONITORING USING ECHO INTEGRATION

In addition to knowledge about the behaviour of individual fish, it is sometimes of interest to gather information about the group within which the individuals occur. Such *en masse* tracking of groups has been carried out using echo integration to monitor the vertical positions of schools of fish.

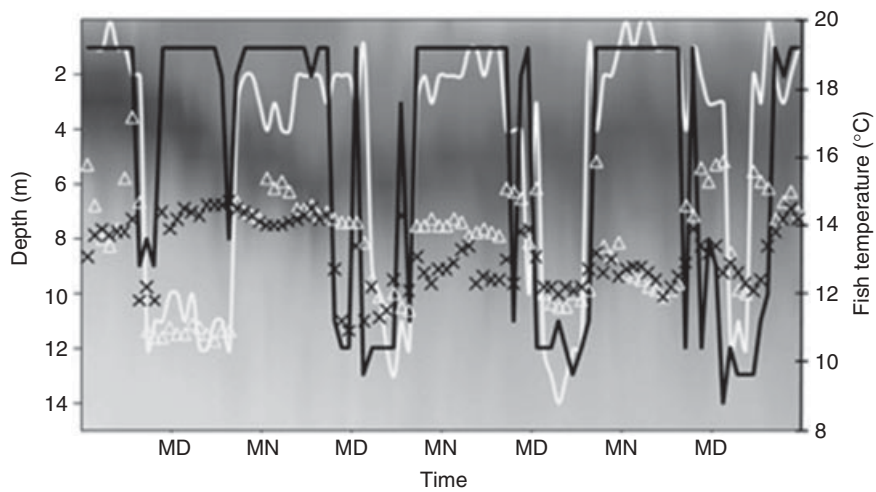


**Figure 3.7.** The use of data storage tags to monitor behaviour of farmed fish in relation to environmental conditions. Swimming depth and individual body temperature of two Atlantic salmon in a production cage during a 4-day period in mid-autumn (Julian days 271–274). The left vertical axis represents the depth from 0–15 m and the right vertical axis individual body temperature (°C). The horizontal axis represents successive days. MN = midnight. MD = midday. The swimming depth (white and black solid lines) and body temperature (white triangle and black ×, respectively) of two fish with different diel behaviours are illustrated. Water temperature is indicated by intensity of shading, ranging from 8 °C to 20 °C. Reproduced with permission from Johansson *et al*. 2009.

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### 3.8.1 Echo integration

A complementary approach to monitoring the position of fish using electronic tags is to use a sonar transducer moored below the sea cage with the acoustic beam oriented upward, for example, a 42° acoustic beam suspended at a depth of approximately 17 m. The sonar echoes are used to detect the presence, position and in some cases the size of fish in the sonar beam path. The transducer scans for the echo densities and a dedicated decoder and software display the fish population density from the bottom to the surface of the sea cage. Both Bjordal *et al*. (1993) and Juell *et al*. (1994) describe computer-based echo integration systems.

A sonar system allows continuous monitoring of swimming depth and relative density of fish, giving information on group distribution and space utilization. Echo intensity, which is directly proportional to fish density, can be recorded at specific depth intervals and converted into relative echo intensity in each interval and thereby provide information on fish density at specific depths. Typically, 60 observations (pings) per minute are recorded and mean values are stored in the computer. Observed fish density in kg $m^{-3}$ at each depth interval is calculated and swimming depth distribution over a longer interval (usually every hour) is transformed into a single value that identifies the preferred swimming depth of the fish. To quantify preferences in the fish for certain depths, a preference index can be calculated for each depth, positive values indicating preference and negative values indicating avoidance. The preference index is a standardised index that integrates depth intervals and fish density and can therefore be used to compare space utilisation at different sites and seasons (Oppedal *et al*. 2007).

### 3.8.2 Examples of the use of echo integration to monitor the behaviour of farmed fish

Oppedal *et al*. (2007) used echo integration to investigate behavioural responses of Atlantic salmon to different light intensities in a thermally stratified environment. Underwater lamps were deployed at different depths and swimming depth and fish densities recorded. Fish position was influenced by light intensity; for example, with the underwater light at 10 m (Figure 3.8) the fish aggregated near the water surface by day, but were more dispersed at night. Bégout Anras *et al*. (2000) combined an acoustic positioning system that detected individual movements with echo integration to monitor positions of groups of fish in sea cages. Similarly, Johansson *et al*. (2009) combined DST and echo integration techniques. In both cases, behavioural indicators based on individual activity patterns and group positioning that emerged from these studies have potential to improve the understanding of complex trade offs such as thermo- and photo-regulatory swimming behaviours (Oppedal *et al*. 2007).

## 3.9 MEASURING FEEDING BEHAVIOUR IN FARMED FISH

Fish appetite can fluctuate on time scales ranging from hours and days to weeks and months and also changes with environmental conditions (Chapter 7; Alanärä 1992a, b; Anthouard *et al*. 1993; Rubio *et al*. 2003b). Therefore, monitoring feed intake in groups of fish and how this relates to growth is crucial for the success of fish farming (Martins *et al*. 2005). Further, minimisation of individual variation in food consumption and growth increases production efficiency, reducing food waste and improving water quality, so knowledge of how much individual fish eat is also important (Jobling & Baardvik 1994). Several methods are used to investigate food intake in farmed fish (Jobling *et al*. 2001). Non-destructive methods include direct video observation of feeding and recording from on-demand feeding systems (Kadri *et al*. 1997; Smith *et al*. 1993, 1995; Juell *et al*. 1994; Ang and Petrell 1997; Houlihan *et al*. 2001).

### 3.9.1 X-ray detection of feed intake

One technique for estimating food intake is based upon X-radiography, in which fish are presented with feed labelled with a radio-opaque marker (Talbot & Higgins 1983; Christiansen & Jobling 1990; McCarthy *et al*. 1992; Jobling & Baardvik 1994; Jobling *et al*. 2001). Some hours after being fed labelled feed, fish are anaesthetised and X-rayed and the number of opaque particles present in the gut counted. With calibration of the average number of particles per pellet and depending on the time food takes to pass through the gut, this can be translated into the amount of food eaten by the fish. This method has been used for the examination of feed-growth relationships, of feed preferences and dietary selection, in investigations of social interactions, for the study of temporal changes in feeding and growth and to track the onset of anorexia in maturing fish (Christiansen & Jobling 1990; McCarthy *et al*. 1992; Jobling & Baardvik 1994; Kadri *et al*. 1997; Jobling *et al*. 2001).

### 3.9.2 Self-feeding systems for controlling and monitoring feed delivery

A useful approach to monitoring feed intake, both for research and on commercial farms, is the use of systems that feed the fish according to appetite. Such systems often record how much feed is delivered, in which case they can track fish feeding over time, as well serving to deliver food.

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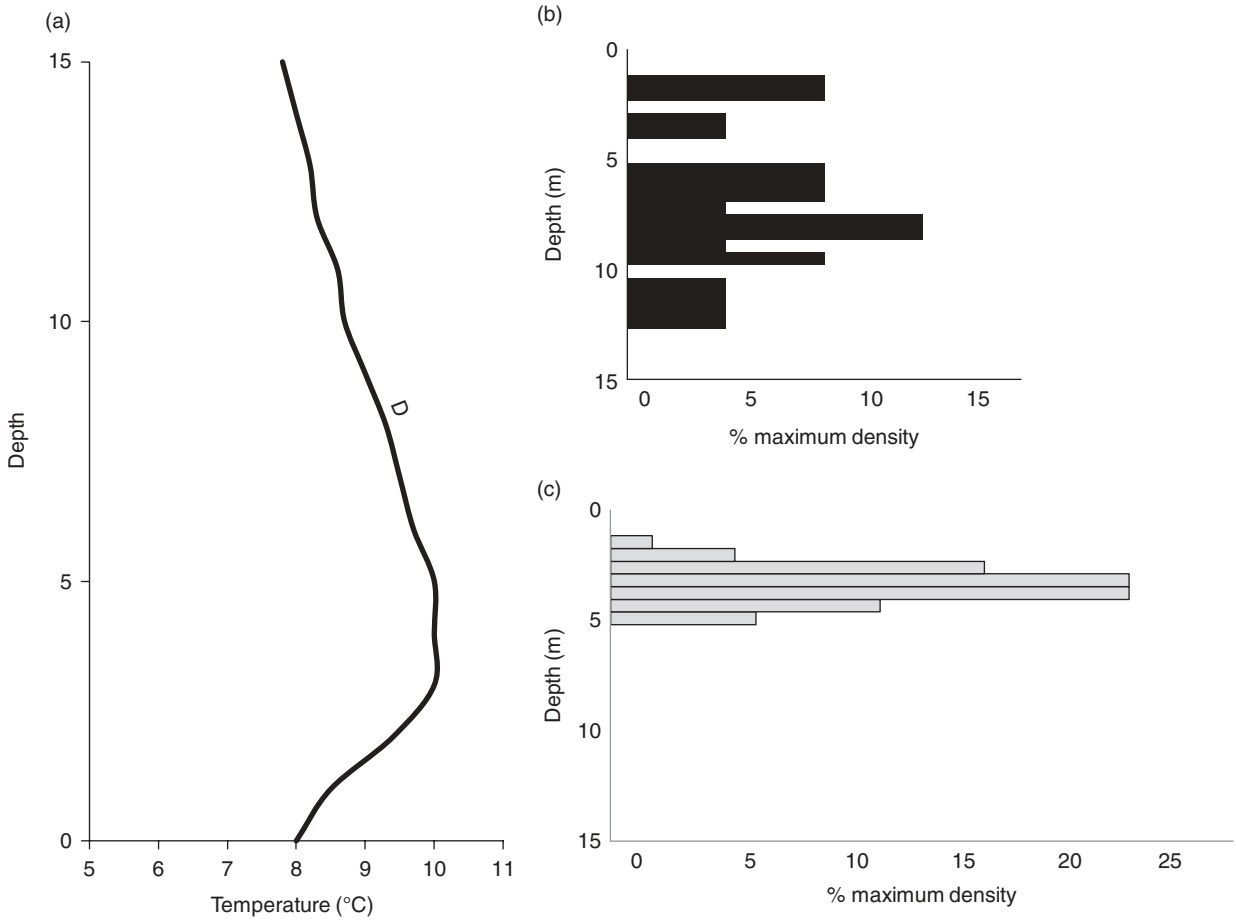


**Figure 3.8.** Using echo-integration to monitor density (kg $m^{-3}$) at different water depths in Atlantic salmon held in a sea cage (stocking density 5 to 10 kg $m^{-3}$) over a 3-day observation period during the summer, with an additional light source positioned at depths of 10 m. (a) Temperature profile in °C. (b) Percentage of maximum observed fish density (% maximum density) at each depth during the night and (c) Percentage of maximum observed fish density (% maximum density) at each depth during the day. Reproduced with permission from Oppedal *et al*. 2007.

There are various types of demand feeding system, the two main kinds being self-feeders, in which feed delivery is triggered by the fish performing a specific action such as pressing a lever, and feedback monitoring systems, where a feeder is controlled by some proxy for appetite such as detection of fish position in the water column or the monitoring of uneaten feed.

On-demand feeding technology provides a tool for matching feed delivery to appetite variation, so as to reduce food wastage (Chapter 7). On-demand feeding systems, in the form of self-feeders, were first used in laboratory studies of feeding by fish (Bitterman *et al*. 1958; Rozin and Mayer 1961, 1964; Adron 1972; Landless 1976; Grove *et al*. 1978), but have also been used in commercial production systems, for example in rainbow trout production in tanks, raceways and ponds (Statler 1982; Kindschi 1984; Tipping *et al*. 1986). Systems have been developed to monitor feed delivery to groups of cultured fish using electromechanical sensors coupled to feed hoppers (Anthouard & Wolf 1988) and the use of an on-demand feeder in commercial production was mentioned by Meriwether (1986). A self-feeder was tested in a pond of tilapia (*Tilapia aurea*) over a 10-week period to estimate labour savings and to compare production of fish fed by the demand feeder with fish fed by hand to satiation. Fish fed by self feeders gained more weight than hand-fed fish,

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although feed conversion and survival rates were not significantly different between the two feeding methods.

Later, Alanärä (1992a, b) used self-feeders to study the effect of a restricted ration as opposed to access to a demand feeding system for cage-reared rainbow trout; the objective was to identify the access time and food supply that optimised growth rate and feed conversion efficiency. The feeding system consisted of a trigger, in this case a pendulum ending with a rubber knob hanging below the water surface in the centre of the cage, with the trigger being connected to the feed hopper through an electronic unit that controlled sensitivity and running time. To avoid accidental triggering the trigger had to be bitten by a fish in order to release food and it was inactivated for 15 seconds after each actuation, to prevent fish from 'playing' with the trigger and releasing more food than required. The daily period during which the trigger could be activated for food release could also be adjusted using a timer function. The feeders were placed in the corner of each cage, spreading the feed in a plume over most of the water surface. Systems of this type allow calculation of the daily feed ration demanded by a fish population, which can then be related to environmental conditions such as temperature, or to culture practices.

To avoid accidental release, feeders can be operated through activation of screened triggers such as a metal rod surrounded by a PVC cylinder with enough space to allow a fish to enter the cylinder and bite the rod. Feed dispensers can be set to distribute either a certain weight of food or a certain number of feed pellets per actuation (Covès *et al*. 2006). How much food is delivered per actuation is often a compromise between minimizing wastage and optimising feed allocation to the group. When such systems are used in combination with waste-feed collectors, they provide information about feed consumed at the tank or group level over time scales ranging from a single meal to days or seasons. As such, on-demand self-feeding systems are valuable for the investigation of feeding rhythms.

It was recognised early on that all fish do not operate the trigger with the same frequency and several studies have been conducted to investigate this phenomenon. The monitoring of individual triggering rates requires equipment that combines self-feeding with individual identification; PIT tags have proved particularly valuable in this context. For example, using PIT-tagged Arctic charr (*Salvelinus alpinus*) and a small detection loop antennae placed around the trigger of a self-feeder, Brannäs & Alanärä (1993) mapped the self-feeding activity of individual fish and showed that one or two individuals monopolized the trigger and had the highest growth rate. Such use of a self-feeder coupled with a PIT tag detection antenna has since been used in a range of studies covering several fish species (Covès *et al*. 1998, 2006; Rubio *et al*. 2004). These systems can be deployed over long periods so represent a powerful tool for monitoring feed intake in farmed fish.

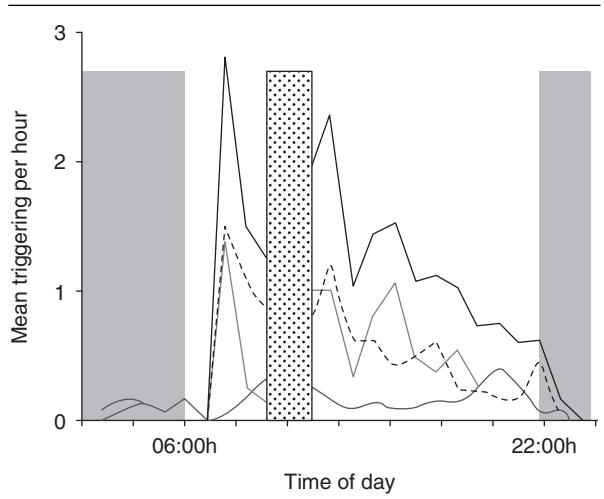


**Figure 3.9.** Mean triggering activity per hour in different individuals (indicated by different line styles) over the 24h cycle in an experiment in which sea bass (mean body weight = 299 g. $N = 48$) were fed using a demand feeder. The grey rectangles represent the dark phase and the dotted rectangle represents the animal care period during which no recordings were made. Reproduced with permission from Covès *et al*. 2006.

### 3.9.3 Examples of the use of self-feeding on-demand systems to monitor feeding in farmed fish

Covès *et al*. (2006) used a computerised self-feeding system in combination with PIT tag monitoring to study the feeding behaviour of seabass stocked in 1 $m^3$ tanks over 55 days. About 70% of the fish actuated the trigger at least once, but just one or two fish within a tank accounted for about 80% of the total triggering activity (Figure 3.9). In another study, individual seabass that activated the trigger of a self-feeding system were found to have higher growth rates than did non-triggering fish. Further, when there was an imbalance between feed intake and feed demand, in other words, when there was feed wastage, this was largely the result of an increase in demand rather than a decrease in consumption; such wastage could often be linked to particular husbandry events, such as measuring or sampling Millot *et al*. (2008).

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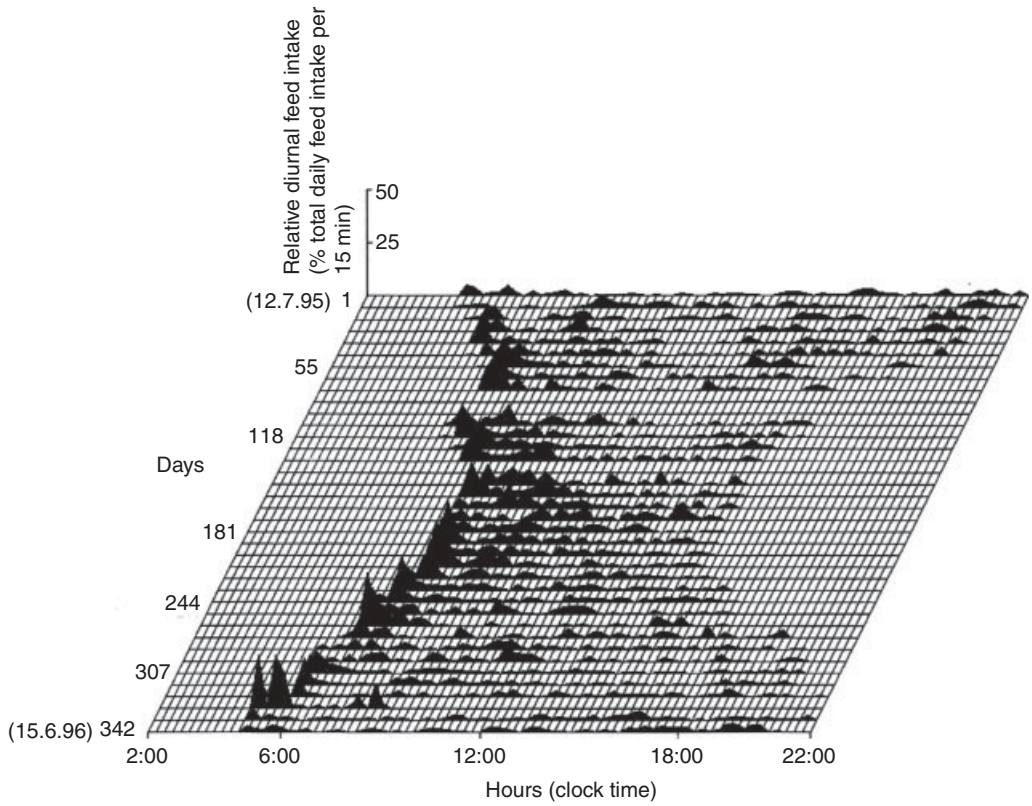


**Figure 3.10.** Percentage of the total daily feed intake taken in each 15 min interval across the day (% intake/15 min) from 12 July 1995 to 15 June 1996 in one cage of Atlantic salmon fed using a demand feeding system based on detection of uneaten pellets. Each horizontal grid represents 9 days of data. Reproduced with permission from Blyth *et al.* 1999.

### 3.9.4 Feedback systems for controlling and monitoring feed delivery

In general, interactive feedback systems work by monitoring the feeding activity of groups of fish and using this to adjust rates of feed delivery. The information recorded by such systems can be used as a resource for research, since it provides a continuous track of feeding activity. Such systems are particularly useful for collecting data about feeding in large populations held at commercial stocking densities, where the use of self-feeders may not be feasible or appropriate. The data used to control feed delivery can be either the detection of uneaten feed or changes in the behaviour of the fish. Uneaten feed can be detected by hydroacoustic transducers that detect the movement of feed through the water column (Juell 1991; Juell *et al.* 1993) or along tank outflow pipes (Summerfelt *et al.* 1995). Alternatively, IR sensors placed below the feed delivery system may monitor uneaten food as it falls through the water column (Blyth *et al.* 1993, 1999) or as it is carried along tank outlet pipes (Chen *et al.* 1999). Uneaten pellets may also be detected by video monitoring (Foster *et al.* 1995). In each case, information about the presence of uneaten pellets is passed to a control system that adjusts feed delivery rate or switches a feeder off when uneaten pellets are detected.

In systems where feed delivery is controlled by the behaviour of the fish, this may be detected either hydroacoustically or by means of video monitoring. Hydroacoustic transducers can be used directly to detect the sound of fish feeding (Lagardère & Mallekh 2000), or indirectly to monitor vertical distribution of fish as a proxy for feeding activity. The latter is possible because fish such as Atlantic

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salmon held in sea cages tend to approach the surface when feeding on pellets delivered from above (Bjordal *et al.* 1993). Video cameras have also been used for data collection in the operation of feedback systems (Foster *et al.* 1993; Ang & Petrell 1997; Petrell 2001a, b; Parsonage & Petrell 2003). In each case, the delivery of feed is adjusted or stopped when the monitored proxy passes a predetermined threshold.

### 3.9.5 Examples of the use of interactive feedback systems to monitor feeding in farmed fish

Blyth *et al*. (1999) used an interactive feeding system (described in Blyth *et al*. 1993) to acquire data about daily and seasonal variation in feeding rates throughout the year for Atlantic salmon held in sea cages from shortly after transfer to seawater until harvest about 11 months later (Figure 3.10). A major feeding peak occurred regularly soon after dawn, with feeding rates remaining high for approximately 1 hour. Over the remainder of the day, the fish fed at lower rates. Daily feed intake varied with season, being high in summer and declining sharply in the autumn, followed by a further decline until fish reached harvest size at the beginning of the following summer.

## 3.10 SYNOPSIS

Monitoring and quantifying the behaviour of farmed fish, whether groups or individuals, is challenging, but various tools have been developed for doing this reliably and accurately. With the advent of cheap video systems, filming fish, either from the surface or using underwater cameras, has become relatively easy. Once analysed, the resulting films can provide valuable information about the behaviour of farmed fish. In addition, a number of electronic tagging techniques have been developed specifically to meet the challenge of tracking one or a few fish among many in three dimensions and in conditions of poor visibility. Together with echo-integration systems for monitoring fish density in production systems, such techniques have been used to obtain information about the behaviour shown by farmed fish and how this relates to environmental conditions. Finally, tools developed for feed management purposes, particularly on-demand feeders, provide a valuable source of information on feeding patterns in farmed fish, which can be enhanced through simultaneous use of electronic identification systems.

All this technology has given researchers a powerful array of tools for quantifying the behaviour of fish in production systems that, combined with other sources of data, allow many aspects of behaviour to be investigated. The results of such studies will appear in later chapters, as will a discussion of how fish farmers might exploit the knowledge and understanding that this research provides. In addition to the scientific information generated by these techniques, they may also provide fish farmers with improved systems for monitoring their stock. Short-term variation in behaviour is common in commercial rearing systems where the fish are subjected to fluctuating abiotic and biotic factors, as well as to handling procedures. This has led to an increased focus on the development of systems that are capable of monitoring such short-term changes in behaviour. For example, information on fish positions within large cages provided by echo integration has been used to fine-tune the placement of lights to suppress maturation (Oppedal *et al*. 2007). Additionally, information from electronic tags can potentially be used to monitor health and welfare of fish in production cages.

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# 4
# Movement and Orientation

*Felicity Huntingford, William Hunter and Victoria Braithwaite*

**Abstract:** The ways in which fish use space in nature are described, distinguishing between movements within a home range, dispersal and directed migration, as are the mechanisms that determine how fish use space. The external stimuli to which fish respond, how they use these cues to find their way around and the role of hormones in migration are also covered. An account is then given of how movement and orientation change with age, the evidence for inherited differences in these aspects of behaviour and environmental effects on development of space use patterns. The benefits that accrue to fish from moving in particular ways are described, as are adverse consequences of such movements, in the form of energetic costs and exposure to predators and pathogens. The ways in which benefits and costs are balanced against each other are discussed, with special reference to diurnal vertical migration. Although cultured fish usually inhabit confined spaces, their natural patterns of orientation and movement can cause a number of problems in aquaculture and some of these are described. Such problems are amenable to biological solutions and these are considered in the final section of this chapter, which also looks at the potential for using what is known about how fish move about to improve the effectiveness of general husbandry practices.

**Keywords:** compass orientation; disorientation; dispersal; home range; homing; interactions with wild fish; mental maps; migration; olfactory imprinting; ontogenetic habitat shifts; route based orientation; tidal stream transport.

## 4.1 INTRODUCTION

Fish live in a three-dimensional world and have several adaptations for both holding station in and moving efficiently through the water (Chapter 2). In spite of their swimming abilities, most fish only occupy a very small part of the space available to them, often concentrating their movements within particular areas, using restricted habitats within these areas and moving about within and between them in more or less predictable ways (Metcalfe *et al*. 2008). This chapter describes how fish in the wild use space, the mechanisms that underlie these space use patterns, how genes and experience combine to determine the way fish move about and how adopting particular movement patterns contributes to individual fitness. Wherever possible examples are taken from cultivated species, but non-cultivated species are also covered where these have proven to be particularly good models for studying movement and orientation. In spite of the fact that cultured fish usually inhabit relatively confined spaces, their natural patterns of orientation and movement can cause a number of problems in aquaculture. Such problems are amenable to biological solutions and these are considered in the final section of this chapter, which also looks at the potential for using what is known about how fish move about to improve the effectiveness of general husbandry practices.

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### 4.1.1 Space use in wild fish

Patterns of movement in fishes can be loosely separated into movements within a defined area or home range, dispersal from such a home range and migration. The term 'home range' refers to a localised area in which an individual animal (or group of animals) confines its activities. An example is provided by a reef fish, the stout bodied chromid (*Chromis chrysurus*), where individual fish inhabit a clearly defined home range, within which they spend their time, moving between a number of good foraging sites (Noda *et al*. 1994). Sea-horses also inhabit a home range and, perhaps not surprisingly given their limited swimming ability, are among the most strongly site-attached of fishes. For example, in *Hippocampus whitei* both sexes confine their activity to home ranges of about 10 $m^2$ in seagrass beds, females having somewhat larger ranges than males (Vincent *et al*. 2005). Fish that use home ranges will often return to them after displacement. For example, another small reef fish, the Bangaii cardinalfish (*Pterapogon kauderni*) lives in groups around aggregations of sea urchins, which give them protection from predators; if these fish are moved from their home site and released 50 m from the point of capture, within a day many return to the site at which they were captured (Kolm *et al*. 2005). Common carp have flexible movement strategies, some individuals moving distances of up to 650 km in a year within a river system and others moving smaller distances between rivers and floodplain areas rich in macrophytes. For those fish that have home ranges, these are not used randomly; instead, there are core areas of intensive use within a larger area to which movement is mainly confined (Figure 4.1; Crook 2004). The greatest movements seem to be related to reproduction and spawning, but the fish may also move over quite large distances when foraging and then return to a more restricted home area (Bajer *et al*. 2010).

Many species of reef dwelling cleaner fish occupy home ranges centred on their cleaning stations, often on coral heads (White *et al*. 2007). These stations may also act as a focus for the client species of fish. Clients use information about the location and nature of individual cleaner fish in complex ways. For example, long-nosed parrotfishes (*Hipposcarus harid*) with home ranges large enough to encompass cleaning stations of more than one cleaner wrasse (*Labroides dimidiatus*) often return to the same cleaning station. They are less likely to do so if during the previous interaction the cleaner fish took a bite of flesh rather than removing ectoparasites (Bshary & Shäffer 2002). Juvenile French angelfish (*Pomacanthus paru*) have cleaning stations on seagrass sandflats near to the reefs on which many of their client species live. The angelfish restrict their movements to an area of 1–3 m around their cleaning stations; clients still visit the stations when the cleaners are removed, so they seem to be attracted to the cleaning location rather than to the angelfish itself (Sazima *et al*. 1999).

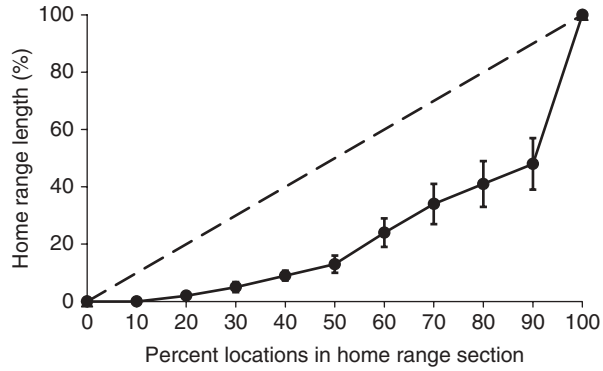


**Figure 4.1.** Home ranges in carp. Mean (±SE) minimum percentage of home range lengths containing selected percentages of the total number of radio locations in tagged common carp. More than 50% of locations of radio tagged carp are concentrated within 20% of their total home range. Adapted with permission from Crook 2004.

Dispersal, or ranging, refers to movement away from a particular area, often when conditions become unfavourable. Movements during dispersal are not necessarily in a fixed direction and they cease once favourable conditions are encountered (Gerlach *et al*. 2007). For example, females of the cichlid *Neolamprologus multifasciatus* lay their eggs in empty mollusc shells and if these are in short supply the fish emigrate, presumably in search of an area where there are more shells (Schradin & Lamprecht 2002).

The term migration refers to directed movements from one well-defined area to another, with migrants usually returning to their original location. Migration may take place over short time scales, such as daily; they may also occur over longer periods, which may be seasonal, annual or related to life-history events. For example, the clients of juvenile French angelfish leave the reefs on which they live and move to sandflats to visit cleaning stations, returning to the reefs once cleaned (Sazima *et al*. 1999). Another reef fish, the brown surgeon (*Acanthurus nigrofuscus*), makes daily migrations of up to 1.5 km from shelters in shallow water used at night, to off-shore feeding sites during the day (Mazeroll & Montgomery 1995). Many fish show regular daily vertical migrations for the purpose

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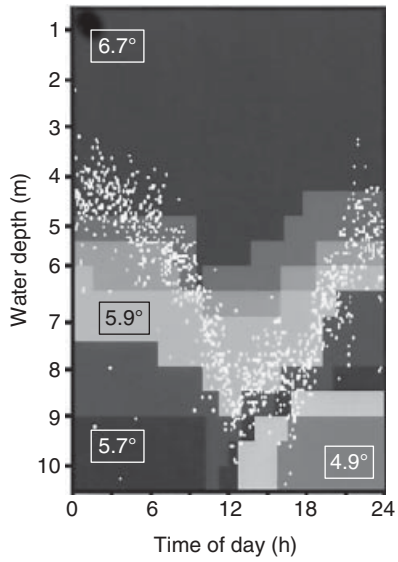


**Figure 4.2.** Daily pattern of vertical migration in Atlantic cod. Shading depicts the thermal stratification within the water column (temperatures indicated), in relation to depth (vertical axis) and time of day (horizontal axis). The white spots indicate the presence of fish. Adapted from Claireaux *et al.* 1995.

of feeding and for avoiding predators. This is seen in many species of marine fish that inhabit the middle layers of the water column (mesopelagic fish), which tend to track light of a particular intensity; these fish sometimes make vertical migrations of several hundreds of metres each day. Atlantic cod may occur in deeper, cooler water during the day and move into shallower, warmer water at night (Claireaux *et al*. 1995; Figure 4.2). As a final example, bearded gobies (*Sufflogobius bibarbatus*) spend the day on the muddy hypoxic substratum of the coastal waters in which they live, but by night they rise into more oxygenated waters nearer the surface (Utne Palm *et al*. 2010).

Other migrations take place over longer time scales and larger distances, often in association with life history events such as spawning. For example, in the summer Arcto-Norwegian cod migrate north from their spawning grounds to feeding areas in the Barents Sea, and then return to spawning sites many hundreds of kilometres further south. Cod of other populations, for example some from the North Sea, migrate shorter distances, while yet others are resident within limited areas, such as a coastal fjord (Robichaud & Rose 2001). In cod, migration takes place entirely within the marine environment, whereas in other species migration is entirely within freshwater, such as when Siberian sturgeon (*Acipenser baerii*) move from the lower reaches of large rivers upstream to the spawning grounds, and post-hatching fish subsequently move back downstream (Khodorevskaya *et al*. 2009). In some species, migration may involve movement between marine and freshwater environments, as in the case of some eels and salmonids (Groot & Margolis 1991; Pennell & Barton 1996; Tesch 2003; Hinch *et al.* 2006). Eels are catadromous, spawning in saltwater and having feeding areas in fresh water, whereas the salmonids are anadromous, with feeding grounds in the sea, and spawning in fresh water. Many important fisheries are based on migratory species and several migratory species are either farmed directly for food or for use in supplementation and sea-ranching programmes (Chapter 1).

## 4.2 MECHANISMS

The previous section has shown how patterns of space use in fish range from directed movement within a small familiar home range to long-distance migrations. This section describes some of the mechanisms, behavioural and physiological, that enable fish to perform such feats of orientation and movement.

### 4.2.1 Spatially informative cues in the aquatic environment

There are several spatially relevant cues that control and direct the patterns of movement of fish (Chapter 2), affecting behaviour in different ways. First, the response of fish to such stimuli may simply involve a change of rate of movement, in which case it lacks a directional component and is called a kinesis. For example, larval brook lampreys are stimulated by light to make lateral movements of their body and when burrowing they continue to make these movements until they are completely buried in the substrate and no longer exposed to light (Jones 1955). Alternatively, fish may respond to a stimulus with movement oriented in a specific direction, in which case the response is called a taxis. For example, many species of fish maintain their body in the correct vertical orientation by the dorsal light reaction, which involves keeping their dorsal surface directed towards the main light source, which in most circumstances is sunlight coming from above.

#### *Visual cues*

Light intensity is the primary guiding stimulus for the daily vertical migrations shown by many species of fish, including juvenile sockeye salmon in lakes. These fish move through the water column tracking light conditions of a preferred intensity and the depth at which the fish

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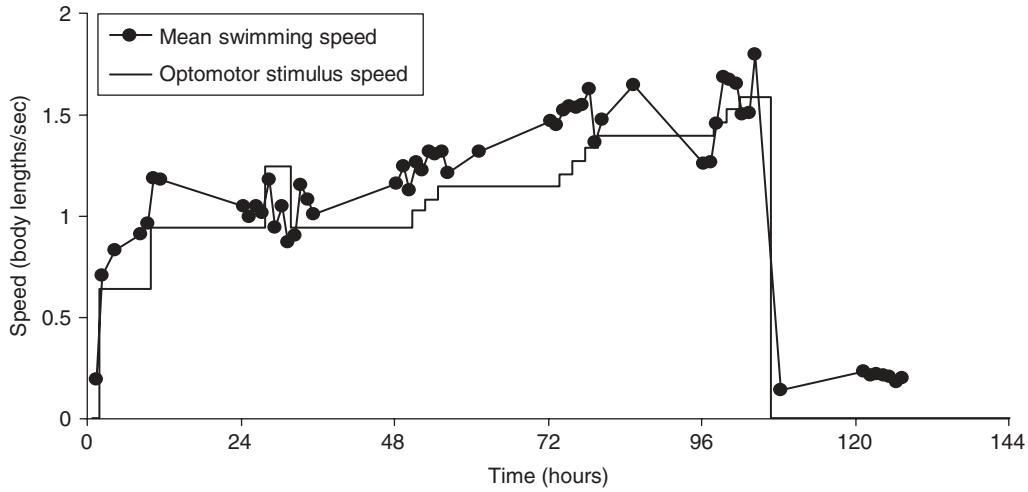


**Figure 4.3.** The optomotor response. Average hourly swimming speed (body length/s) in an individual horse mackerel (*Trachurus trachurus*) tracked within a group of 3 held in dark conditions (black circles) in response to a visual target apparently moving at varying speeds (solid line). The target consisted of 24 Luxaura light guide rods in an outer ring with one lighting group moving sequentially around the tank. Swimming speed in unstimulated fish is approximately 0.25 body lengths/s. Neil Herbert, unpublished data. Reproduced with permission.

are found changes throughout the 24 h cycle (Scheuerell & Schindler 2003). Another important visual determinant of orientation and movement in fish is the optomotor response, whereby a vertical stimulus moving across the visual field elicits a following response (Figure 4.3). This response allows fish to control their position, for example holding station against a current in a stream or keeping pace with other fish in a school.

### *Mechanosensory cues*

Externally generated water movements, or currents, control many aspects of movement and orientation in fish; responses to water currents are called rheotaxes and may be positive or negative. For example, during migration to feeding grounds in lakes, sockeye salmon that emerge from nests in outlet streams show positive rheotaxis, swimming upstream, whereas those from nests in inlet streams show negative rheotaxis, moving downstream towards the nursery areas (Brannon 1972). Currents also provide a source of directional information for fish when they are moving around a home range; for example, sticklebacks can use the direction of water flow to help them remember the position of profitable feeding sites (Braithwaite & Girvan 2003). The ambient noises of the sea are rich in low-frequency sounds generated by turbulence along the edge of ocean currents, waves at the surface and reflections from features of the underwater landscape. Fish make use of such sounds to find their way about. For example, at the point of transition from planktonic larva to benthic juvenile, reef fish of many species, including several that are harvested for capture-based culture, use sounds to orient towards and select appropriate reef habitat on which to settle (Simpson *et al*. 2005).

### *Olfactory cues*

Juvenile fish may use olfactory cues to locate a suitable home-site. For example, different reefs have different bouquets of smells; settling juveniles use these (Doving *et al*. 2006) as well as sounds to locate suitable reefs (Gerlach *et al*. 2007). Olfactory cues are important determinants of movement in other contexts. For example, black rockfish (*Sebastes inermis*) use olfactory cues to return home following displacement (Mitamura *et al*. 2005). Mature sea lampreys (*Petromyzon marinus*) migrating to the streams in which they spawn are attracted to chemicals released by larval conspecifics, presumably an indicator of suitable spawning habitat, as well as by sex pheromones released by mature conspecifics (Vrieze & Sorensen 2001).

### *Temperature*

Since fish are ectotherms, their activity is influenced by ambient temperature. In many cases fish movements are

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finely tuned to local temperature regimes; for example, herring can detect and orient themselves in relation to temperature differences of less than 1 °C (Shelford & Powers 1915) and sea bass move vertically and horizontally to track water of 10 °C, the optimal temperature for maturation (Metcalfe *et al*. 2002). In other words, some of the movements of fish are associated with behavioural thermoregulation in which fish search for, and then remain within, waters of a particular temperature (Wood & McDonald 1997).

***Electric and geomagnetic cues***

Weakly electric fish, sometimes cultured for the ornamental fish trade, live in turbid water and orient themselves using active electrolocation (see Chapter 2). For example, elephant nose fish (*Gnathonemus petersii*) generate an electric field around themselves and continually monitor the status of this field. Information on the strength of the returning signal is combined with information about outgoing signal strength along the length of the body to generate a three-dimensional electrical picture of the world. This enables the fish to locate and identify structures in their environment and to avoid collisions with both inanimate objects and living organisms (Von der Emde *et al*. 1998). A number of fish, for example yellowfin tuna (*Thunnus albacares*), can detect magnetic fields (Walker 1984; Walker *et al*. 1984) and it is suggested they may use this ability during migration (Willis *et al*. 2009).

### 4.2.2 How fish use spatial information

Fish use spatial information to explore novel areas, to find their way around familiar areas, to return to their home range after being displaced and to migrate between geographically distinct areas. They achieve this through a variety of mechanisms, ranging from moving towards landmarks to the formation of mental maps (Braithwaite & Burt de Perera 2006). Knowing about the mechanisms that allow fish to move around and exploit efficiently the resources in their natural environment can help to explain how cultured fish behave and in managing what they do in production systems.

***Selective tidal stream transport***

Where currents are predictable in direction, fish can move between locations on various geographic scales by opting to move into and out of these. For example, juvenile plaice (*Pleuronectes platessa*) move from offshore waters to nursery areas in shallow water near the shore. They do this by moving up into the water column during rising tides that carry them shorewards and descending to the substrate, out of the current, during falling tides. Adults also use selective tidal stream transport when migrating between their feeding and spawning grounds. Combined with an ability to recognise their destination, as long as current direction is predictable, this is a reliable mechanism of migration used by many fish species (Metcalfe *et al*. 2008). It should also be noted that currents can flow in different directions at different depths in the water column, so by making vertical movements fish can sometimes ensure that they remain within water masses that are flowing in the appropriate direction in relation to their migratory route. In addition, exploiting the water movements in directional currents means that speed over the ground can be much greater than swimming speed.

***Route-based orientation***

Fish may move efficiently around an area by keeping track of their own previous movements, or in other words by using self-referential inertial guidance. For example, when foraging in an eight-armed maze, corkwing wrasse (*Crenilabrus melops*), which are sometimes used on salmon farms for louse control, can find a food item by using the simple rule of visiting every third arm, thereby avoiding revisiting the same place; to do so, they must be able to keep track of their movements (Hughes & Blight 1999). The ability to use such a system offers the possibility of route-based navigation, whereby animals can return to a starting point after an outwards trip using an integrated memory of movements made on the outward trip; this is called inertial guidance, path integration or dead reckoning. Migrating plaice may possibly use inertial guidance based on infra-sound, at frequencies below 20 Hz, to maintain a steady heading (Harden Jones 1984, cited in Sand & Karlsen 2000), but path integration has never been fully demonstrated in migrating fish. This may be because the complex currents and water movements that fish experience would make this an inaccurate way of navigating over longer distances, with a strong likelihood of drifting off route (Braithwaite & Burt de Perera 2006).

***Compass orientation***

A reliable way to maintain a particular direction over long distances is to orient in relation to a stable directional cue in the environment; in other words, fish may use a compass to maintain a particular bearing. A number of fish species are known to use the sun as a compass; for example, sockeye salmon migrating in large lakes are able to orient by the sun's position, as well as by polarised light patterns and by the Earth's magnetic field (Dittman & Quinn 1996). The use of multiple directional cues for compass orientation provides a back-up when one cue is obscured, for example polarised light can be used when the sun is hidden from view by clouds.

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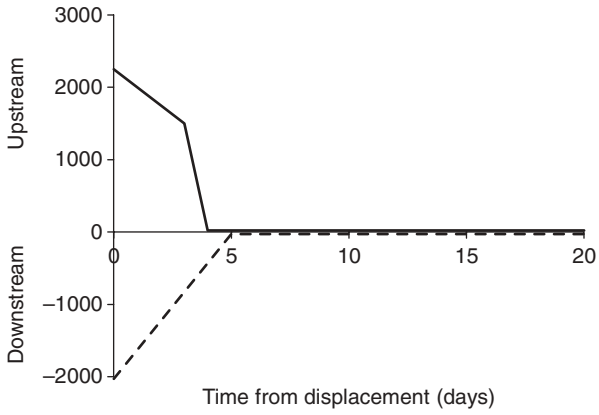


**Figure 4.4.** Site fidelity and homing in carp. Distance (m) moved by two carp translocated upstream (solid line) and downstream (broken line) of their home range (0) in relation to days after release. Adapted from Crook 2004.

### *Landmarks*

Fish can use localised cues detected from a distance, sometimes called landmarks, to direct their movements in both familiar and unfamiliar surroundings. For example, common carp show fidelity and homing, probably based on the use of landmarks (Crook 2004; Figure 4.4). In addition, juvenile Atlantic salmon can use visual cues to direct foraging activity towards profitable feeding sites (Braithwaite *et al*. 1996). Landmarks can also control movement on a larger scale; migrating surgeonfish (*Acanthurus nigrofucus*) alter their routes when landmarks are displaced, pausing for several minutes both at the point at where the displaced landmark used to be and at its new location before resuming swimming along the migratory route (Mazeroll & Montgomery 1998). A landmark can be olfactory, as when mature Arctic charr swim towards scents produced by smolts of their natal population (Selset & Døving 1980) or when adult salmon direct their upstream migration towards their natal waters (Døving & Stabell 2003). Sockeye salmon use both visual and olfactory cues to guide them to the mouth of their natal river (Ueda *et al*. 1998).

Fish can use a series of familiar landmarks to guide movement over longer distances, a form of navigation that is called pilotage. Evidence for the ability of fish to learn a sequence of landmarks comes from studies on blind cavefish (*Astyanax fasciatus*), which use their lateral line organs to detect perturbations in the flow field that forms around them as they move about (see Chapter 2). The fish use this system to detect and orient to a sequence of landmarks, providing 'an ordered list of learnt places' by which they pilot themselves through their home range (Burt de Perera 2004). Several species of butterfly-fish follow predictable paths as they swim between feeding patches on coral reefs, using a sequence of visual features to guide their movements (Reese 1989). During downstream migration, salmonid smolts may learn to recognise a series of odorants that they use in reverse when they return to their natal river as maturing adults (Harden Jones 1968).

### *The formation of mental maps*

As well as using conspicuous features directly as landmarks, some fish can remember topographical relationships between environmental features and use this information to form a spatial cognitive map. The spatial information in such maps allows fish to move efficiently around a familiar area, heading towards particular goals from unfamiliar starting positions using varied and novel routes. For example, the frillfin goby (*Bathygobius soperator*) may be trapped in a small pool by the falling tide and if attacked by a predator, the fish escapes by jumping into another pool, even when the second pool is out of sight. The gobies follow such effective escape routes using a spatial cognitive map developed as they swim about at high tide (Aronson 1951, 1971). An ability to form spatial maps has been demonstrated in blind cave fish (*A. fasciatus*), which encode the distance between and relationships among landmarks and use this to identify their current position (Burt de Perera 2004). The lateral pallium in the brain telencephalon (Chapter 2) seems to play a critical role in the ability of fish to form mental maps. For example, the rate of protein synthesis is higher in the lateral pallium of goldfish after they have learned a spatial task (Vargas *et al*. 2000, 2006) and the ability to use spatial maps, but not to use landmarks, is impaired if the lateral pallium is destroyed (Rodriguez *et al*. 2002; Broglio *et al*. 2003; Vargas *et al*. 2006).

## 4.2.3 Effects of hormones on migration

Migration often coincides with key life history events, such as maturation. The occurrence of migration is therefore indirectly linked to secretion of the hormones that control such events (Chapters 2 and 10). This is relevant to aquaculture because, even when held in captivity with no possibility for migration, fish will experience natural hormonal changes, which prompt behavioural changes. Thyroid hormones often play a key role in the control of movement and migration in fish. For example, the change from negative to positive phototaxis that causes juvenile brook charr to emerge from the redd coincides with an

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increase in thyroid hormone production (Hinch *et al*. 2006). Some of the changes that accompany parr–smolt transformation in salmonids coincide with a surge in circulating thyroid hormones; these may include body silvering, olfactory imprinting and behavioural changes as the fish switch from living within a defined home range to a migratory, schooling way of life. In Atlantic cod, levels of thyroxine increase at the start of the autumn migration from coastal to offshore areas, with this thyroid hormone possibly inducing increased metabolism and swimming capacity (Comeau *et al*. 2001).

### 4.2.4 Summary of the causes of space use and orientation in fish

There are many spatially relevant cues in the environment and as a group fish make use of all of these to control movement and orientation on a range of spatial scales. The mechanisms involved can be relatively simple, as in the non-directional kineses shown by burrowing lamprey larvae and following a moving stimulus during the optomotor response that stimulates swimming in many species. They can also involve more complex processes in which behaviour is controlled and oriented by cues with a directional component. Among the capabilities that enable fish to move effectively in three-dimensional space are: self-referential systems, such as when wrasse avoid searching for food in areas that they have already visited; the use of landmarks, such as when juvenile Atlantic salmon learn to use landmarks to identify profitable feeding sites; pilotage, such as when juvenile salmonids leaving their natal river learn a sequence of odours that they use in reverse when returning to breed; and the formation of cognitive spatial maps, such as when blind cave fish build up a representation of their home range on the basis of the mechanosensory cues that they detect when moving around. Large-scale migrations, which feature in the lives of many species of fish, cultured or otherwise, often occur in association with critical age-dependent habitat shifts. The behaviour patterns that fish show at these times are often modified by the same hormones that control morphological and physiological adaptations to the fishes' new habitat. Understanding the mechanisms that control fish movement and use of space may help to prevent a variety of problems that occur when fish are cultured.

## 4.3 DEVELOPMENT

### 4.3.1 Ontogenetic changes in movement patterns

In all fish, orientation and movement patterns change with age and this dictates the space and other conditions that they require, both in the wild and when held in captivity. For example, many marine fish have a planktonic larval phase and development includes metamorphosis, during which there are dramatic changes in body form and habitat. At metamorphosis, sea bass change their body shape and muscle structure and they also start to develop scales. These changes are accompanied by reduced propensity to swim against a current as the fish move from epipelagic waters to near the seabed (Koumoundouros *et al*. 2009).

Changes in space use and movement with age have been well documented for salmonid fishes. On hatching, the young fish, called alevins, remain hidden in the gravel redd and are relatively unresponsive to current and moving visual cues. When the yolk is absorbed and fish need to feed, they emerge from the gravel and move to nursery areas by passive drifting and active swimming (Veselov *et al*. 1998). As the fish become older, in the case of Atlantic salmon they often move from shallow riffles with moderate current to habitats with a faster current over a coarser substrate. The young fish tend to concentrate their activity in localised home ranges, which may sometimes be defended as territories (Armstrong *et al*. 1997 and see Chapter 9). Within these home ranges the fish hold station at one or a number of favourable feeding positions (Godin & Rangeley 1989), taking shelter when disturbed. They usually return to their home range following displacement (Saunders & Gee 1964) or disturbance (Armstrong *et al*. 1998; Huntingford *et al*. 1998). Individuals vary in their patterns of space use, with fish that occupy a localised territory coexisting with mobile and less sedentary individuals (Figure 4.5; Bradford & Taylor 1997; Armstrong *et al*. 1997; McLaughlin *et al*. 1992).

While juvenile Atlantic salmon are occasionally found in lakes, this is always the case for sockeye salmon (*Onchorhynchus nerka*), which initially settle in shallow, littoral areas, but later adopt a pelagic life style. Here they show vertical migration on a daily basis, moving close to the surface at dusk, spending the night in shallow water and returning to relatively deep water at dawn (Levy 1987; Hinch *et al*. 2006; Scheuerell & Schindler 2003). Once they reach an appropriate size, juveniles of many salmonid species undergo parr–smolt transformation that prepares them for life in seawater. The main smolt migration takes place in spring, the exact timing depending on species, latitude and temperature. The parr–smolt transformation involves changes in morphology, physiology and behaviour (Pennell & Barton 1996; Le Francois *et al*. 2010). Behavioural changes include reduced sensitivity to flow and to moving visual stimuli (Veselov *et al*. 1998), reduced feeding and a switch from site attachment to mobile schooling. During downstream migration, fish orient with

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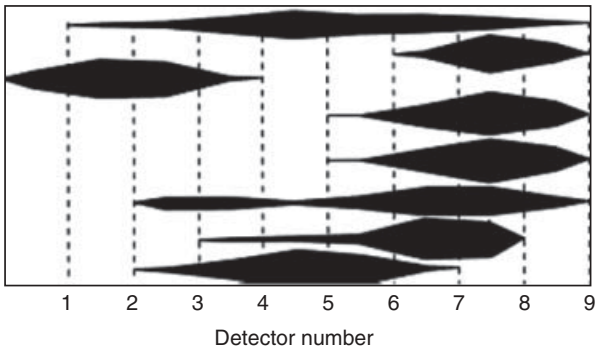


**Figure 4.5.** Individual variability in space use patterns in juvenile Atlantic salmon. Estimated use of sections of stream by 8 PIT-tagged fish, using flat bed PIT detectors placed across a small stream. Width of each dark area represents the intensity of space use by a given fish at a given location. Reproduced with permission from Martin Smith & Armstrong 2002.

and are carried by the current, but they also swim actively (Moore *et al*. 1995; Lacroix & McCurdy 1996).

On reaching the estuary of their natal river, migrating smolt start moving towards their marine feeding sites, initially showing irregular, but directed, movement close to the coast (Thorstad *et al*. 2004). In sockeye salmon, coastal migration routes follow circulation patterns of the surface water, but the fish also swim actively, periods of migration being interspersed with periods of feeding. After up to a year on the continental shelf, sockeye move further offshore, before initiating a migration to rich oceanic feeding grounds. Large-scale movements during this phase are dictated by major oceanic current systems, but fine-scale choices are made in relation to water temperature and food availability (Groot & Margolis 1991; Pennell & Barton 1996; Hinch *et al*. 2006). Ocean-going salmon swim within a few metres of the surface, often meandering and backtracking, presumably following localised food, and travelling many thousands of kilometres in the process (Hansen & Quinn 1998). After a period of oceanic feeding, rapid growth and accumulation of energy reserves, salmon begin their homeward journey to spawning sites in the rivers in which they hatched.

Norwegian Atlantic salmon returning from feeding grounds around the Faroe Islands and Greenland initially swim in a southerly direction at speeds of 22–46 km/day and gradually approach the Norwegian coast (Hansen *et al*. 1993). Sockeye salmon move at speeds of up to 70 km/day, still foraging actively and building up energy reserves as they approach the Pacific coasts (Groot & Quinn 1987). Chum salmon migrating towards coastal areas travel as far as 2500 km at speeds of *ca* 36 km/day and maintain orientation towards their natal area (Tanaka *et al*. 2005). As the migrating fish approach the coast, they follow the shoreline until they reach the mouth of their natal river, where they may remain for some weeks before beginning the final phase of upstream migration. The timing of this phase is related to how far the fish have to travel to the spawning grounds and to local flow regimes; fish with longer and more difficult journeys enter the river earlier and with larger energy reserves than do salmon that spawn closer to the sea. During the upstream migration, salmon typically stop feeding, orient into the current and swim upstream, sustaining speeds of more than 40 km/day for long periods (Hinch *et al*. 2006).

### 4.3.2 Inherited differences in space use

Some age-related changes in space use and orientation are the result of gradual development of the systems needed for effective movement, largely under genetic influence. For example, as juvenile Atlantic salmon become older and larger they are able to hold station at higher current speeds and to cope better with turbulence and this changes how they use space (Vaselov *et al*. 1998).

Several lines of evidence point to the existence of inherited differences in patterns of movement and orientation in fishes. For example, three-spine stickleback (*Gasterosteus aculeatus*) specialised for benthic foraging in the structured vegetated littoral zone of a small lake (Chapter 5) learn to use a landmark to find food more quickly than do sticklebacks that forage in the open-water pelagic zone (Odling Smee *et al*. 2008). Dwarf lake whitefish (*Coregonus clupeaformis*) prefer higher parts of the water column than do fish of the normal form, which favour deeper water. Hybrids between the normal and dwarf forms show intermediate depth preference, indicating an inherited component to the variability (Rogers *et al*. 2002). Differences in space use and migration between genetically distinct stocks reared under standard conditions also suggest that the behaviour patterns concerned are inherited. For example, there are both migratory and non-migratory stocks of Atlantic cod and among migratory stocks there are sub-stocks that travel in different directions and for different distances (Ruzzante *et al*. 2000; Knutsen *et al*. 2003; Metcalfe *et al*. 2008). Table 4.1 summarises some studies demonstrating strain differences in movement patterns in salmonid fish. At a very different level, zebrafish with particular mutations move and orientate differently to normal fish. For example, the mutant *belladonna* results

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**Table 4.1.** Some evidence for strain differences in movement patterns in salmonid fishes.

| Species | Observations | Source |
|---|---|---|
| Atlantic smolts | Naturally-spawned fish from a lower tributary (hence with a shorter seaward journey) begin migration later than those from an upper tributary in the same system, even when transferred to the upper catchment as unfed fry. | Stewart *et al*. 2006 |
| Atlantic adults | Stock-specific migration patterns exist, with hybrids showing intermediate behaviour, indicating both maternal and paternal effects. | Kallio-Nyberg *et al*. 2000 |
| Coho smolts | At the point of migration into coastal waters, coho salmon from different stocks head in different directions, some going predominantly north and others predominantly south. | Weitkamp & Neely 2002 |
| Chinook adults | Non-random use of fish ladders by different stocks occurs, with fish using the ladder adjacent to the side of the river that their tributary joins. Route segregation increases as fish approach their natal tributary. | Keefer *et al*. 2006 |
| Sockeye adults | Populations of sockeye originating from sites further upriver start the return migration earlier and carry larger energy stores. | Crossin *et al*. 2003 |

in defects in the optic chiasma and the fish display a reversed optomotor response and an abnormal form of swimming called looping (Huang *et al*. 2009). That inherited differences in patterns of movement and migration exist is important for fish culture, because it may be possible to carry out selective breeding to generate fish that display particular orientation behaviours and patterns of movement.

### 4.3.3 Effects of experience on space use and migration

Environmental factors provide another source of variability that may influence space use and movement patterns in fish. The effects may be of a general nature, as when temperature and food supply combine to influence growth rates in juvenile salmonids and thereby determine the timing of migration to the sea (Jonsson *et al.* 2005; Olsson *et al*. 2006). In other cases, environmental effects on the development of movement patterns may be somewhat more specific. For example, exercise during early development in zebrafish increases swimming efficiency (Bagatto *et al*. 2001), probably through modification of neuromuscular development (Bagatto *et al*. 2001; Pelster *et al*. 2003). Effects of experience on movement patterns may also be highly specific, as when fish remember locations by learning about landmarks and use these to direct behaviour (Odling-Smee & Braithwaite 2003; Braithwaite & Burt De Perera 2006). The capacity for learning about landmarks continues throughout life, but long-term influences of experience with landmarks can be seen in developing fish. For example, hatchery-reared juvenile cod exposed to both variable food and variable visual landmarks are more likely to explore a novel area than are those reared in a simple environment (Braithwaite & Salvanes 2005). Such findings are important when considering the effects of captive rearing on the behaviour of fish reared for release. There is evidence that some young fish learn migratory routes from older, more experienced members of the same species. For example, during their first spawning migration, young herring follow older fish that are themselves following landmarks learned in previous years (McQuinn 1997; Fernö *et al*. 1998) and young plaice and charr may also learn traditional migration routes from older fish (reviewed in Metcalfe *et al*. 2008).

Effects of early experience on migration later in life are seen in several salmonid species, which use the bouquet of scents from their natal stream to guide their movements in the latter stages of their spawning migrations (Hasler & Scholz 1983. Odling-Smee *et al*. 2006). This may be based on olfactory imprinting, which in its simplest form involves the learning of home stream odours during exposure at a sensitive period around the parr–smolt transformation. Evidence that this occurs comes from studies of the effects of translocation of juvenile salmon away their natal stream; provided the fish are translocated before they undergo parr–smolt transformation, the adult fish tend to migrate to the translocation site rather than their natal stream. Additional evidence comes from the fact that salmon exposed to artificial chemicals such as morpholine during parr–smolt transformation are attracted to these scents during their subsequent upstream migration as maturing adults (Hasler & Scholz 1983). The surge of thyroxine that

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occurs at around the time of the parr–smolt transformation is thought to play a central role in olfactory imprinting, by stimulating neurogenesis in the olfactory epithelium (Morin & Døving 1992; Dittman & Quinn 1996). Further, artificial exposure of younger fish to thyroxine stimulates the formation of long-term memories of specific odours (Scholz 1980, reviewed in Dittman & Quinn 1996). During upstream migration of adults, enhanced cortisol secretion is associated with somatic and neural degeneration, but may enhance the recall of home stream odours by priming the olfactory regions of the brain (Carruth *et al*. 2000).

There are a number of areas of uncertainty relating to the olfactory imprinting hypothesis as it applies to migrating salmonids. For example, imprinting may not necessarily be a one-off event occurring at a single critical point. As they get older, many salmonids move away from the site at which they hatched, eventually transforming into smolts at points far downstream, yet they still return to natal areas (Dittman & Quinn 1996). It therefore seems that olfactory imprinting can take place over a relatively long period, starting well before and finishing well after the time of the parr–smolt transformation. Salmon undergoing their downstream smolt migration may learn a sequence of odours and follow this in reverse when returning to their natal areas as maturing adults; fish deprived of experience of part of the downstream migration path usually fail to return to the natal area.

It is also unclear whether scents produced by small conspecifics are important in attracting the maturing adults, thereby controlling the migratory movements of the larger fish to the spawning grounds in their natal streams. Certainly, streams vary in their bouquet and fish can distinguish among them. On the other hand, fish are very sensitive to conspecific odours. Salmonids are attracted to water containing the scent of their own species and can discriminate among populations and recognise their siblings on the basis of scent (Quinn & Tolson 1986). An alternative to the olfactory imprinting hypothesis is that homeward migration involves following a pheromone trail left by related smolts migrating in the opposite direction. Transplantation experiments using charr and trout show that both species can sometimes home effectively without having had previous exposure to water from the natal stream and therefore with no opportunity for site imprinting. It is suggested that while at sea the fish join relatives from their river of origin and migrate with them (Nordeng & Bratland 2006). Salmonids probably use several cues when migrating towards their natal rivers in the sea and then when locating spawning areas once they have entered fresh water. Whatever turns out to be the case, the process of olfactory imprinting is important in aquaculture because, among other things, it offers the possibility of controlling the behaviour of salmonids released into the wild, possibly making sea ranching a feasible operation. In addition, it will to some extent determine the impact of farm escapees on natural populations.

#### 4.3.4 Summary of the development of space use and orientation in fish

How fish use space changes with age and stage of development and such changes are often linked to a metamorphosis, such as when pelagic larvae metamorphose to become juveniles and start to live on or near the substratum. Changes in movement patterns also occur as fish grow larger and both their swimming capacity and their need for resources increases. Some differences in orientation and movement between and within species are inherited. For example, Atlantic salmon from different areas within a watershed have different distances to travel upstream to their natal streams and start their spawning migrations at different times. Movement, orientation and migratory patterns may also be influenced by differential experience, such as in olfactory imprinting by which young salmonids learn the scent of their natal stream and use this to direct their spawning migration some years later.

### 4.4 FUNCTIONS

Fish use space in many different ways, determined by complex underlying control mechanisms and developmental histories. The fish gain benefits by adopting particular patterns of space use, but these also incur costs that must be balanced against such benefits.

#### 4.4.1 Benefits of adopting particular space use patterns

***The benefits of moving rather than staying put***

Fish may move about to avoid unfavourable conditions, including the presence of predators (Chapter 8); for example, small juvenile brown trout (*Salmo trutta*) move away from open water towards the river bank to reduce the risk of being attacked by predators (Bremset & Berg 1999). They may also move about to track resources, as when juvenile Atlantic salmon use visual landmarks to track a spatially variable food supply (Braithwaite *et al*. 1996). Movement may serve to bring fish to and keep them in conditions that optimise various functions; for example, both seabass (Pawson *et al*. 1987, 2000) and spawning sockeye salmon track water of a temperature (9–11 °C) that is optimal for sexual maturation (Newell & Quinn 2005). Moving to warm water may also help to control

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pathogens and 'behavioural fever' has been described in several fish species (Covert & Reynolds 1977). Movement itself may have beneficial consequences. Thus fish that have undertaken sustained swimming may show low stress levels and fast growth (Jobling *et al*. 1993; Davison 1997; Chapter 1). Sockeye salmon that have exercised against a current show accelerated maturity, females are more successful than unexercised fish at depositing eggs and both females and eggs survive better (Patterson *et al*. 2004).

***The benefits of forming maps rather than simply following cues***

When fish move within a large area they could rely on chance encounters to bring them into contact with resources. However, by developing an internal representation of the area and the distribution of important elements within it, in other words forming a cognitive, spatial map, a fish can increase the efficiency with which it finds and exploits resources. Stout-body chromids exhibit organised search strategies as they feed on patches of zooplankton, allowing them to forage without retracing their steps (Noda *et al*. 1994) and corkwing wrasse use memorised visual cues to discriminate among sites in which resources are replenished at different rates (Hughes & Blight 2000). As an additional example, the ability of clients of cleaner fish to return to cleaning stations at which they have had ectoparasites removed and to avoid those where they were bitten by the cleaner fish (Bshary & Schaffer 2002) would seem clearly beneficial and is likely to involve some sort of spatial memory.

***The benefits of regular migration***

The benefits of migration on a small scale are illustrated by female yellow tail damselfish (*Microspathodon chrysurus*), which briefly leave their territories to spawn some distance away. Some females complete spawning before returning to their territory, while others frequently interrupt spawning to return to their territory and this may reduce the likelihood of territorial intrusions by other fish (Sikkel & Kramer 2005). By moving into muddy, hypoxic, sulphidic areas by day, bearded gobies gain protection from predation, since other vertebrates avoid such areas (Utne Palm *et al*. 2010). Regular large-scale migrations between two or more areas, often feeding areas and spawning areas, can be explained by the fact that the environmental requirements of adults and young usually differ, so a habitat that suits one life history stage is unlikely to suit another. One driving force favouring migration may be the need for subadults to reach feeding grounds where they can achieve fast growth and obtain sufficient resources to enable successful reproduction. A second driving force for migration is the assurance of juvenile survival and growth, which may be favoured in habitats that are not suitable for adults. In the case of homing to a particular spawning area, by definition, the conditions in the place at which the mature, adult fish hatched must have been adequate for survival, development and growth. If conditions in spawning areas are reasonably stable over time and if the costs of returning to these areas are not too high, returning to the natal site for spawning is a good option. In addition, when fish breed on several occasions, returning to a familiar area could help to bring fish in contact with suitable breeding sites and mates (Mitamura *et al*. 2005). This may be the case for black rockfish (*Sebastes inermis*), which congregate in specific spawning areas in which males defend breeding territories (Shinomiya & Ezaki 1991).

### 4.4.2 The costs of adopting particular space use patterns

The costs of moving include the energetic costs of swimming, increased predation risk and increased risk of exposure to disease.

***Energetic costs of swimming***

Movement involves a number of costs. In the first place, during fast ascents and descents swim bladder volume will change in response to depth-related changes in hydrostatic pressure and will often deviate from the optimum for neutral buoyancy. There is a lag because of the time required to void gases from, and secrete gases into, the bladder as the fish moves up and down in the water column. This constrains rapid vertical movement in most teleosts and also incurs costs. Fish that are ascending and descending in the water column will not be neutrally buoyant and this imposes increased swimming costs associated with the need to generate dynamic lift or counteract the forces that will cause the fish to rise too rapidly. There are also costs involved in the development of organs and tissues required for increased swimming capacity; for example, both heart size and muscle metabolic capacity increase in Atlantic salmon prior to their smolt migration (Leonard & McCormick 2001). In addition, swimming is an energetically costly activity (Figure 4.6; Farrell *et al.* 2003). For each size and species of fish, there is an optimum swimming speed at which the energetic costs per distance moved are minimized. When moving over long distances, such as when migrating, fish of several species, including Atlantic salmon and Atlantic cod, most frequently swim at speeds that are close to the optimum (Jobling 1994). The energetic

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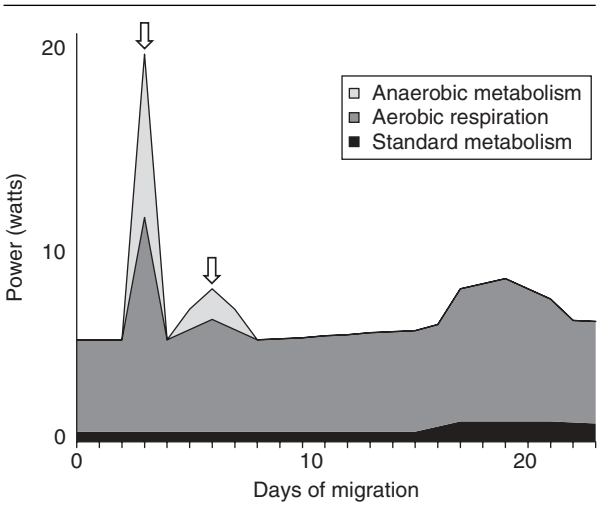


**Figure 4.6.** Costs of migration. Estimated power consumption by various activities during migration from the mouth of a North American river to spawning grounds, for an average female sockeye salmon, based upon metabolic costs calculated by electromyogram telemetry and bioenergetics modelling. Light grey = anaerobic respiration. Dark grey = aerobic respiration. Black = standard metabolism. Arrows indicate passage through hydraulic barriers. Reproduced with permission from Hinch *et al.* 2006.

costs of migratory swimming are particularly striking since migrating fish, like migrating birds, often cease or drastically reduce feeding and rely upon stored reserves for energy. For example, during upstream spawning migration salmonids may deplete up to 75% of their body fat, equivalent to half their total energy reserves (Brett 1995) and costs of spawning migration can be as high as 18 kJ/kg/km (Dodson 1997).

Migrating fish have a number of adaptations for minimising swimming costs, for example by adopting selective tidal stream transport, 'riding' favourable currents and descending to the substrate under unfavourable flow conditions. Migrating salmon select low current paths where possible (Standen *et al*. 2004), minimising the costs per unit of distance covered (Hinch & Rand 2000). Pink salmon (*Oncorhynchus gorbuscha*), which have relatively small energy reserves, minimise the costs of upstream migration by following routes that offer the least resistance (Crossin *et al*. 2003), making use of small-scale flow reversals and vortical flows in turbulent water (Liao *et al*. 2003; Liao 2004). Migrating salmon can also reduce costs by making vertical movements into water of temperatures that allow them to swim with increased metabolic efficiency (Tanaka *et al*. 2000). Even with such adaptations, energetic costs of migration are high, and these must be traded -off against some other characteristics. For example, male chinook salmon with higher than normal migration costs have reduced secondary sexual characters, with smaller dorsal humps and shorter upper jaws, used in competition for spawning opportunities (Chapter 10; Kinnison *et al*. 2003).

***Predation and disease costs***

Predation risk is increased during migration, partly because moving fish are conspicuous and partly because they may be physiologically stressed and in poor condition. For example, more than 50% of wild sea trout smolts are eaten by herons and cormorants (Dieperink *et al*. 2001), while (hatchery-reared) Atlantic salmon smolts are a major prey for Atlantic cod during the smolt migration (Hvidsten & Møkkelgjerd 1987). Being physiologically stressed may put migrating fish at increased risk of disease and movement into new areas may expose migrating fish to novel parasites and diseases. The relationship between migration and disease can be complex. For example, before migrating up-river, late run sockeye salmon spend some weeks in cool, brackish waters of the river mouth as maturation proceeds towards completion, rather than immediately entering the warmer fresh water of the river. Since sea lice develop rapidly in warm water, staying in cool water may prevent a build up of lice (González & Carvajal 2003). On the other hand, like many ectoparasitic marine organisms, sea lice are relatively intolerant of fresh water, so passing immediately from the sea to fresh water would reduce lice infestation even more.

### 4.4.3 Integrating costs and benefits

In functional terms, a fishes' pattern of space use depends on the balance of benefits and costs; this has been examined in detail in the case of daily vertical migrations. A common pattern is for fish to stay in deep water during the day, ascending into shallower water at dusk, and spending the night close to the surface. Movements follow the changes in illumination that occur at dawn and dusk. There are several proposed functions of diel vertical migration and these relate to the fact that ambient light levels and temperature are both usually lower in deeper water. Diel vertical migrations are potentially relevant to aquaculture when the culture environment is vertically stratified. The effectiveness of some husbandry practices may be determined by the depth at which the fish congregate and attempts by cultured fish to express diel migration in a confined space can cause crowding.

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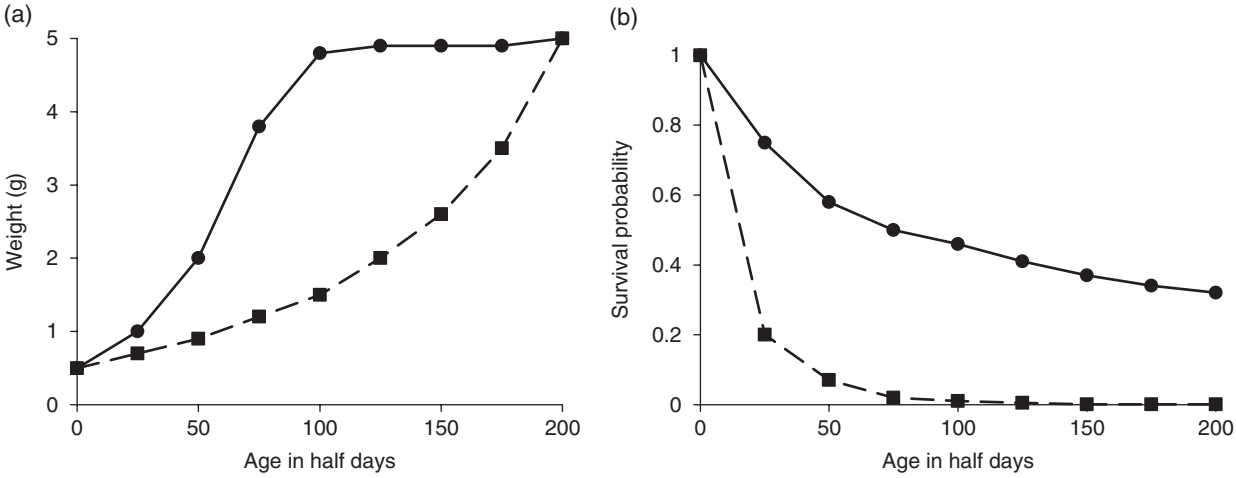


**Figure 4.7.** The costs and benefits of daily vertical migration in juvenile salmonids. Estimated values for (a) growth rate and (b) survival against time in fish that show daily vertical migration (black circles and solid line) and those that do not (black squares and dashed line). From Mangel & Clark, 1989 *Dynamic Modeling in Behavioral Ecology*, copyright Princeton University Press. Reprinted by permission of Princeton University Press.

In general, fish may derive three main benefits from diel vertical migration; these are not mutually exclusive. First, vertical movement may allow fish to follow their prey in space and time, thereby maximising foraging. This is, for example, the case for basking sharks (*Cetorhinus maximus*; Sims *et al*. 2005) and siscowet (*Salvelinus namaycush siscowet*; Hrabik *et al*. 2006). Second, daily vertical movement may allow fish to avoid predation, with fish using darker deep water to hide from visually hunting predators during the day; this may be the case for ciscoes in large North American lakes (Jensen *et al*. 2006). Finally, daily vertical movement may promote energetic efficiency. Under conditions where fish have a limited supply of food, both growth rates and food conversion efficiency are generally better at low temperature than at high. This means that when food is limited, bioenergetic advantages are likely to accrue for fish that undertake vertical diel migrations, feeding in warmer surface waters where there is most food and then moving into cooler deeper water where the energetic costs of metabolism are reduced. For example, dogfish (*Scyliorhinus canicula*) can lower daily energy costs by adopting a 'hunt warm–rest cool' strategy, spending the day in relatively cool water, but making short forays into shallower, warmer water to feed during the night (Sims *et al*. 2006).

Fish can optimise growth and survival by making continuous trade-offs between the need to forage and feed, to avoid predators and to conserve energy. This may underlie the daily vertical movements of lake-dwelling juvenile sockeye salmon. These fish feed on zooplankton in the upper water layers, but are in turn preyed on by visually hunting piscivores. Sockeye undertake diel vertical migrations, ascending close to the surface at dusk, spending the night in shallow water and descending at dawn to relatively deep water. Daily changes in food availability and vulnerability to predation considered in isolation cannot account for these vertical movements, but a model that combines the two selection pressures works well (Clark & Levy 1988, described in Mangel & Clark 1988). Key elements of the model are functions that define the relationship between feeding rates and the fish's visual range, for both the planktivorous sockeye and its predators. Based on cruising speeds, visual range, prey density and prey handling time, the model considers how feeding rate varies with visual range and defines the point at which reduced light intensity begins to affect the feeding rates of the planktivorous sockeye and its predators.

The feeding rate inflection points are at about 1 cm for the planktivore and 2.5 m for the piscivore, but these vary as surface illumination changes, and hence with time of day. Output from the model shows that there are specific conditions under which the planktivores can forage efficiently but the piscivores cannot, offering a predation-free window for the planktivores. Model planktivores that migrate into surface waters to feed at dawn and dusk grow faster (Figure 4.7a) and survive better than those that do

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not show daily vertical migration (Figure 4.7b; Mangel & Clarke 1988). Real vertically migrating juvenile sockeye do indeed experience a daily antipredation window, the length and timing of which varies with season (Scheuerell & Schindler 2003), indicating that the trade off between feeding efficiency and predator avoidance may in principle explain why juvenile sockeye salmon show daily vertical migration (Clark & Levy 1988).

The mechanisms involved in behavioural thermoregulation may also be an important aspect of vertical migration of plantivorous fish such as sockeye, because the shallower water in a lake is often warmer as well as having higher prey concentrations than deep water (Wood & McDonald, 1997). Juvenile kokanee salmon, which is the freshwater form of sockeye salmon, feed in warm surface waters and then descend into deeper cooler waters during non-feeding periods, when digestion takes place more efficiently (Bevelhimer & Adams 1993).

### 4.4.4 Summary of the functions of space use in fish

Fish derive benefits from the way they use space; for example, forming spatial maps of a restricted area can improve the efficiency with which resources are harvested and movements from adverse to suitable areas can promote fitness. Swimming generally, and long distance movements in particular, may incur considerable costs, primarily energetic but sometimes in terms of risk of predation and disease. Over evolutionary time, natural selection has moulded the ways in which fish use space so that they balance these costs and benefits, unconsciously trading them off in such a way as to maximise fitness. The complex balance between the need to acquire food and to avoid being attacked by predators is exemplified by the daily vertical migrations shown by several species of fish.

## 4.5 IMPLICATIONS FOR AQUACULTURE

How fish move in their three-dimensional world is an important aspect of their biology and considerations of fish movement are also important when it comes to aquaculture. Fish that are farmed extensively spend much of their lives in environments that are not very dissimilar to those experienced by wild fish. Under such circumstances farmers may experience few problems arising from the natural space use patterns of their fish. In the case of intensive culture, the spatial environment in which fish are held is very different from that experienced by their wild counterparts. Most obviously, since the fish are confined in a restricted space, their capacity for moving around is limited. In addition, the culture environment may expose fish to spatially relevant cues to which they cannot respond effectively in the space available. Moreover, in many instances the culture environment will be impoverished in terms of provision of spatially relevant cues. These attributes of the culture environment and the responses of fish to them could potentially cause problems during the production process, when fish are being reared to a size at which they can be used. Abnormal space use can also cause problems in fish that are cultured for release, for the ornamental trade or for science. Fortunately, it may be possible to use what is known about the way fish respond to spatially relevant cues to solve some of these problems. It is also possible to use knowledge of how fish respond to such cues to devise ways of making practices in fish culture more effective. These topics are discussed in turn in the following sections.

### 4.5.1 How fish use space in culture system

It is important to know how cultured fish move about and whether they display patterns of movement and orientation similar to those seen in their wild counterparts. This information is not easy to obtain, but for a few species and culture systems, for example, Atlantic salmon held in sea cages, several techniques have been used to collect this sort of information (Chapter 3).

On the subject of swimming patterns in cultured fish, information collected using acoustic tags has confirmed that Atlantic salmon often swim in circular patterns along the perimeter of sea cages, with circular swimming being interrupted by feeding. Swimming pattern also depends on stocking density; at moderate densities fish swim constantly in a counter-clockwise direction, but this pattern breaks down at lower densities. Swimming speed is usually higher during the day than at night, increasing from shortly before sunrise to a peak of about 0.5 body lengths per second (bl/s) at midday and falling to its lowest level, about 0.15 bl/s, soon after sunset (Figure 4.8; Juell & Westerberg 1993). Such swimming speeds are maintained over long periods, with fish in the same cage tending to move at comparable speeds, suggesting a degree of structured schooling behaviour (Dempster *et al*. 2009). In general, salmon tend to form schools when swimming actively during the day and to become more dispersed as well as less active at night (Fernö *et al*. 1995). The vertical position of Atlantic salmon in sea cages is influenced by temperature and light regimes, and hence by season, as well as by feed delivery. The change in light intensity that occurs over a 24 h cycle is reflected in the swimming depth of the fish, with farmed salmon descending to deeper water at dawn and ascending at dusk (Fernö *et al.* 1995). Superimposed

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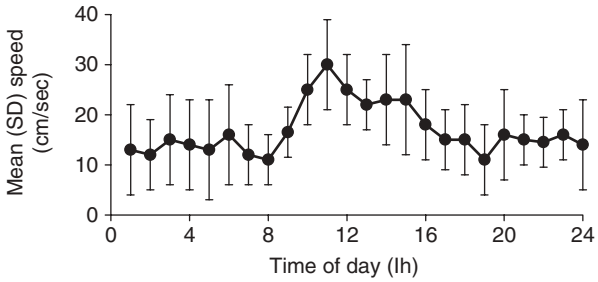


**Figure 4.8.** Swimming patterns and speeds in Atlantic salmon in marine net pens. Mean (±SD) swimming speed in relation to time of day in one Atlantic salmon held at low stocking density and fitted with an acoustic tag. Adapted from Juell & Westerberg 1993.

upon this is a seasonal effect, with deeper swimming depths in the summer than in the winter, as the fish avoid the more intense light at the surface.

The behavioural mechanisms responsible for the patterns of space use by salmon in sea cages have been explored by means of a simulation model (Føre *et al*. 2008), in which it is assumed that behaviour is driven by a combination of a motivation to remain within preferred ranges of light and temperature, while at the same time responding to food. Specifically, model fish approach or ignore food depending on hunger level, avoid collision with the net walls of the cage and keep a minimum distance from other fish to avoid collisions. The model accurately reproduces several features of the behaviour of salmon in cages, such as swimming trajectories around the cage periphery and changes in fish density with water depth in relation to time of day. The significance of these predictions is that they arise directly from simple behavioural rules. The fact that they are reasonably accurate means that space use by salmon in sea cages is driven by the same kind of mechanisms as are movements of fish in the wild, namely responses to key spatially structured cues interacting with current internal state.

Little is known about space use by other fish species and in other culture systems, but information is available from a few studies. Ultrasonic tags have been used to monitor movement patterns of rainbow trout in large tanks and the data reveal that space use is influenced by stocking density and time of day; individuals differ in space use, some fish swimming actively and using much of the tank area, whereas others are sedentary (Bégout Anras & Lagardere 2004). Information obtained by filming underwater and data from acoustic tags has revealed that Atlantic cod held in offshore sea cages are diurnally active, do not school strongly and tend to occupy the lower half of cage, but move higher in the water column when being fed (Rillihan *et al*. 2009).

Direct observation of wrasse in sea cages with Atlantic salmon showed that goldsinny (*Ctenolabrus rupestris*), which naturally have small home ranges, spend most of their time hovering in restricted areas close to the net walls of the cages, browsing on fouling organisms. On the other hand, rockcook (*C. exoletus*) stay near the bottom of the cages. The salmon tend to be concentrated at depths between 2 and 5 m and are never abundant close to the cage bottom, but the wrasse make occasional forays into shallower water during which they remove sea lice from the salmon (Tully *et al*. 1996). Taking a final example from a fish cultured for the ornamental trade and for conservation, the seahorse *Hippocampus guttulatus*, is diurnally active, tends to remain close to the bottom of tanks near water inlets and shows strong preferences for vertical holdfasts and plants (Faliero *et al*. 2008).

### 4.5.2 Problems during production arising from the ways in which fish use space

The ways in which fish move, including how fast and in what direction they swim, have implications for the effectiveness of culture, as does the way they respond to the spatially relevant stimuli to which they are exposed. How these aspects of the behaviour of cultured fish change with age is also relevant for fish culture, since this will determine how easy it is to provide appropriate environmental conditions and to manage the changes in space use that take place as fish develop and mature. How effectively fish are able to function in the spatial environment they experience will determine their growth and survival, so understanding the implications of costs and benefits of space use might help to unravel and ameliorate some of the problems experienced when cultivating fish. Some of these problem areas are summarised in Table 4.2.

#### *Problems arising from interactions with wild fish*

Problems may arise for the farmer, the farmed fish and the environment from the movements of wild fish. In some cases, wild fish may come into the vicinity of fish farms during their natural movements and in others cases the wild fish may congregate at farm sites, attracted by the food sources the farms provide. For example, wild fish are attracted to large coastal salmon farms in Norway (Fernandez-Jover *et al*. 2010) and juveniles of 20 species of wild fish may settle in the vicinity of Mediterranean seabass and sea bream farms, feeding on the zooplankton that flourishes in the water around the farm cages. The fatty

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**Table 4.2.** Some possible consequences for aquaculture of the natural space use patterns of fish and some potential problems caused by these.

| Consequences | Implications for production | Implications for welfare | Implications for the environment |
|---|---|---|---|
| Interactions with wild fish | Possible source of cross-infection in cultured fish | Compromised welfare of individual fish through disease-induced ill health | Possible source of cross infection within wild fish<br>Altered population density and community structure |
| Restricted opportunity for directional swimming | Benefits of sustained swimming not exploited | Possible inability to meet a behavioural need | Less efficient use of food due to stress means that more feed is needed and wasted |
| Inappropriate space use through natural responses in a constrained environment. | Crowding and increased levels of injury and disease<br>Exposure to pathogens | Crowding-induced stress responses in individual fish<br>Compromised welfare of individual fish through injury and disease | Increased general levels of disease<br>Less efficient use of food due to stress, higher feed requirements and greater feed waste |
| Disorientation due to lack of access to spatial information | Collision-induced damage and mortality<br>Inefficient food capture and growth | Compromised welfare of individual fish through injury and disease<br>Compromised welfare of individual fish through inadequate access to food<br>Impaired welfare through lack of predictability and controllabilit | Less efficient use of food due to stress, higher feed requirements and greater feed waste |
| Failure to make effective habitat switches at metamorphosis | High mortality<br>Malformations | Compromised welfare of individual fish through inappropriate immediate conditions and long term malformation | |



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acid profiles of juvenile fish caught near farms can differ from those of fish caught at a distance from farm sites, indicating that fish farms may influence local food webs (Fernandez-Jover *et al*. 2009).

Wild fish are sometimes attracted by waste feed arising from over-feeding of farmed fish held in sea cages. For example, wild fish are abundant near cages in which groupers (*Epinephelus fuscoguttatus* and *Cromileptes altivelsi*) and rabbitfish (*Siganus* spp.) are farmed, with the wild fish swimming around the margins of the cages when the farmed fish are being fed and eating much of the wasted feed (Sudirman *et al*. 2009). In Chile, more species may be found in areas where salmon are farmed than in other locations and feed pellets are found in the stomachs of more than 50% of native fish captured around salmon farms (Sepúlveda *et al*. 2004).

It has been suggested that the presence of salmon farms has caused wild Atlantic cod to change their migration habits, avoiding the fjords where they have traditionally spawned because of odours from salmon farms. Some wild cod avoid water containing metabolites and waste from salmon farms, even at very low concentrations. Farmed cod do not do so and wild cod caught close to fish farms show relatively weak avoidance responses, possibly having learnt to associate the odours from farms with the presence of food (Sæther *et al*. 2007). Studies of the movements of tagged wild cod have produced ambiguous results; there are no differences in movement patterns between intact fish and those with an ablated olfactory sense, which argues against avoidance on the basis of olfactory cues. However, cod that are released in the outer part of a fjord and have to pass fish farms to reach the spawning areas tend to leave the fjord without visiting the spawning grounds, whereas cod released in the inner part of the fjord do not leave (Bjørn *et al*. 2009).

There is also concern that interactions between wild and cultured fish at farm sites could facilitate the exchange of pathogens between them. For example, the natural movement patterns of wild fish, acting together with attraction to salmon farms, may bring wild fish into contact with farmed salmon, promoting the transmission of pathogens and parasites. In a Chilean example, two ectoparasites and one endoparasitic species have transferred from wild fish to farmed salmon (Sepúlveda *et al*. 2004). Transfer of parasites in the opposite direction, from farmed to wild fish, is also a possibility; this has been widely discussed in the case of the sea-lice that infest salmonids (see Krkošek *et al*. 2006, 2008; Riddell *et al*. 2008). In brief, the transmission of sea-lice between adult and juvenile Pacific salmon is usually minimal because in nature the life cycles of these salmonids means the two life stages are segregated in both time and space (Groot & Margolis 1991; Pennell & Barton 1996). This segregation may be compromised if cages of farmed salmon are located near smolt migration routes, leading to the possibility that the juvenile fish could become infested with lice at an earlier age than normal (Krkošek *et al*. 2006). Dispersal of larval sea-lice at distances of up to 30 km from fish farms has been reported and secondary production of lice from migrating wild fish infected at farms has been detected up to 75 km away (Costello 2006). The most pragmatic conclusion to be drawn is that transfer of parasites between farmed and wild fish is a potential problem for aquaculture, arising because of the natural movement patterns of fish.

### *Problems arising from restricted opportunity for sustained, directional swimming*

Problems could arise from the fact that sustained directional swimming is usually prevented by the confines of intensive culture systems. This raises the question of whether the welfare of cultivated migratory species is compromised by keeping them in captivity. It could be speculated that fish that undertake long-distance migrations might be driven by an internally generated 'need' to swim. However, fish of migratory species might also undertake long journeys because they are tracking widely dispersed food or other resources. In the first case, holding these fish in captivity poses welfare problems, but in the second, keeping the fish in a confined space is not a direct cause for concern on the grounds of welfare. For the vast majority of migratory fish that are farmed for food, the relevant migrations are those made by juveniles to feeding grounds, rather than migrations of adults to spawning grounds, because food-fish are usually harvested before they mature. Studies of the oceanic movements of wild salmon suggest that the fish track food at local scales. For example, patterns and speeds of movement shown by Coho salmon suggest that the fish search for patches of food, and backtrack to stay in profitable areas (Ogura & Ishida 1992, reviewed in Hinch *et al*. 2006). On the other hand, it remains to be established whether any fish species has an inherent need to swim over long distances and if so whether depriving them of the opportunity to do so compromises their welfare. Resolving this difficult question would require observation of what fish do when given swimming opportunities, how hard they will work to obtain such an opportunity and perhaps whether they show any indication of an intention to migrate at a particular time of year, as is seen in caged individuals of some species of migratory birds.

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Studies of the costs and benefits of movement in fish have identified a number of beneficial consequences arising from sustained swimming in a range of fish species. These include increased swimming capacity, more rapid recovery from exhaustive swimming, muscle hypertrophy, increased schooling behaviour and reduced aggression, faster growth, more efficient food conversion and reduced levels of stress (Jobling *et al*. 1993; Davidson *et al*. 1997). For example, growth is more rapid and feed conversion more efficient in Japanese flounder (*Paralichthys olivaceus*) exposed to water flowing at a rate equivalent to 0.9 bl/s than in fish exposed to water flowing at lower or higher speeds (Ogata & Oku 2000). Likewise, in Arctic charr, growth rates are higher and less variable in fish swimming against a current at a speed of *ca* 1.5 body lengths/s in comparison with those of fish held in standing water and so not stimulated to swim (Jobling *et al*. 1993; Chapter 1). As such, the absence of sustained swimming contributes to lost production in some species that are intensively cultivated as food-fish.

### *Problems arising from natural responses to spatial cues in a constrained environment*

A number of adverse consequences could arise from the expression of natural responses to spatially relevant cues by fish held in a restricted space. For example, the natural responses of Atlantic salmon to gradients of temperature and light can create a conflict when fish are held in sea cages and food is provided at the water surface. Such conditions can result in aggregations of fish that are sufficiently dense to cause collisions and to seriously deplete oxygen concentrations (Johansson *et al*. 2006). There may be several costs associated with being close to the water surface. For example, the fish may be easy prey for aerial predators, and the infective stages of some species of ectoparasites, such as sea-lice, are more frequent in surface waters than deeper in the water column (Juell & Fosseidengen 2004).

Behavioural thermoregulation, involving the ability to seek out water of a temperature that optimises physiological function, is important to both farmed and wild fish and growth may be compromised if restricted space prevents farmed fish from undertaking this form of thermoregulation (Wood & McDonald 1997; Oppedal *et al*. 2007). It is worth noting that with night-time attraction to lights within a thermally stratified water column, the fish may divide to form distinct subgroups, some fish being attracted to the light and others seeming to select position according to temperature preference (Juell & Fosseidengen 2004). This may reflect the expression of individual variability in space use, which might be the result of differences in motivational state, of recent experience or of inherited behavioural predispositions.

### *Problems arising from lack of spatial information in culture systems*

The problems considered above come about because fish show appropriate behaviour to spatially relevant cues, but in an inappropriate context. Another set of potential problems may arise due to lack of important spatial cues. This could, for example, arise as a result of background noise compromising the ability of fish to detect and respond effectively to spatially relevant mechanosensory stimuli. For example, exposure to noise above 140 dB can cause temporary hearing loss and physiological stress responses in Atlantic salmon, European seabass and common carp (Bart *et al*. 2001). Unpredictable stimuli are more stressful than continuous noise, perhaps because fish habituate to continuous noise (Wysocki *et al*. 2007). Recordings made on fish farms indicate that background noise from equipment such as aerators, pumps and filtration systems may reach about 130 dB (Bart *et al*. 2001), approaching levels that can cause temporary hearing loss (Popper 2003; Amoser & Ladich. 2003).

Problems in fish culture may come about through lack of a range of spatial cues. For example, when transferred to small net cages from tanks at about 30 dph, juvenile bluefin tuna (*Thunnus thynnmus*) experience mortalities of up to 50% per night. This is a consequence of damage and stress resulting from collision with the net wall of the cage (Figure 4.9; Ishibashi *et al*. 2009). The reason for collision is that juveniles of this species have poor scotopic vision, meaning that they do not see well when the light intensity is low, and this is reflected in poor optomotor responses in dim light. The problems that arise due to poor vision may be particularly acute at dawn, when the fish become disorientated as their eyes change from being dark-adapted to being light-adapted (Masuma *et al*. 2001). In nature, older fish with good swimming ability can avoid visual disorientation by behavioural compensation, making vertical movements to track appropriate light levels during the period of visual adaptation. Younger fish do not have the scope for making such movements, especially when held in small cages that are limited in depth. In the wild, the small fish are usually found close to the surface at night, often in association with floating objects (Ishibashi *et al*. 2009).

If there is a deficiency of spatial cues and landmarks, as is the case in many captive environments, the abilities of the fish to use spatially relevant cues to improve the efficiency with which they exploit resources may be impaired.

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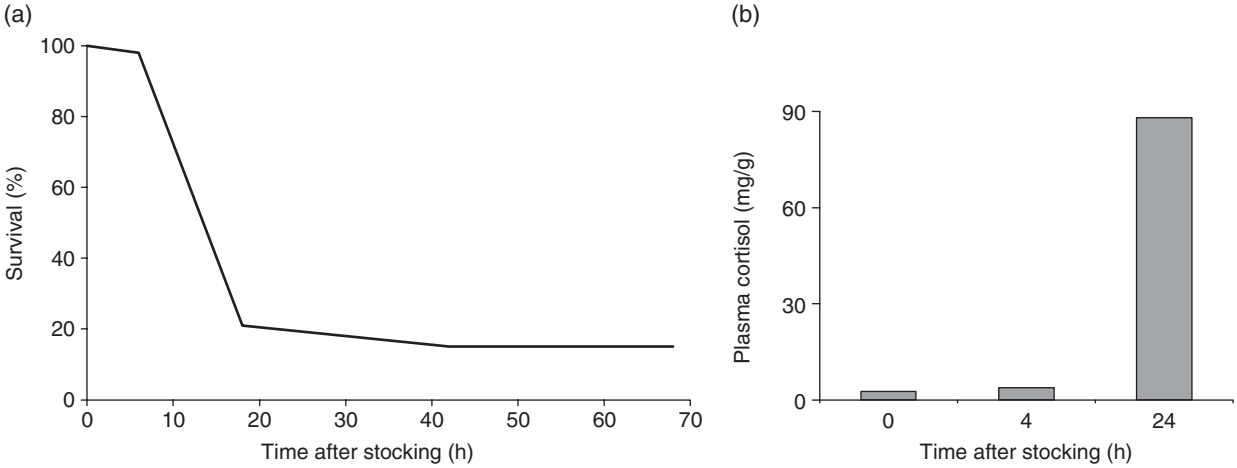


**Figure 4.9.** Mortality and stress caused by disorientation in farmed fish. (a) Percentage of juvenile Pacific bluefin (33 dph) surviving and (b) Mean (± SD) whole body cortisol in juvenile Pacific bluefin (33–36 dph) in relation to time after stocking into sea net cages. Data plotted at 24 h is the average of samples taken at 18 and 24 h. Adapted with permission from Ishibashi *et al.* 2009.

For example, in the absence of structures or landmarks, Atlantic salmon and Arctic charr fail to show spatially organised behaviour in the form of territoriality (Mikheev *et al*. 1996). In the case of wrasse on Atlantic salmon farms, sea cages often lack identifiable landmarks at which wrasse can establish cleaning stations and the salmon also lack the spatial information needed to allow them to seek the attention of the wrasse for the removal of ectoparasites (Treasurer 1996; Deady *et al*. 1995; Tully *et al*. 1996).

The dearth of landmarks, and hence an impaired ability of fish to form and use mental maps in culture systems, may compromise effective space use and may also influence welfare through effects on the predictability of potentially stressful events. One approach to animal welfare based on appraisal theories indicates that the emotional effect challenging events depends on whether or not such events are predictable (Désiré *et al*. 2002). For example, lambs show weaker startle responses to a sudden looming stimulus if its appearance is signalled in advance by a light (Greiveldinger *et al*. 2007) cortisol levels are higher in Mozambique tilapia subjected to confinement stress when this is unpredictable than when it is predictable (Galhardo *et al.* 2011). Given that captive fish may have limited opportunities to form maps and make associations, they may have a reduced ability to predict events and so are likely to be easily stressed.

### *Problems arising from ontogenetic habitat shifts*

Ontogenetic changes in space use mean that appropriate holding conditions differ between life history stages and transitions must be carefully managed. For example, larval seabass and sea bream need access to the air–water interface to fill their swim bladder and if the water is covered by a surface film access to the air may be prevented. This often results in the failure of the fish to fill the swim-bladder and in some instances can lead to the development of spinal deformities, because the fish adopt an abnormal body posture during swimming (Planas & Cunha 1999; Moksness *et al*. 2004). The transition from pelagic larva to benthic juveniles is a major event in the life of flatfish; settlement is accompanied by a metamorphosis that includes a 90° change in posture, migration of one eye around the body, changes in the orientation of the skeletal elements of the jaws and the development of asymmetrical pigmentation patterns. In the wild, there may be reduced growth during this transition, but there is no evidence of increased mortality during metamorphosis (Geffen *et al*. 2007). However, in flatfish culture aberrant metamorphosis commonly leads to physical deformities and malpigmentation (Moksness *et al*. 2004), which compromise subsequent survival and the commercial value of the fish. In addition, variable growth rates around the time of metamorphosis can lead to problems; in summer flounder (*Paralichthys dentatus*) large, early metamorphosing fish make cannibalistic attacks on smaller, late metamorphosing fish. This problem can be reduced by frequent grading, but this is stressful to the fish as well as being labour-intensive (Gavlik & Specker 2004).

The transition from fresh water to seawater that occurs during the smolt migration of salmonids is a

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well-documented example of an ontogenetic change in space use. The solutions to problems that arise in salmon aquaculture during the transfer of smolts from fresh water to seawater have mostly been developed on the basis of knowledge about the physiology of the fish (Pennell & Barton 1996; Stead & Laird 2002; Le Francois *et al*. 2010), but the problems originate as a result of a behavioural event in the life history of the fish, specifically migration from one habitat to another.

### 4.5.3 Space use problems when cultivating fish for purposes other than food

When fish are reared for release it is important that they show appropriate space use and patterns of movement in the water bodies into which they are released. Domestication and captive rearing can have profound effects on many aspects of the biology of fish (see Chapter 1), so it is important to establish the extent to which orientation and movement are affected. Captive-reared fish may have smaller brains than wild fish (Kihslinger & Nevitt 2006; Chapter 1). Female guppies reared in the laboratory have a 19% smaller telencephalon and a 17% smaller optic tectum than do wild-caught females, although is not directly linked to specific features of the spatial conditions in which the fish were reared (Burns *et al*. 2009). The relationship between the size of particular brain regions and their behavioural functions is complex (Healy & Rowe 2007), but such variation in parts of the brain known to be involved in spatial learning suggest that differences in space use may exist between captive-reared and wild fish.

In general terms, the migratory behaviour of hatchery-reared salmon is similar to that of wild fish, to the extent that farmed smolts move downstream and imprint on olfactory cues (Hansen *et al*. 1993) and post-smolts move away from coastal waters (Finstad *et al*. 2005). However, the behaviour of wild and hatchery-reared fish may be different in detail. For example when Atlantic salmon of wild and farmed origin are reared under common conditions in a lake, the proportion of juvenile salmon that migrates in autumn is higher in the wild than in the farmed stock, possibly because more males in the farmed stock mature without migrating to sea (Chapter 10).

The duration of migration tends to be both longer and more variable in wild salmon than in hatchery-reared, domesticated stocks, with hybrids being intermediate. Such differences may have arisen due to inadvertent selection over generations when targeting for production of smolts during a narrow time window (McGinnity *et al*. 2007). Fewer farmed than wild Atlantic salmon captured at the mouths of rivers are subsequently found further upstream and, although wild and farmed fish travel at a similar speed (approx 2 km/day), only wild salmon swim faster in response to higher currents (Thorstad *et al*. 1998). Table 4.3 summarises the results of a number of studies that have compared movement patterns in wild and farmed fish.

Behavioural differences between captive-reared and wild fish have potential implications for the success of release, restocking and sea-ranching programmes. If captive-reared fish fail to exploit the habitat effectively due to poor responses to spatial cues, survival and growth are likely to be compromised. In addition, how captive-reared fish respond to environmental cues and when they arrive at feeding and breeding grounds will determine how they interact with fish from natural populations. For example, hatchery-reared Atlantic salmon in the Baltic Sea show different migration patterns to those displayed by wild fish, being commoner in the Gulf of Bothnia and less common in the Baltic main basin. Since the Baltic main basin is intensively fished, this difference makes the hatchery-reared salmon less vulnerable to the salmon fishery than are their wild conspecifics (Jutila *et al*. 2003).

Many fish reared in hatcheries for restocking do not survive for long following release into the wild (Olla *et al*. 1998; Brown & Day 2002). The failure of released fish to survive may be due in part to the relatively impoverished rearing environment experienced during early development. For example, juvenile Atlantic cod reared under standard hatchery conditions are less likely to explore a novel habitat than are fish reared in a more complex environment (Braithwaite & Salvanes 2005). As a second example, very few juvenile white sea bream (*Diplodus sargus*) released onto artificial reefs survive, many being eaten by predators on the night following release. This high mortality may be due to behavioural deficits, because captive-reared sea bream swim actively around the reefs and initially make few attempts to use reef structures for shelter (D'Anna *et al*. 2004). As well as giving rise to fish with specific deficits in feeding, predator avoidance and social behaviours, captive-rearing might also produce deficits in several aspects of space use, including an impaired ability to move around natural habitats and to locate unpredictable resources.

How cultured fish respond to spatial cues can also influence their value as ornamentals in display aquaria. Comparisons of the behaviours of wild-type and domesticated fish reared for the ornamental trade have mostly involved feeding and reproduction, but domesticated Koi carp are less likely to remain close to the bottom than are feral-strain carp reared under identical conditions (Matsuzaki *et al*. 2009). Domesticated zebrafish show more

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**Table 4.3.** Examples of differences in movement patterns between wild and domesticated fish.

| Species | Observations | Source |
|---|---|---|
| Atlantic salmon | • Of fish tagged at the mouth of a large river, 87% of wild fish are recorded upriver compared to 50% of farmed fish, which also travel up river more slowly | Heggberget *et al*. 1993 |
| | • Compared to wild-caught fish of the same (endangered) stocks, fish reared in hatcheries up to smolting make shorter feeding migrations in the Baltic and return to freshwater sooner than do wild fish | Jutila *et al*. 2003 |
| Masu salmon | • Newly-emerged hatchery-reared wild fish move and disperse downstream from the release site; hatchery-reared domesticated fish tend to stay at the release site or move upstream | Nagata *et al*. 1994 |
| Japanese flounder | • Domesticated fish are more tolerant of high salinities and move less after release than wild reared fish reared in hatchery conditions | Shimada *et al*. 2007 |

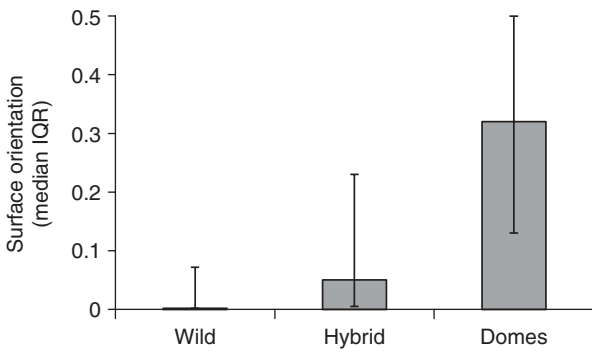


**Figure 4.10.** Effects of domestication on orientation. Mean and interquartile range (IQR) of an index of orientation towards the water surface (percentage of time spent above the midline of the tank) in laboratory-reared zebrafish of wild origin (4 generations removed from capture), domesticated stock ('Domes') and in hybrids between them. Adapted with permission from Robison & Rowland 2005.

surface orientation than do wild-type fish when reared under standard conditions and hybrids show intermediate behaviour (Figure 4.10; Robison & Rowland 2005). As a final example, guppies reared at low densities are more likely to shoal and are better at using social information to learn a spatial task (finding food in a maze) than are guppies reared at high stocking density (Chapman *et al.* 2008).

### 4.5.4 Solving problems in aquaculture arising from the biology of space use in fishes

Having identified potential problems for aquaculture that arise from space use in fish, the next task to consider is how these might be solved. There is relatively little scope for intervention to prevent interactions between wild fish and farmed fish held in sea cages, though positioning of fish farms away from the natural migratory routes of wild fish may help. In addition, if it transpires that attraction of wild fish to farm sites causes problems, it might be possible to change husbandry routines to reduce the attraction of the wild fish, or to use aversive stimuli to repel wild fish and deter them from approaching sea cages.

#### *Mitigating the effects of reduced opportunity for sustained swimming*

Potential problems here might be avoided by increased concentration on the cultivation of non-migratory species, or non-migratory forms within a species, especially in the intensive farming of fish for food. Given that fish of several species are known to have discrete migratory and non-migratory populations, or non-migratory components within a population, it may be possible to select fish with reduced migratory tendency for use in breeding programmes.

For fish that are already being farmed, it is possible to promote sustained swimming within cages and tanks, either by generating water currents to stimulate rheotactic movements, or by using visual stimuli to elicit an optomotor

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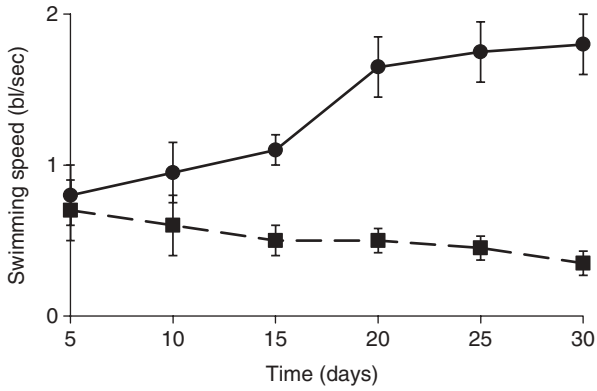


**Figure 4.11.** Using lights to control swimming in farmed fish. Swimming speed (body lengths/s) in Atlantic salmon post-smolts exercised by a light-induced optomotor response (black circles and solid line) and in control fish (black squares and dashed line) on successive days after deployment of the light device. Redrawn with permission from data presented in Herbert *et al.* 2011.

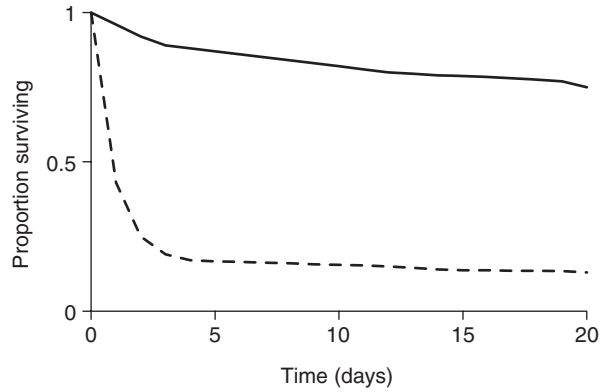


**Figure 4.12.** Using lights to improve survival in farmed fish. Cumulative survival after stocking into sea net cages in juvenile (38 dph) Pacific bluefin tuna held with (solid line) and without (dashed line) artificial lighting, up to 20 days after stocking. Adapted from Ishibashi *et al.* 2009.

response. A range of farmed species are known to benefit from sustained swimming and the generation of water currents is exploited in the tank culture of several species, especially salmonids (Chapter 1). As an alternative to the use of water currents, the optomotor response can be exploited to encourage farmed fish to swim. For example, Atlantic salmon can be stimulated to swim for several weeks in an optomotor device (Figure 4.11; Herbert *et al.* 2011). As is the case for fish swimming against a current (Chapter 1), optomotor-induced swimming promotes growth, improves feed conversion efficiency and reduces plasma concentrations of cortisol, suggesting that the exercised fish are less stressed than controls. This example illustrates how knowledge of the mechanisms that control movement in fish, combined with an understanding of the beneficial effects of swimming, can be used to improve fish culture.

### *Mitigating the effects of natural responses to spatial cues in a constrained environment*

Atlantic salmon in sea cages may experience a number of problems arising from their responses to spatially stratified cues. This includes excessive density, exposure to adverse water conditions such as low oxygen, lack of opportunity to track optimal temperatures and increased exposure to infectious stages of parasites. For this reason, the annual patterns of temperature, light and water stratification should be taken into account when selecting and managing farm sites, for example making sure that the fish always have access to water in which environmental factors are within acceptable ranges for survival and growth (Oppedal *et al*. 2007). Further, environmental manipulation may be used to alleviate potential problems. For example, within sea cages elective densities can be controlled and the risk of both excessive crowding and exposure to poor-quality water reduced by the judicious placement of lights to which the fish are attracted (Juell & Fosseidengen 2004).

### *Reducing disorientation due to lack of access to spatially relevant cues*

Where cultured fish are disorientated because of husbandry-related noise, attempts should be made to reduce levels of background noise so that spatially important mechanosensory cues are not masked. Where cultured fish are disorientated through lack of or inaccessibility of spatially relevant cues, it may be necessary to redesign or modify culture systems. For example, mortality of juvenile yellowfin tuna on transfer to cages can be reduced by providing additional light, because this reduces the chance of the fish colliding with the cage walls at night when their vision is poor (Figure 4.12; Ishibashi *et al.* 2009). In the wild, small tuna associate with floating objects at night, so additional improvements might be achieved by placing floating objects in sea cages. Beneficial effects of placing structures

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in sea cages have been reported when using wrasse for the control of sea-lice in Atlantic salmon farming. For example, goldsinny wrasse make use of shelters, specifically, lengths of pipe, that provide a refuge from currents and from attacks by other fish; such shelters might also act as landmarks around which the fish can organise their behaviour (Deady *et al*. 1995).

### *Managing metamorphosis and migration*

The changes in space use that occur during development can create problems, including some that are related to incomplete or abnormal metamorphosis. Such problems often arise at the physiological level, but may also have their origins in behavioural events at specific life history stages. For example, in larviculture, problems may arise if the small fish are prevented from gulping air at the surface to fill the swim bladder (Moksness *et al*. 2004). The problems include the development of vertebral deformities accompanied by aberrant and uncoordinated swimming patterns. These can be significantly reduced by the installation of surface-skimmers on tanks; these remove surface debris and oily films from the water surface, giving the fish access to the air–water interface and allowing them to fill the swim bladder. The problem of cannibalism by large, early-metamorphosing summer flounder on smaller conspecifics is currently addressed, but not completely solved, by carrying out labour-intensive size-grading. An alternative approach uses what is known about the cues that control the switch from a planktonic to benthic life style in wild fish, one cue being a drop in salinity, which can be manipulated in culture systems. Exposure of flounder larvae to water of 20 ppt salinity late in development (from 26 days post hatching onwards) increases the percentage of fish settling by 54 days (Figure 4.13) and reduces the variability in developmental stage at settlement, thereby reducing cannibalism (Gavlik & Specker 2004).

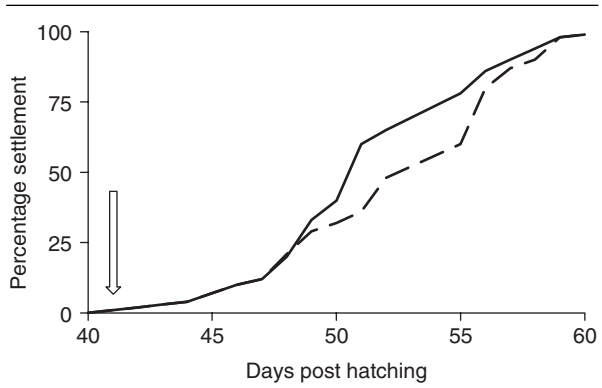


**Figure 4.13.** Controlling patterns of larval settlement in flounder by manipulating salinity. Percentage of summer flounder larvae settling onto the substratum on successive days in control groups held at a salinity of 30 ppt (broken line) and in groups exposed to a change of salinity from 30 to 20 ppt at a point indicated by the vertical arrow (solid line). Adapted from Gavlik & Specker 2004.

### *Mitigating the effects of domestication and captive rearing*

Understanding the factors that control the timing and nature of migrations can help promote the aims of aquaculture when fish are reared for purposes other than food. For example, dispersing juveniles of various species of reef fish are attracted to the sounds and smells of reefs (Simpson *et al*. 2006; Gerlach *et al*. 2007). This raises the possibility of developing traps for harvesting reef fish for subsequent rearing for the ornamental fish trade or for conservation, and of doing so at times that might minimise ecological impact. Settlement is a time of high mortality for reef fish, so collecting fish in moderate numbers prior to, or around the time of, settlement should not have any major adverse effects on recruitment (Heenan *et al*. 2009).

Various changes in the rearing environment may improve survival in fish cultured for release; for example, maintaining hatchery-reared juvenile steelhead on reduced rations for one month prior to release, which lowers their nutrient reserves, makes the fish move rapidly away from the release site and improves survival (Tipping & Byrne 1996). Increasing the complexity of the rearing environment can also have beneficial effects; for example, cod reared in hatchery tanks furnished with variable spatial cues and a spatially variable food supply are more likely to explore a novel environment and are generally more flexible in their behaviour than are fish reared in a standard tank (Braithwaite & Salvanes 2005; Figure 4.14). Thus, relatively simple changes to the rearing environment can alter the behaviour of fish in a way that is likely to promote survival after release.

## 4.5.5 Improving the effectiveness of general husbandry practices

The previous sections show that a number of problems experienced by fish farmers, and those who buy their products, arise from the natural space use patterns of cultured fish and also demonstrate how such problems can potentially be solved by using what is known about the biology of the behaviour patterns concerned. It is also possible to use this same body of knowledge to devise more effective general husbandry practices, solving problems that are caused by factors other

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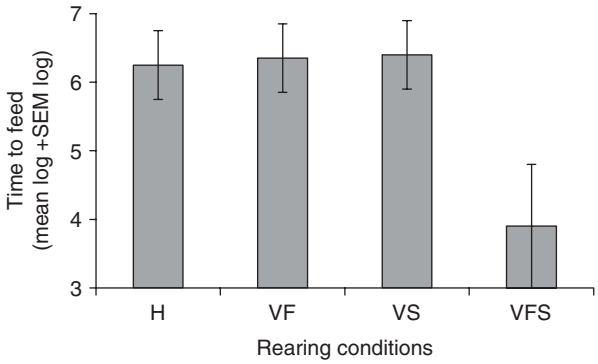


**Figure 4.14.** Effects of a spatially variable environment during development. Mean (± SE) log time to respond to novel live prey (mysis shrimp) in juvenile cod reared in standard hatchery tanks (H), in tanks in which food was variable (VF), in tanks in which the position of spatial features was variable (VS) and in tanks where both food and spatial features were variable (VFS). Adapted from Braithwaite & Salvanes 2005.

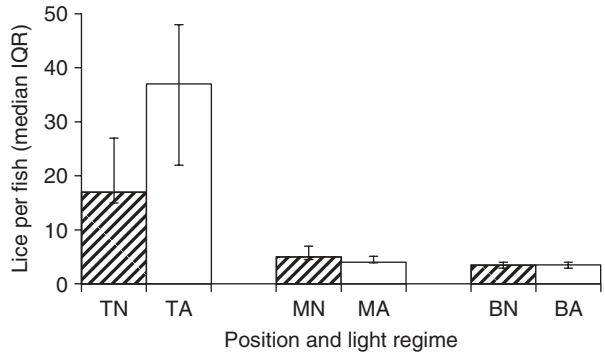


**Figure 4.15.** Effect of additional lighting on lice infestations in salmon in marine pens. Median (IQR) number of lice on fish captured at different depths (T=0–4 m; M=4–8 m; B=8–12 m) held under normal light regimes (N) or with additional light (A). Fish in the top depth have more intense lice infestations than those in deeper water, especially when artificial lights are present. Adapted from Havrøy *et al.* 2003.

than the natural movement patterns of the fish concerned. Examples are given in the final section of this chapter.

### *Improving hatchery survival*

Losses of cultured fish at and around hatching can be substantial and there are good reasons for seeking improvements. For example, alevins of Arctic charr and some other salmonids reared in tanks with grooved bases, or with other types of substrate such as artificial turf in which they can position themselves vertically, survive better and start taking exogenous feed later and at a larger size than do fish held in tanks lacking a substratum. This is associated with the physical support given to the fish by the substrate, reducing the need for positional movements; the fish also make fewer horizontal movements and show less swimming against the current (Benhaim *et al*. 2009). Thus, by introducing measures that manipulate the posture and movements of the small fish, general husbandry efficiency is improved.

### *Improving feed delivery*

Several features of the movement patterns of fish have been used for regulating feed delivery (Chapter 3). For example, the gradual descent of fish detected by hydroacoustic monitoring during the course of a feeding session can be used as an indicator of satiation, with feeding being terminated when fish have descended to a certain depth (Fernö *et al*. 1995). In addition, continuous electromyogram recordings of rainbow trout show that patterns of activity closely correlate with feeding motivation, although this has not been exploited in a commercial setting (McFarlane *et al*. 2004).

### *Reducing disease*

Taking account of fish movement patterns when selecting sites for fish farms, and the placement of sea cages within farms, can help to reduce the risk cross infection between wild and farmed fish. In addition, the risk of infections can be further reduced by adopting appropriate culture system designs and husbandry practices. For example, the infectious stage of the sea louse is pelagic and strongly positively phototactic and so tends to be found in shallow water layers during the day or, in the case of artificially lit sea cages, in areas of relatively high illumination. Holding farmed fish in deep cages allows them to avoid infection by moving into the deeper parts of the cage, with the result that salmon held in deep cages or held at depths of 4–12 m by artifical lights have lower levels of infestation with sea lice than those in shallow cages or at shallower depths (0–4 m, Figure 4.15; Hevrøy *et al*. 2003).

### *Manipulating elective stocking density*

Submerged lights can be used to control the distribution of farmed Atlantic salmon in sea cages, thereby avoiding the establishment of excessively high densities (Oppedal *et al*. 2007).

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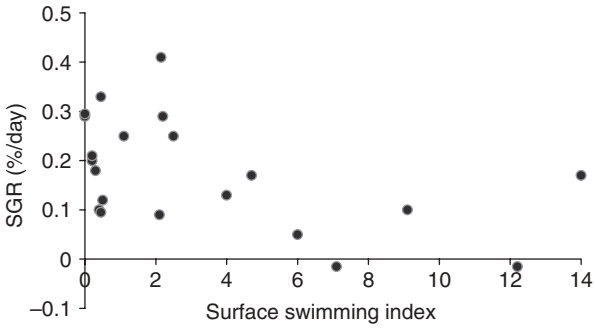


**Figure 4.16.** Space use in farmed fish as an operational welfare indicator. Specific growth rates (percentage change in body weight per day) in relation to an index of tendency to swim at the surface (average number of registrations at a PIT antennae placed just below the water surface) in PIT tagged Atlantic halibut held at low densities. Adapted from Kristiansen *et al.* 2004.

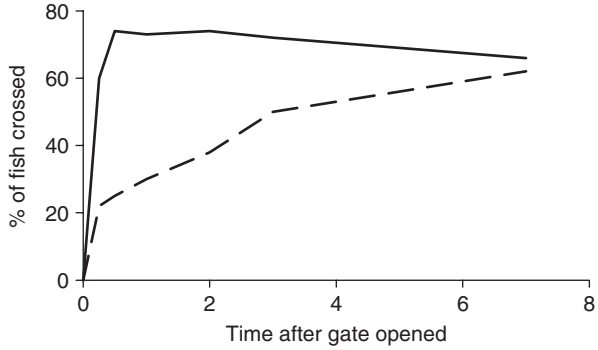


**Figure 4.17.** Using natural phototactic responses to move fish between tanks. The proportion of fish moving through a gate between two tanks at different times after the gate was opened when light conditions were equal in the two tanks (dashed line) and when the tank on the far side of the gate was brighter (solid line). Adapted from Lekang & Fjæra 1995.

***Protection from adverse weather conditions***

During times of severe weather, sea cages may be submerged to avoid potential storm damage (see Chapter 1). Over periods of a few weeks, this has few adverse effects on fish such as Atlantic salmon, although with longer submersion lack of opportunity of fish in submerged cages to replenish swim bladder gas by gulping air at the water surface may cause buoyancy problems. When Atlantic salmon are held in cages that are submerged to just below the water surface they do not change their swimming depth, but fish in submerged cages swim faster than fish in cages with open access to the air-water interface, perhaps to gain dynamic lift (Dempster *et al*. 2009). In this case, the movement patterns and space use of fish dictate the fact that a husbandry intervention can be used with relatively little ill effect.

***Monitoring growth and welfare***

There is a recognised need for easily applied indicators of welfare in cultured fish (Chapter 1). Some candidate indicators, often used by fish farmers, include aspects of movement and positioning of cultured fish, whether and how fast the fish are swimming, whether they are schooling and whether they rise in the water column to feed. For example, a measure of impaired reflexes, including aspects of orientation and movement, can be used to predict stress levels and mortality rates in several species of farmed fish (Davis 2010). In halibut, the frequency with which fish swim in a vertical posture with the head above the water surface is negatively correlated with growth (Figure 4.16), so this could be used as an indicator of whether of not rearing conditions are completely appropriate (Kristiansen *et al.* 2004).

***Moving fish about***

The natural response of fish to cues with a spatial component opens the possibility of developing techniques for moving fish with minimum stress. For example, olfactory stimuli such as amino acids or sex pheromones can be used to attract fish and induce them to move from one area to another (Næss *et al*. 1991, cited in Lines & Frost 1999) and the positive rheotactic response shown by some species and life history stages can be used to move fish between tanks (Fjæra & Skogesal 1993; Lekang *et al*. 1994). The tendency for some species to show positive phototactic responses can also be exploited. Thus light can be used to attract fish from cages in which light levels are kept low to other cages with brighter conditions, stimulating movement of the fish into the cage with brighter illumination (Lekang & Fjaera 1995; Figure 4.17).

Methods for moving fish can also be based on learned behaviour, such as conditioned responses to acoustic stimuli that can be established by pairing sound with the presentation of food (Abbott 1972). Such responses can be exploited to facilitate sorting and grading. For example, positive rheotactic and conditioned responses to light cues can be used to move fish through sub-surface size grading grids (Fjæra & Skogesal 1993). Guppies can be induced to enter small containers by

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means of their positive phototactic and rheotactic responses; they can then be photographed, classified, assessed and graded automatically, rather than by more labour-intensive and stressful manual methods (Karplus *et al*. 2005). A similar system based on a conditioned response to light can be used to separate fish according to species (Zion *et al*. 2000).

### *Reducing stress at harvest*

Handling and harvesting, whether for transport or slaughter, can be highly stressful for the fish, compromising some of the aims of fish culture through impaired product quality and poor welfare. Harvesting methods might be based on the exploitation of natural patterns of orientation and movements of the fish. For example, $CO_2$ avoidance provides a method of 'herding' tank-held rainbow trout either towards the inlet of a fish pump or to a specific location in the tank from which they can be harvested by net or pump (Clingerman *et al*. 2007, cited in Summerfelt *et al*. 2009).

Harvesting fish from ponds may be difficult when the ponds have an irregular shape or parts of their sides and bottoms are obstructed. Fish ponds are often constructed with channels and deeper sumps that create favourable water flows that encourage the fish to swim towards harvest points when pond water levels are reduced by draining. As another example, young perch, which are naturally positively phototactic, can be harvested from ponds using a large lift net with lights suspended above it to which the fish are attracted; this is more efficient than conventional seining in terms of catch per unit effort and also causes less damage to the fish (Manci *et al*. 1983). Learned responses can also provide an aid to harvesting fish from ponds. For example, following training to approach an acoustic stimulus by pairing sound with food, cichlids are attracted to, and can be captured in, nets at which the conditioned stimulus is presented (Levin & Levin 1994).

### *Managing the behaviour of escaped and ranched fish*

Fish that escape from culture systems represent lost production, as well as being a potential threat to wild fish populations, so the development of systems for 'recalling' escapees would represent a valuable advance. As an example, both rainbow trout and Atlantic salmon trained to approach an acoustic signal for food, a response that they learn easily and retain for at least 7 months, can be attracted to the vicinity of sea cages by presentation of the conditioned stimulus (Tlusty *et al*. 2008).

Sea-ranching of some species is considered an attractive proposition, as it may overcome some of the problems of fish welfare and environmental impact associated with holding fish in captivity for extended periods (see Chapter 1). The success of ranching depends on being able to harvest the fish once they reach an appropriate size and both innate and learned responses to spatially-informative cues can potentially be used to control their behaviour (Lines & Frost 1999). For example, olfactory imprinting can be used to manipulate sea-ranched salmonids to return to specific sites for harvesting (Scholz *et al*. 1976), although the olfactory imprinting to unfamiliar chemicals is rarely completely successful (Mazeaud 1982). Captive-reared juvenile striped jack (*Pseudocaranx dentex*) may be released into coastal waters for ranching purposes. The young fish form schools and associate with floating objects. The combination of floating and underwater structures (sometimes called fish aggregation devices) and training the fish to associate a broadcast sound with food may be a way to ensure that the fish remain within particular areas (Kuwada *et al*. 2000).

## 4.6 SYNOPSIS

Fish live in a complex three-dimensional environment and patterns of movement and space use depend on species, gender, life history stage and environmental conditions. Space use varies from local movements within a small home range in some coral reef fish to long oceanic migrations in some salmonids. For certain species much is known about the effects of various external stimuli and the use of spatial information by fish to organise their patterns of movement.

The way that fish use space in culture systems is based on the same processes that control the behaviours of wild fish, but captive fish generally operate within a restricted space. This poses a number of problems; captive fish are not free to move about as their wild counterparts do, spatial cues within a culture system may lead the fish to experience unfavourable conditions and a lack of landmarks may reduce the efficiency with which captive fish exploit their environment. In addition, domestication and captive rearing can generate fish that differ from their wild counterparts in various aspects of their spatial behaviour. This may compromise their suitability for subsequent use, for example when released into the wild in supplementation and sea-ranching programmes.

Some of these problems can be solved using biological solutions based upon knowledge of space use in fishes; rheotactic and optomotor responses can be used to stimulate sustained swimming in intensively cultured fish and rearing fish in units with complex and variable spatial features can promote the development of appropriate behaviours in fish destined for release into the wild. In addition, husbandry

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practices including transport of fish between rearing units, grading and the aggregation of fish for harvesting and slaughter might be made more efficient and less stressful by exploiting these behaviours.

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# 5
# Feeding Biology and Foraging

*Malcolm Jobling, Anders Alanärä, Sunil Kadri and Felicity Huntingford*

**Abstract:** This chapter, the first of three dealing with feeding behaviour, describes the different kinds of food that fish eat and the many different ways in which this is harvested. The sensory cues used by fish to locate food are considered, as well as the trophic apparatus used to gather and consume food and the way these are adapted to the kinds of food being eaten. The development of effective feeding movements as fish grow and as their nutritional needs change and the role of genetic variation and differential experience in determining fish foraging are also considered. The benefits and costs of eating different food types and of using different foraging strategies and the way these are balanced to enhance Darwinian fitness are described. Attention then shifts to the implications of natural foraging behaviour for aquaculture. Information is given on how cultured fish species are fed and on problems for production, welfare and the environment that arise from the expression of natural feeding behaviour in an aquaculture context. Some effects of domestication and captive rearing on the foraging of cultured fish are also described. Finally, an account is given of possible solutions to these various problems, based on a knowledge of the natural behaviour of the species concerned.

**Keywords:** cannibalism, carnivory, food capture methods; gastrointestinal tract; herbivory, omnivory; piscivory; trophic apparatus; trophic polymorphism.

## 5.1 INTRODUCTION TO THE FEEDING BIOLOGY OF FISHES

It is critical to the success of aquaculture that fish, irrespective of the purpose for which they are being reared, are offered nutritionally-balanced diets that are presented correctly, in sufficient amounts at the right time. Much research effort has been devoted to the study of what fish eat, how they find and harvest food, what and how much they choose to eat and at what times. A failure to accomodate the natural feeding behaviour of fishes in aquaculture can lead to problems relating to production and can also compromise fish welfare and lead to adverse environmental impact. Many such problems can be solved through an understanding of the behavioural biology of feeding in fish and for this reason three chapters in this book are dedicated to the topic of feeding, nutrition and foraging behaviours.

Acquiring food involves a sequence of events that starts with locating a suitable foraging area and proceeds through detecting food, moving towards and making contact with it, then grasping and ingesting it (Figure 5.1). Once food has been ingested it is either swallowed and the resulting nutrients processed and absorbed, or else it is rejected. The sequence of events can break down at a number of points, due to actions of the forager or, in the case of carnivorous species, of the prey.

How fish search for and exploit areas containing food has been considered briefly in Chapter 4. The present chapter addresses general feeding biology and foraging

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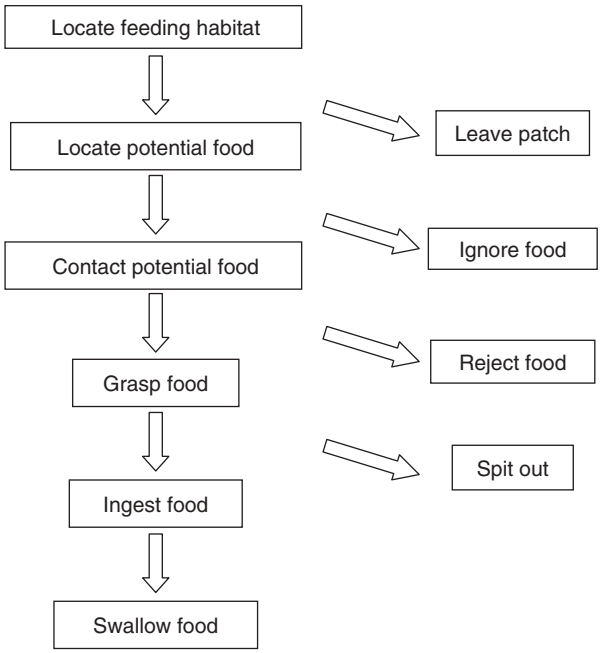


**Figure 5.1.** Schematic of the sequence of events that occurs during food acquisition.

strategies, considering what types of food fish eat and how food is detected and harvested. This provides a general background to Chapter 6, which covers in detail the processes by which fish evaluate food and choose what to eat, and Chapter 7, which deals with the factors that control appetite in fish, how much they eat as they pass through different life history stages and how feeding varies with the seasons and during the day. There is, of course, a close connection between the processes that control how much a fish eats and how much it chooses to eat of different types of food.

## 5.2 FORAGING STRATEGIES OF WILD FISH

### 5.2.1 What fish eat

There are some 28,000 extant species of fish living in a wide range of different habitats, so it is not surprising that the group as a whole displays great diversity in feeding habits, in terms of both their main source of nutrition and how this is harvested (Gerking 1994). These two aspects of feeding biology are of critical importance when it comes to aquaculture, since they determine how easy it is to provide cultured fish with food that they will eat readily. In terms of the main source of nutrition, a first important distinction is between fish that, as adults, eat plants (herbivores), those that eat animals (carnivores) and those that eat the organic remains of plants or animals (detritivores). Many important cultured species eat a combination of plant and animal material; in other words, they are omnivores. Within these general categories, feeding habits can be further subdivided by the kind of plant or animal that is eaten, whether it is eaten whole or in part and how it is gathered.

Fish exploit a range of plants, including phytoplankton, benthic algae (including periphyton and filamentous algae growing on or around structures) and macrophytes. Fifty percent of the fish species on coral reefs are herbivores, plants being a prominant part of the diet in labrids, pomacentrids (damselfish and butterflyfish) and pufferfish, for example. There are many herbivorous species among the cichlids of the African Great Rift Lakes; these include *Tilapia esculenta*, which eats phytoplankton, *Hemitilapia oxyrhynchus*, which eats periphyton, *Oreochromis rendalli* which feeds on macrophytes, *Pseudotropheus zebra*, which scrapes algae off rocks and *P. fuscus*, which feeds on filamentous algae. Several characids in the Amazon drainage system, for example the tambaqui (*Colossoma macropomum*), often move into flooded areas of the forest and wait below mature trees for fruit and seeds to fall.

Fish also exploit a range of animal foods. Zooplankton (comprising adults of some invertebrate species and larvae of both invertebrates and fish) is a prominant part of the diet of many fish, including adults of many smaller ornamental species and juveniles of many larger species. It is common for fish to feed as predators on benthic invertebrates that live either in or on the substratum or in vegetation growing on the substratum. Some gobies (*Gobeidae*) ambush invertebrate prey from shelters and several wrasse species feed on hard-bodied prey such as crustaceans, gastropods and sea urchins. It is also common for fish to feed on other fish (piscivory), this being second to feeding on benthic invertebrates as a general feeding strategy. In many species, some of which are cultured for food, piscivory may involve cannibalism; examples include Atlantic cod (*Gadus morhua*), in which there is a period of intense cannibalism in young fish, and pike, in which larger fish prey on smaller conspecifics throughout life. Most piscivorous fish ingest their prey whole, but some feed on bitten-off parts. For example, the Asian glass-fish (*Chanda nama*) often feeds on the scales of other fish; the prey are approached steathily and the glass-fish dislodges scales from the flanks of the prey by raking movements of the extended lower jaw (Grubh & Winemiller 2004). Bluefish (*Pomatomus saltatrix)* eat fish such as small juvenile striped bass whole, but eat just parts of larger fish (Scharf *et al*. 1998).

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Detritus, non-living organic matter at various stages of decomposition, is a complex mixture of plant and animal remains. It forms a major component of the diet of some fish, including the menhaden (*Brevoortia patronus*) and the mrigal (*Cirrhinus mrigala*, which is a cyprinid) and is included to a lesser extent in the diet of many other cyprinids, of tilapias (for example, *Oreochromis mossambicus*) and of the ictalurid, channel catfish (*Ictalurus punctatus*).

Some broad biological principles relate to the diversity of dietary habits in fish and these are relevant when it comes to selecting and managing cultured species. For example, amongst both freshwater and marine species dietary diversity is greater in fish at low latitudes than at high. At high latitudes, almost all fish are carnivorous and there are very few herbivores; herbivory is more widespread amongst fish of the tropics and sub-tropics (Choat & Clements 1998). Trophic diversity is particularly high in fresh waters of tropical lowlands, such as the Amazon basin. Here the full range of fish feeding habits are represented, including herbivorous fish that feed extensively on the fruits and seeds produced by the forest trees, herbivores that consume algae and other water plants and carnivorous fish specialising on other fish, insects, molluscs, a variety of benthic invertebrates or on zooplankton. There are also omnivores and detritivorous fish that feed on the remains of a variety of other animals and plants (Gerking 1994; Jobling 1995; Rust 2002). In the marine environment, trophic diversity is greatest on tropical coral reefs, which supply many of the fish that are used in the ornamental fish trade. Here there are fish that feed on algae, on coral polyps, on the sponges and other sessile animals that grow as encrusting species, on the mobile benthic crustaceans, echinoderms and fish that live among the corals or on the invertebrates and fish that inhabit the water column in the vicinity of coral outcrops.

### 5.2.2 How fish acquire food

Within their feeding mode, fish use a variety of methods to acquire food. Such variety is well illustrated by the fish communities found on low-latitude coral reefs. Thus, algal-feeding fish may either crop large algae or graze on algal mats. Some damselfish, for example *Stegastes* spp., practise 'algal farming', feeding selectively and promoting growth of preferred algal species and defending their feeding territories against other herbivores (Gobler *et al*. 2006; Chapter 9). Fish that feed on coral may do so either by delicately biting off individual polyps or by crushing the calcareous coral skeleton to obtain the soft parts within. Fish that feed on benthic invertebrates may pick up individual animals or sift through the substratum. Likewise, fish that feed on zooplankton may take individual animals or filter large numbers. The rich communities of coral reefs also attract piscivorous fish that feed on the smaller reef residents.

Among piscivores, some specialise in taking parts of their prey, as in the piranha, which may strip flesh from other fish without first killing them. Having encountered a large prey, eels twist and rotate their body, breaking off pieces of flesh from the prey. Other fish feed on tissues such as blood, as in *Trichomycterid* catfish, or scales, as in many cichlids and characoids among freshwater species and some blennies and jacks among marine species. Many groups of fish (labrids and gobies, for example) contain members that act as cleaners, nipping at and removing ectoparasites from the skin, oral and gill cavities of larger fish. Cleaner fish, which may also eat damaged tissue, scales and mucus from their clients, have been used in aquaculture for control of sea lice. The sabre tooth blenny (*Aspidontus taeniatus*) is a mimic of the cleaner wrasse (*Labroides dimidiatus*). It resembles the cleaner wrasse in morphology and behaviour and approaches client fish slowly before making a rapid dart to tear off fin tissue using the large canine-like teeth in its lower jaw.

Most piscivores swallow their prey whole and use a variety of tactics for prey capture. Some achieve this by hiding (helped by camouflage and lures in anglerfishes and frogfishes), stalking (as in the case of trumpetfish *Aulostomus chinensis*), chasing (as in the yellowtail, Carangidae) and ambush. The pike is a good example of an ambush predator (Hart 1996). Tiger musky (a hybrid between an *Esox lucius* male and *Esox masquiningy* female) use different strike methods depending on the distance from which they initiate their attack. Attacks on distant prey start with bending the body into an S shape, followed by rapid acceleration. Strikes take 50–300 ms to complete and are 2% successful. Closer prey are attacked more quickly (17–100 ms) and attacks are 95% successful (Webb & Skadsen 1980). Finally, some predatory fish hunt cooperatively in schools or in looser groups, as in the case of jack mackerel (*Trachurus* spp).

### 5.2.3 Variability in foraging within species

Although fish species are often classified according to their broad feeding habits (as herbivores, planktivores, benthophages, piscivores and omnivores), many species display considerable intraspecific variation in trophic habits (Hyatt 1979; Gerking 1994; Smith & Skúlason 1996). In some cases, this reflects an ability to alter feeding habits in response to temporal, seasonal and spatial changes in food availability. For example, juvenile lumpfish (*Cyclopterus lumpus*) switch from actively searching when

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prey densities are low to sit-and-wait foraging when prey is abundant (Killen *et al*. 2007). Perch (*Perca fluviatilis*) also show flexibility in foraging strategy, actively pursuing prey in open habitats that contain few refuges for the prey, but adopting a sit-and-wait strategy when their prey have many places to hide (Eklöv & Diehl 1994).

In other cases, variation in foraging patterns or types of food eaten represents individual specialisations, with fish taking only a small proportion of the prey types exploited by the population as a whole. Such trophic polymorphism is common in fish, including a number of species that are cultured, and is usually associated with a range of behavioural, morphological and physiological adaptations (Smith & Skúlason 1996). Two well-documented cases are presented here.

Juvenile perch (*Perca fluviatilis*) are usually considered to be visually-orientated predators that forage on planktonic prey in clear, well-lit waters; they are less proficient at feeding on benthic organisms, especially at night (Schleuter & Eckmann 2006). Nevertheless, some lake-dwelling perch have distinct differences in body form that are related to differences in feeding mode. Some individuals are slim and relatively streamlined, whereas others have a deep body (Svanbäck & Eklöv 2006). The streamlined perch, which are found in open water, cruise over quite long distances, searching large volumes of water for their planktonic prey, which they capture efficiently. They are less efficient at feeding on bottom-living (benthic) prey and at hunting for and capturing prey in aquatic vegetation. Hunting in confined spaces requires good manoeuvrability, precise movement and good steering and braking abilities (Chapter 2). The deep-bodied perch, which occur most often in the vegetation that grows in shallow lake margins, are able to make precise swimming movements and feed effectively on bottom-living prey, on prey that is attached to aquatic plants and on the planktonic organisms that swim close to the underwater vegetation (Svanbäck & Eklöv 2004). As a second example, Arctic charr that inhabit a single water body may display considerable morphological variation related to the food upon which they feed (Smith & Skúlason 1996; Jonsson & Jonsson 2001; Andersson *et al*. 2005). Some lakes contain as many as four sympatric morphs, specifically planktivores, small and large benthivores and piscivores, that are reproductively isolated from each other (Smith & Skúlason, 1996; Jonsson & Jonsson 2001).

## 5.3 MECHANISMS

There are many differences between fish species, and sometimes within them, in what is eaten and how food is acquired; this diversity is accompanied by variation in the mechanisms by which fish detect and capture different types of food. What kind of food fish eat, the cues they use to detect it and exactly how they harvest it are very important for aquaculture, since these traits dictate how easy or difficult it is to provide particular species of fish with the appropriate conditions for them to feed effectively. This section describes the cues that fish use to detect and locate food and how they capture and engulf it once located.

### 5.3.1 The sensory cues that fish use to locate food

Chapter 2 gives a general account of the sensory cues that are detected and used by fish and of the sense organs involved. All of the senses may be involved in foraging, details depending on species. In some cases, the stimuli concerned may be very specific, with a given feeding pattern being mediated through a single sensory system, as in the case of knifefish, which detect prey by means of distorsion in self-generated electric fields. More often, however, foraging is initiated and maintained by the combined effects of several types of stimuli; for example, in the piscivorous musky (*Esox masquinongy*), visual cues are important when prey are being stalked, both vision and mechanosensory input via the lateral line are involved in the initiation of a strike and mechanosensory cues are critical for prey capture (New *et al*. 2001).

#### *Vision*

Visual cues are important in the search for and location of food for many fish species (Douglas & Djamgoz 1990; Hawryshyn 1998; Rust 2002; Utne-Palm 2002). As discussed in Chapter 2, the determinants of visibility of a potential food item include its shape, size, colour, degree of transparency and whether it is moving or stationary. Many planktivorous fish select the prey that appears largest, either because it is indeed large or because it is small, but close by. At any given light intensity fish will generally be able to detect prey at greater distances if they are large rather than small (Figure 5.2) and will have a higher feeding efficiency on larger prey (O'Brien *et al*. 1990; Holzman & Genin 2005). Although many zooplanktonic species are transparent, they are often preyed upon by visually-feeding fish and detection distance is a major factor that determines the vulnerability of the zooplankton to predation. Fish can locate moving targets more easily than those that are motionless, so prey activity can increase the likelihood of detection by predators. The overall consequence is that under some circumstances motion may be more important than size in determining whether or not prey is detected and attacked.

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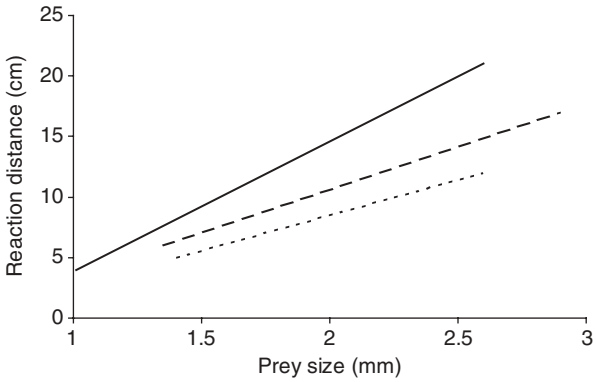


**Figure 5.2.** Visibility and prey size. Reaction distance (cm) in relation to prey size (mm) in lake trout feeding on prey of different degress of conspicuousness. Solid line = heavily-pigmented *Daphnia*. Dashed line = moderately-pigmented *Daphnia*. Dotted line = unpigmented *Daphnia*. Adapted from O'Brien 1979.

As discussed in Chapter 2, in order for an underwater object to be visible it must differ sufficiently from the background, so fish that detect their prey by vision depend upon an adequate degree of contrast between the prey and the background against which it is to be detected. This depends on the amount of available light, the degree of turbidity and the backscattering of light between the fish and its food. At very low light intensities fish experience difficulties in detecting their food by vision, but some are able to feed visually even under such conditions. Turbidity is caused by suspended material, including small inorganic particles, organic detritus and phytoplankton suspended in the water column. There are differences in light absorbing and scattering properties of phytoplankton and suspended inorganic material such as clay particles. Therefore the ability of predators to detect and capture prey may differ in waters that contain high concentrations of phytoplankton compared to those where turbidity is the result of suspended inorganic material (Radke & Gaupisch 2005). As water becomes more turbid the distance at which visually feeding foragers are able to detect food is reduced (Utne-Palm 2002). In general, species that live in turbid water or at depth have more sensitive eyes than those that live in clear, shallow waters,or close to the water surface (Kestemont & Baras 2001; Stoner 2004). The effects of water turbidity on feeding can differ between species and circumstances, depending, for example, on the visual abilities of the species concerned and their reliance on vision and other senses during foraging (Stoner 2004; Gadomski & Parsley 2005; Lehtiniemi *et al*. 2005; Radke & Gaupisch 2005). Predatory fish can compensate for reduced visibility due to low light levels or turbidity by increasing their activity, thereby maintaining rates of encounter with prey (Utne-Palm 2002; Granqvist & Mattila 2004; Stoner 2004).

The detection of ultraviolet (UV) light may be important for prey detection and feeding, as well as other aspects of fish behaviour (Utne-Palm 2002; Jordan *et al*. 2004; Flamarique 2005; Modarressie *et al*. 2006). Many zooplanktonic organisms are semi-transparent and reflect very little light within the wavelengths of the normal visible spectrum, making them effectively transparent within the 400–700 nm range of wavelengths and so difficult to detect by potential predators such as small fishes. Zooplanktonic organisms are, however, relatively opaque at UV wavelengths (280–400 nm), due to increased light scattering and the presence of UV-protective pigments. They will be visible to predators that possess photoreceptors capable of detecting UV wavelengths. The conspicuousness of transparent objects may also be increased in polarised light. Many zooplanktivorous fish (including larvae and juveniles of several species) have visual pigments that are sensitive to UV wavelengths and these fish may also be sensitive to the polarization of the light; these two visual adaptations increase the conspicuousness of zooplanktonic prey. The environmental factors that determine the ability of fish to locate their food visually are likely to have an important influence on the effectiveness with which cultured fish are able to acquire food.

### *Mechanosensory systems*

Fish that locate and strike at prey by means of mechanosensory cues tend to have an elaborate lateral line canal system on the head, with prey-generated signals usually being detected head-on (Bleckmann 1993; Janssen 1997; van Netten 2006; Chapter 2). Long-distance detection requires predators to be sensitive to minute water velocities and lateral line sensitivity can be increased either by proliferation of superficial neuromasts and/or by wide membraneous canals. Self-generated noise has the potential to mask signals from external sources and when searching for prey fish may employ a saltatory search strategy, with short movements interspersed with periods during which the fish reduce self-generated noise by ceasing to swim. This is the case for dwarf scorpionfish (*Scorpaena papillosa*), which detects respiratory movements of potential prey (commonly crabs) using the lateral line (Bassett *et al*. 2007). Self-generated noise may also be reduced by adopting slow gliding movements when foraging rather than more active

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propulsion that involves side-to-side displacement along much of the body length (Montgomery *et al*. 1995).

***Chemoreception***

Olfactory input has an important influence upon detecting and locating food (Hara 2006; Rust 2002; Kasumyan & Døving 2003). Several types of chemical compounds have been identified as potent odorants for fishes. These include amino acids, metabolites of sex steroid hormones, prostaglandins and bile acids (Hara 2006; Chapter 2). For carnivorous fish, amino acids play a major role in the olfactory detection of potential prey (Wyatt 2003) and the discriminatory ability for different amino acids appears to be very high (Friedrich 2006). The amino acids that are most stimulatory for the fish olfactory system seem to be short-chain neutral amino acids (Hara 1975, 1992, 2006; Yacoob *et al*. 2004). As such, cysteine, a very potent olfactory stimulating agent, serves to initiate feeding behaviour in a range of fish species (Hara 2006). Aromatic amino acids, on the other hand, are generally much less effective as olfactory stimulants and odorants for fish and have a lesser role in the stimulation of feeding behaviour.

Gustation is also extremely important in the detection and ingestion of food by fish. As described in Chapter 2, unusually among vertebrates, fish often have taste buds both in the mouth and pharynx and on the lips, barbels, fin rays and on the skin, particularly in the head region close to the mouth (Hara 2006; Lamb 2001; Kasumyan & Døving 2003; Ishimaru *et al*. 2005). In sturgeon, extraoral gustatory receptors are used to determine the palatability of food, with a preliminary investigation being essential to induce feeding behaviour; following this the final assessment of palatibility is made using the oral gustatory receptors (Kasumyan & Døving 2003).

***Electrical cues***

Fish can detect and capture prey by means of both passive electroreception, detecting the electrical cues produced by the prey, and active electroreception, detecting prey from deformations in an electrical field generated by the foraging fish itself. For example, Australian lungfish possess ampullary receptors (Chapter 2) that are capable of detecting weak electric fields from external sources. Feeding responses are more common when electric cues from prey are present than when such cues are blocked, irrespective of the presence of olfactory cues (Watt *et al*. 1999). Juvenile paddlefish use ampullary receptors on the extended snout, or paddle, to detect and capture prey in swarms of *Daphnia*; if presented with dipole electrosensory cues similar to those generated by *Daphnia* they are attracted to these (Wilkens & Hoffman 2007). Similarly, cartilaginous fishes such as sharks and rays have well-developed electrosensory systems that are used in detecting and locating prey. Gymnotid knifefish of the genus *Apteronotus* use active electroreception to detect prey. When searching for prey, the fish swim slowly with the head pointing downwards and the dorsal surface as the leading edge. Upon detecting prey the fish reverse thrust to bring the prey item in line with their mouth (Nelson & MacIver 1999).

### 5.3.2 The structures that fish use to gather food

The trophic apparatus of fish includes the mouth and jaws, the teeth (which are found on pharyngeal bones set far inside the mouth as well as in the jaws and some other skull bones), the gill rakers (protrusions from the gill arches that help to collect food) and the gastrointestinal tract. There may also be extraoral appendages, such as barbels or free fin-rays, that are used for detecting and locating prey.

The feeding habits of fish are reflected in the morphology of their feeding apparatus (Wootton 1990). For example, planktivores and other fish that feed on small food items usually have small jaws and jaw teeth, while fish that take larger prey usually have a large gape, large jaw teeth and a non-restrictive pectoral girdle that allows large prey to be swallowed whole. Fish that eat corals and other food items with hard spines or a thick exoskeleton usually have specialised dentition for removing food items from the substrate and for crushing them. They may also employ a 'winnowing' movement to separate the soft edible parts of the prey from the hard skeletal fragments. In such cases, the jaw teeth, which are usually blunt and molariform or fused to form strong plates, will most often be used for scraping or wrenching the prey from the substrate, whereas the crushing of the exoskeleton may be carried out by either the jaw teeth or by plates of strong, blunt teeth located in the pharynx (the pharyngeal mill).

Pharyngeal teeth are common in fish and their form reflects the feeding habits of the species concerned. For example, the cichlid family, which consists of more than 1500 species, forms an important component of the freshwater fish faunas in Africa and parts of Central and Southern America, as well as being cultured for food and as ornamental fish. Cichlids eat a wide variety of food types and their pharyngeal teeth, which play a central role in food processing, take a wide variety of forms. The pharyngeal teeth range from long, slender and hook-like teeth, to large, rounded molariform teeth with flat crowns. The slender, hook-like pharyngeal teeth provide a mechanism for processing fine particulate food, such as microscopic plants that are first trapped in mucus secreted by cells in the mouth

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**Table 5.1.** Summary of the substrates and actions of the main digestive enzymes in fish.

| Macronutrient substrate | Chemical bond affected | Digestive enzyme involved | Site of | |
|---|---|---|---|---|
| | | | Production | Action |
| Carbohydrates | Glycosidic | Carbohydrases | | |
| | | Amylase | Pancreas | Intestine |
| | | Cellulase | Gut microflora | Intestine |
| | | Chitinase | Pancreas & intestine Gut microflora | Intestine |
| | | Disaccharidases | Intestine | Intestine |
| Lipids (fats) | Ester | Lipases/esterase | | |
| | | Lipase | Pancreas | Intestine |
| | | Phospholipase | Pancreas | Intestine |
| | | Esterase | Pancreas | Intestine |
| Proteins/polypeptides | Peptide | Proteases/peptidases | | |
| | | Pepsin(ogen) | Stomach | Stomach |
| | | Trypsin(ogen) | Pancreas | Intestine |
| | | Chymotrypsin(ogen) | Pancreas | Intestine |
| | | Carboxypeptidases | Pancreas | Intestine |
| | | Aminopeptidase | Intestine | Intestine |
| | | Peptidases | Intestine | Intestine |

and on the gill rakers, before being raked backwards towards the gullet. Strong molariform pharyngeal teeth act as grinders to crush the shells of molluscs, whereas sharp, knife-like pharyngeal teeth serve to cut and slice fish prey (Beveridge & Baird 2000; Hulsey *et al*. 2005). The structures that support the gills (branchial arches and their gill rakers and filaments) are also highly diverse and their morphology is often indicative of feeding habits (Hyatt 1979; Gerking 1994). Fish with numerous, long, thin, closely-spaced gill rakers tend to feed on small food items such as planktonic organisms, whereas fish that have fewer, blunter and more widely-spaced gill rakers usually feed on larger prey (Budy *et al*. 2005; Kahilainen & Østbye 2006).

A fish's diet is also reflected in the structure of its gastrointestinal tract (GI) tract, which is a major interface between the external environment and the fishes' body. The functions of the GI tract include digestion of food, absorption of nutrients, defense against potentially pathogenic bacteria and other harmful agents, salt and water balance and elimination of toxins and metabolic wastes. The fish GI tract houses an array of digestive enzymes that is generally reflected throughout most of the vertebrate lineage (Fänge & Grove 1979; Smith 1989; Jobling 1995; Rust 2002; Table 5.1). The major divisions of the GI tract are the mouth and buccal cavity, pharynx, oesophagus, stomach, intestine and pyloric caeca, and rectum. There are also additional organs with roles that are intimately related to GI tract function, including the liver, gallbladder and pancreas. Sometimes one or more of the GI tract regions or organs may be absent or degenerate. For example, the Cyprinidae (carp-like fishes) lack an acid-secreting stomach, but have a distensible bulb-shaped structure in the forepart of the intestine that receives ingested food items and acts as a short-term food reservoir. Fish stomachs and intestines differ markedly in gross morphology and in their ability to hold, retain and process food. For example, the stomachs of predatory fish species, particularly piscivores, are usually large and sac-like and are capable of expansion to accommodate large meals taken at infrequent intervals. Piscivores and other carnivores tend to have shorter intestines relative to their body length than do omnivores, herbivores and detritivores, which consume foods with a higher non-digestible fibre and roughage content (Kapoor *et al*. 1975; Smith 1989; Jobling 1995; German & Horn 2006). The occurrence of a long intestine is not, however, universal in herbivorous and detritivorous species; some herbivores that have part of the GI tract adapted to form a microbial fermentation chamber have a relatively short intestine in relation to their body length (Choat & Clements 1998).

The relationship between the morphology of the trophic apparatus and diet is seen particularly clearly in fish that

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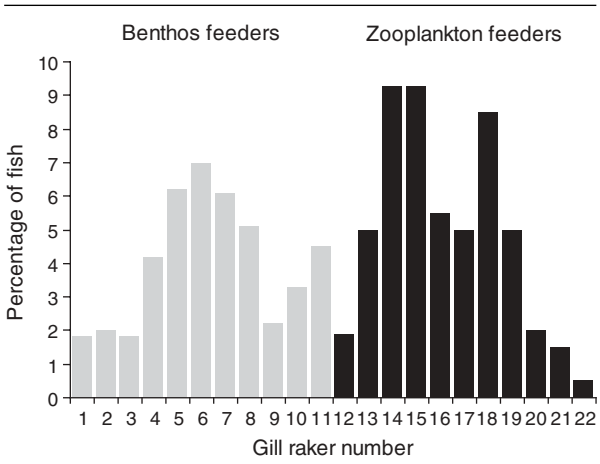


**Figure 5.3.** Trophic polymorphism in whitefish. Frequency distribution of fish with different numbers of gill rakers in whitefish specializing on larger benthic (pale grey bars) or smaller zooplanktonic prey (dark grey bars). Adapted from Amundsen *et al.* 2004.

display trophic polymorphisms. For example, the cichlid *Herichthys minckleyi*, which is endemic to a small number of water bodies in Mexico, exists in three forms that specialise on different diets and also differ in trophic morphology. One form specialises on detritus, algae and soft-bodied invertebrates and has papilliform teeth. Snail specialists have flat, molariform pharyngeal teeth and enlarged muscles that are effective at crushing hard-shelled prey. A third form is piscivorous and has adaptations for this foraging mode (Swanson *et al*. 2003; Hulsey *et al*. 2005). In the European whitefish there is a striking bimodality in gill raker numbers (Figure 5.3), with resulting differences in how densely the gill rakers are packed. The fish with many, densely packed rakers eat zooplankton, whereas the sparsely rakered form eats bottom-living animals (Amundsen *et al*. 2004).

### 5.3.3 Mechanisms for capture and ingestion of food

Once the sensory systems have brought fish into contact with their prey, just how the fish effect food capture can be complex. In parrotfish, jaw movements, locomotion and eye movements are tightly coordinated during prey capture. As a fish approaches a food item, the pectoral fins act as a source of thrust, but during a strike they function primarily for manoeuvring. The jaws open approximately 100 ms before prey capture and the eyes move from looking forward at the target, to looking to the side. This means that although vision is important in initiation and coordination of feeding, its role ends before the fish ingests the prey, perhaps allowing the forager to switch to looking out for predators (Rice & Westneat 2005).

Fish can ingest prey using inertial suction, ram feeding or manipulation (Liem 1980). Suction feeding, the most common form of prey capture, entails an expansion of the oral (buccal) cavity, which results in lowered pressure and the drawing of prey into the mouth, along with some water (Gerking 1994; Ferry-Graham & Lauder 2001). Suction feeding is used in many different ways by foraging fish. Zooplanktivores and surface-feeding fish may take in single prey in this way. Some benthic and detritus feeders scoop up prey or substrate by a series of rapid, non-directional suctions through a downward directed mouth. Adult seahorses capture prey using highly specialised suction feeding; the long-snouted head is rotated rapidly towards the prey, followed by a powerful suction amplified by elastic recoil of the rotated head (Van Wassenbergh *et al*. 2009).

Despite the variety in prey types and feeding conditions, the general pattern of prey capture by suction is consistent across species, with four phases being recognised; the preparatory, expansive, compressive and recovery phases (Ferry-Graham & Lauder 2001). During the preparatory phase the oral cavity is compressed, and this is then followed by a rapid expansion that draws the food and some water into the mouth. The magnitude of the change in the volume of the oral cavity and the speed of expansion both affect the rate of the flow of water into the mouth. The rapid expansive phase is followed by a slower compression, during which water is expelled through the gill covers while the food is retained within the mouth. Finally, during the recovery phase the bones of the jaw and skull and the various muscles involved return to their relaxed, prefeeding condition. Ram feeding, whereby food is engulfed by rapid forward movement of the fish while the mouth is held open, may involve filtration of small food items that impinge on the gill rakers. For example, herring (*Clupea harengus*) filter planktonic food by swimming with the mouth wide open and the opercula flared to allow the water to pass out.

### 5.3.4 Summary of foraging mechanisms in fish

Fish are very varied in terms of the food that they eat and this is reflected in differences in trophic morphology, including jaws, teeth, gill rakers and GI tract. It is also reflected in the sensory cues used to detect and capture food. Depending on species, age and the phase of the foraging sequence, these might involve vision, mechanosensory cues, chemical cues and in some cases electrical

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cues. The circumstances in which potential food is encountered, for example the turbidity of the water, determine how useful the various sensory cues are for its detection. Even though fish eat a wide range of food types, the constraints imposed by moving in water impose a degree of uniformity on how food is actually acquired. The majority of fish use suction feeding, whereby the oral cavity is rapidly enlarged, creating negative pressure and suction. Ram feeding involves fish swimming with mouth agape and opercula flared to collect small food items that are filtered out by the gill rakers or to engulf larger prey.

## 5.4 DEVELOPMENT

Requirements change as fish pass through a larval period of nutritionally demanding early growth and development, a juvenile period of more gradual increase in size and finally reach maturation and prepare for breeding. Such changes in nutritional requirements are often associated with changes in the types of food that fish eat and the methods used to gather them. This is true for most species, but is particularly marked in fish whose life histories include dramatic changes in habitat. Larval rearing is recognised as a major bottleneck in fish culture, and knowing how methods of food acquisition change with age can potentially help in meeting this challenge. In addition, understanding the genetic and experiential processes that mould foraging behaviour has potential applications both in the development of aquafeeds and in identifying and ameliorating deficits in feeding behaviour in fish that are cultured for release.

### 5.4.1 Ontogeny of foraging

Young fish start feeding on exogenous food when most of the nutrients in their yolk sac have been used up. Larval and juvenile fish require high-quality food to sustain growth and most fish larvae feed on small animals (often zooplankton), irrespective of the type of foods consumed later in life. As fish grow, the type of food that they eat often changes. For example, many piscivorous fish (for example, Caribbean groupers and American freshwater bass, Wainwright & Richard 1995) undergo a size-dependent dietary progression from zooplankton to benthic macroinvertebrates and then to fish (Mittelbach & Persson 1998). Ontogenetic changes in diet may correspond to changes in habitat. For example, when juvenile Atlantic cod settle out of the plankton and take up a demersal way of life, they change from feeding on zooplankon to feeding primarily on benthic invertebrates. As they grow to adult size another dietary shift takes place, with fish and large benthic invertebrates such as crabs making up an increasing proportion of the diet (Link & Garrison 2002).

#### *How fish capture food at different ages*

Integrated feeding movements often appear gradually during developement. In zebrafish (*Danio rerio*) larvae hatch about 3 days after egg fertilisation, start responding to food about a day later and the yolk sac is exhausted after 1 week. The typical pattern of prey capture, evident a few days after hatching, is characterised by an initial tracking phase composed of small turning movements, followed by a capture phase during which the larvae strike at potential prey. The capture phase involves a series of small caudal bends to adjust position, followed by one or more large rostral bends propelling the fish towards the prey, accompanied by a series of tail beats, the frequency of which increases with age (Borla *et al*. 2002). Feeding movements in zebrafish develop gradually, as is the case in many other species, but there are a few exceptions to this general rule. For example, on first being released from their father's pouch, young seahorses (*Hippocampus reidi*) are able to feed successfully using extremely rapid, rotation-based suction feeding similar to that seen in the adults. This is possible because of rapid development of the necessary anatomical structures, but also because the larvae, having been brooded and nourished by their father, are relatively advanced by the time they feed independently (Van Wassenbergh *et al*. 2009).

Ontogenetic changes in the type of food eaten and the way in which it is harvested are associated with changes in morphology and behaviour and are often the result of increasing size. For example, patterns of suction-induced flow during prey capture in African catfish (*Clarias gariepinus*) change with size over the range 10–90 cm. As the fish increase in size the expansion phase is prolonged to give a stronger sustained flow (Figure 5.4a) reaching further into the mouth and increasing the distance from which prey can potentially be captured (Figure 5.4b). At the same time the maximal prey size that can be consumed increases, as does the fishes' ability to capture evasive species (Van Wassenbergh *et al*. 2005).

Changes in sensory systems also influence the development of feeding in young fish. For example, zebrafish larvae become sensitive to amino acids one day after hatching, responding to them with an increase in activity and turning rate (Lindsay & Vogt 2004). Seven day old zebrafish attack small prey with a high degree of accuracy in the light but not in the dark, emphasising the importance of visual cues in prey detection at this stage (Gahtan *et al*. 2005). Although small fish may use UV light

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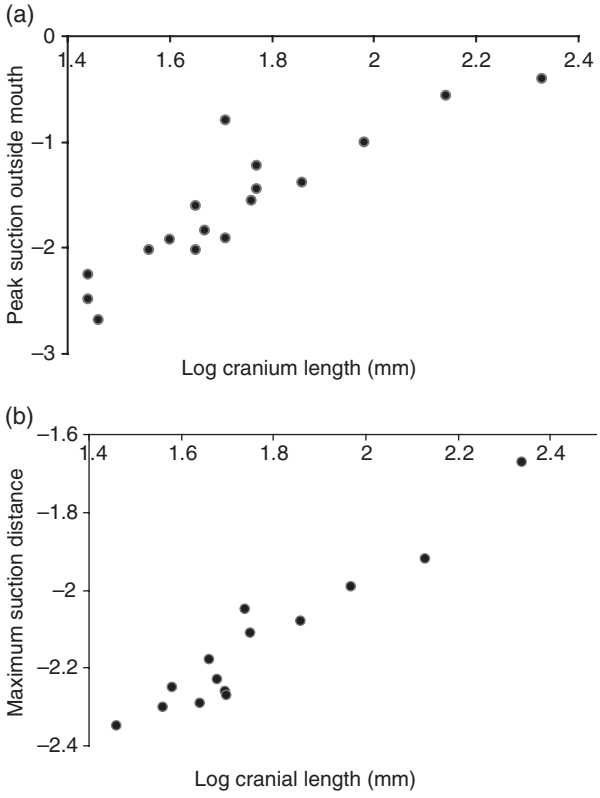


**Figure 5.4.** Ontogeny of suction feeding in catfish. (a) Log peak suction flow 15 mm in front of the mouth and (b) log maximal suction distance external to the mouth for a speed of 0.2 m/s, in relation to log cranial length (mm) in juvenile catfish. Adapted from Van Wassenberg *et al.* 2005.

for detecting their planktonic prey, UV sensitivity may be lost as the fish grow larger and start to feed upon other types of prey. This occurs in rainbow trout (*Oncorhynchus mykiss*) as they increase in size and become less dependent upon zooplankton as a source of food (Hawryshyn *et al.* 1989). Larval striped trumpeters (*Latris lineata*) have superficial neuromasts at hatching and these increase in number over the head and body as the fish grow older and the lateral line develops. Nevertheless it is the development of a functional retina in the eye at day 7 that coincides with the onset of feeding (Cobcroft & Pankhurst 2003).

The red porgy (*Pagrus pagrus*) is a visual feeder. Larvae hatch with little remaining yolk, but without a functional mouth or visual system and with a simple, undifferentiated gut. The eye rods and cones and the gut are functional by 4 days after hatching. By this time the larvae have a well developed capacity for prey capture and this ability increases as they grow (Roo *et al.* 1999). The undeveloped eye and gut in red porgy is in striking contrast to the situation in the clownfish (*Amphiprion percula*), in which the mouth is open and the gut, liver and pancreas are all functional before hatching. Clownfish readily accept rotifers at hatching and change their diet from rotifers to *Artemia* at about 10 days after this (Önal *et al.* 2008). This augurs well for the captive rearing, and hence conservation, of this popular ornamental species.

Once independent feeding is established, what the fish eat and how they eat it may change, due both to increased size and to habitat shifts. For example, after 7–10 days of independent feeding Atlantic salmon (*Salmo salar*) switch from a ram feeding mode to a suction mode (Coughlin 1991). Young black surfperch (*Embiotica jacksoni*) detect prey visually and pick individual prey (small invertebrates) from the substrate, whereas larger fish filter prey from mouthfuls of sedimented detritus. This age-related difference in feeding is associated with a preference for different feeding patches; juvenile surfperch tend to forage around foliose algae whereas older surfperch tend to feed in areas with turf algae (Schmitt & Holbrook 1984).

### 5.4.2 Inherited differences in foraging methods

The broad diet of a given species of fish (whether it is herbivorous, benthivorous, omnivorous or piscivorous, for example) and its method of aquiring food are largely hardwired, in the sense that they develop without specific experience of using particular feeding modes. This is illustrated by the fact that cultured fish that have only experienced artificial food will often feed readily on wild prey, showing species-specific responses to the stimuli these emit (Reiriz *et al.* 1998). This suggests some degree of innate recognition of prey and an inherent tendency to show a particular foraging strategy, dictated by the physical and physiological constraints of the sensory and trophic apparatus of the species concerned.

In addition, several more direct lines of evidence demonstrate genetic influences on trophic apparatus and behaviour. For example, many zebrafish mutants cause differences in the structure, and presumably the functioning of, the trophic apparatus (Schilling *et al.* 1996) and in the sensory systems used to detect food (Gahtan *et al.* 2005). There is also evidence for a genetic component to trophic polymorphism in a number of fishes. Pumpkinseed sunfish can be of a pelagic form, with a long head, long thin pectoral fins and a long, relatively slim body, or a benthic-feeding form, which has the opposite set of morphological features. Pelagic fish retain their long, slim bodies when reared in an environment with benthic prey,

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indicating a genetic component to the morphological difference (Robinson & Wilson 1996). Pelagic and benthic morphs of Arctic charr within a lake are often genetically distinct and the behavioural and morphological differences may have a genetic component, because differences may persist when fish are reared under identical conditions (Smith & Skúlason 1996; Alexander & Adams 2004). Finally, inherited differences in the propensity for cannibalism are indicated by the fact that hybrids between a cannibalistic species (*Poeciliopsis monacha*) and a non-cannibalistic species (*P. lucida)* show levels of cannibalism that are intermediate between those of the parental species (Thibault 1974).

### 5.4.3 Experience and foraging methods

Even though there may be genetic influences on feeding biology, experience plays an important role in how foraging develops in fish, through two main kinds of effects, namely the morphological development of the trophic apparatus and the behavioural effects of experience with particular kinds of food.

#### *Effects of feeding history on trophic morphology*

In the cichlid (*Cichlasoma managuense*) there is an ontogenetic shift from biting at prey to the use of suction, with associated changes in snout shape. Young fish exposed to prey that require biting, such as flaked food and nematodes, retain blunt snouts, whereas those exposed to prey that require suction (*Artemia*, for example) develop pointed snouts sooner (Meyer 1987). In the case of pumpkinseed sunfish, variation in jaw morphology is associated with the proportions of snails that make up the diets of fish from different lakes or habitats (Robinson & Wilson 1996). Differences in jaw morphology and muscle size can be induced by providing pumpkinseeds with diets with or without snails. This indicates that some of the differences among populations are the result of a developmental plasticity that allows the fish to exploit a range of prey types (Mittelbach *et al*. 1999). When young fish from populations with different jaw morphology in the wild are reared in the laboratory on soft bodied prey either alone or supplemented with snails, population of origin has no effect on trophic morphology. However, fish with experience of feeding on snails develop strikingly larger crushing muscles (Figure 5.5) than do fish fed only on soft bodied prey. In this case, the difference in trophic morphology between pumpkinseed sunfish from lakes with and without snails comes about through a plastic response to local foraging conditions rather than being an inherited genetic adaptation.

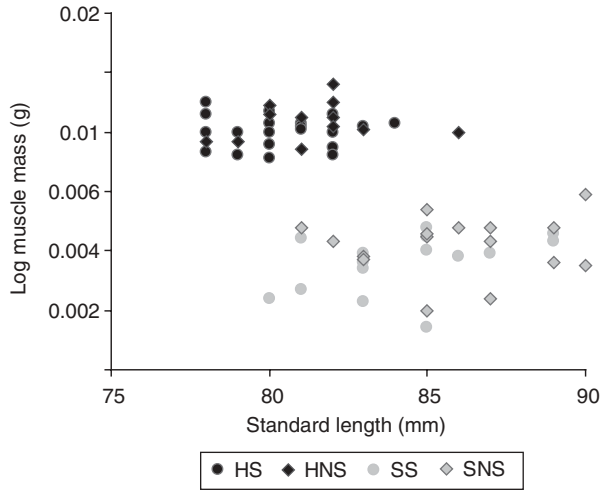


**Figure 5.5.** Effects of experience on trophic morphology. Jaw muscle mass (g, log) in relation to standard length in pumpkinseed sunfish from populations with (S) and without (NS) natural access to abundant snails, reared either on hard (H) or on soft (S) food. Adapted from Mittelbach *et al.* 1999.

In the case of Arctic charr, the divergent morphological and behavioural traits of sympatric morphs specialising on zooplankton or benthic prey would appear to be the combined result of inherited genetic effects and individual foraging experience. When offspring of parents that display different trophic morphologies are reared in a common environment, the morphological differences between offspring of the two forms are still seen, but in a less pronounced form than those seen in their parents. This provides evidence of a phenotypic plasticity in trophic morphology, in addition to the genetic component (Alexander & Adams 2004).

#### *Effects of feeding history on foraging behaviour*

Fish are able to adjust their strategy for acquiring food in the light of experience. In some cases adjustment takes place over a short time scale. For example, foraging bluegill sunfish (*Lepomis macrochirus*) alternate between pauses (during which they scan for prey) and periods of forward movement. The pauses are shorter when the fish are feeding in open water than when they are in weeded areas, presumably because prey that are hiding in weeds are harder to locate (Ehlinger 1989). Sacramento perch (*Archoplites interruptus*) hunt evasive zooplankton more efficiently after experience of such prey (Vinyard 1982) and pumpkinsed

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sunfish feeding on guppies, an unfamiliar prey in the wild, become increasingly effective at capturing these fish (Wainwright 1986). In the longer term, the effectiveness with which fish capture prey increases with experience. During their early life, young Atlantic salmon gradually increase the accuracy with which they attack live prey and they capture them faster. Initially the young salmon show a poor aim and use weak, relatively undirected suctional feeding, but older, more experienced fish have a steadier aim and compress their buccal cavity earlier in relation to mouth opening, generating more effective suction (Coughlin 1991).

### 5.4.4 Summary of the development of foraging patterns in fish

The integrated movements that fish use to gather food begin soon after hatching, with a degree of effectiveness that depends on species. The foods that fish eat, as well as the methods they use to acquire food, change with age. This is partly due to altering nutritional needs; for example, many species that are herbivorous as adults are carnivorous as larvae, when they need a protein-rich diet to sustain growth. It is also partly due to changes in the structures required to detect, gather and process food; for example, fish may switch from an invertebrate diet to piscivory once their jaws and teeth reach the size required to feed on other fish. The foraging strategy of adult fish (the kind of food eaten and how it is gathered) is more or less hard-wired, in the sense of being seen in fish reared without experience of natural prey. In addition, some differences in foraging strategy within species are known to be inherited. Nevertheless, these same traits can be modified by experience, enabling fish to alter their trophic apparatus, digestive functions and feeding behaviour in relation to changes in the types of food that they encounter and hence to exploit a range of food resources (Warburton 2003; Andersson *et al*. 2005; Olsson & Eklöv 2005). Such plasticity is of critical importance for fish culture, since it determines the extent to which it is possible to culture fish effectively on unfamiliar and unnatural food sources.

## 5.5 FUNCTIONS

Since the foraging environment of wild fish is likely to vary in unpredictable ways, those individuals that are best able to exploit the diverse and unpredictable food sources that they encounter are likely to enjoy higher fitness. The following sections encompass the functional consequences of the foraging strategies that fish use, considering the benefits gained and the costs incurred by fish using particular food gathering methods and how such costs and benefits are balanced.

### 5.5.1 Benefits

The benefit of foraging in a particular manner relates to the nutrients gained from consuming the prey concerned. In general, animals represent higher-quality food for fish than do plants (Raubenheimer *et al*. 2005; Skea *et al*. 2005; German *et al*. 2004; Krogdahl *et al*. 2005). Most parts of plants contain a low proportion of protein and the amino acid balance of plant proteins often does not match that required by fish. Plants include a high proportion of long-chain structural polymers (fibres) such as cellulose and lignin, which are not digested by fish. The poor quality of plants as a source of food explains why relatively few species of fish are exclusively herbivorous and why most herbivores supplement their diet by consuming some animal prey. The nutritional consequences of feeding on different kinds of food are discussed in more detail in Chapter 6.

Within a dietary mode, a given foraging tactic is either more or less successful depending on circumstances. For example, where prey are small relative to the size of the predator, successful foraging is largely dependent on effective searching, but when prey are relatively large success depends more upon on pursuit and handling (Hart & Connellan 1984; O'Brien *et al*. 1990). The ease with which different species of piscivorous fish can capture agile prey, and hence the benefits they derive, depend on body shape (Chapter 2). For example, stealth-and-sprint piscivores such as the pike have an elongated body, a deep caudal peduncle and the dorsal and anal fins are positioned towards the hind end of the body. Such fish are good at fast starts, but poor at chasing and at manoeuvering during strikes, so if an attack misses, they are unable turn quickly and give chase. In contrast, deeper-bodied piscivores such as smallmouth bass (*Micropterus dolomieui*) and perch (*Perca fluviatilis*) have somewhat laterally flattened bodies with the paired fins placed anteriorly. These species are poorer than the pike at fast starts, but are good at chasing and at manoeuvering during chases; they are also able to anticipate evasive tactics and rarely miss their prey (Webb 1984). The benefits (in terms of food intake and growth) of ambushing (exemplified by pike) as opposed to chasing (exemplified by bass and perch) depend upon the conditions under which predatory encounters take place. Piscivorous perch feed more efficiently and grow faster when held in small groups than when feeding alone, but pike show no social foraging behaviour and do better on their own (Eklöv 1992).

### 5.5.2 Costs

Eating different kinds of food and gathering it in different ways impose various costs. These may take the form of time spent foraging, energy expenditure, risk of injury or

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harm from the food item and risk of predation on the forager. Considering energetic costs, a predator may be required to expend more energy to find and capture active than inactive prey. Sacramento perch, for example, swim faster and expend more energy when feeding on mobile zooplankon species than when feeding on more sedentary prey (Vinyard 1982). Considering harm caused to the forager; in addition to yielding lower nutritional returns than animal food, eating plants can incur some costs to the forager in the form of ingesting toxic secondary compounds that either have an unpleasant, bitter taste or interfere with digestion and metabolism (German *et al*. 2004; Krogdahl *et al*. 2005; Skea *et al*. 2005; Chapter 6). Animal prey can also be harmful; for example, conger eel stop abruptly and retreat after coming into contact with an electrogenic torpedo ray (Wilson 1953) and when other prey are available pike avoid feeding on stickebacks, in which some of the fin-rays take the form of stiff, sharp spines (Hoogland *et al*. 1957). Further, different foraging strategies may incur different risks of predation; juvenile sharknose goby (*Elacatinus evelynae*) have lower mortality rates when living on sponges and feeding on free-living copepods than when adopting a cleaning strategy on coral heads (56% versus 88% mortality over 30 days). These differences in mortality are probably the result of differences in predation on the fish displaying different types of feeding behaviour (White *et al*. 2007).

### 5.5.3 Trading costs against benefits

Optimal foraging theory seeks to identify the behaviour of foragers that will maximise fitness, or a likely proxy for fitness such as net rate of energy gain. This approach has been applied most often to questions of diet choice (Chapter 6), but some studies have looked at how foragers might trade-off the costs and benefits of different ways of acquiring food. For example, in lumpfish (*Cyclopterus lumpus*), the default foraging mode is sit-and-wait predation, in which the fish cling to the substratum and ambush prey, but they may also show active searching. Metabolic costs are 6–12% higher for active searching than for sit-and-wait foraging and at high prey densities net rates of energy gain are higher for fish using the sit and wait tactic. However, at low prey density active searching yields energy at a faster rate, even though active searching requires a greater expenditure of energy (Figure 5.6a). If lumpfish choose the foraging tactics that maximise energy gain, they should switch from ambushing prey to active searching as prey densities fall below a certain threshold. A 10-fold increase in prey density does indeed cause a switch to active searching. A further trade-off arises from the fact

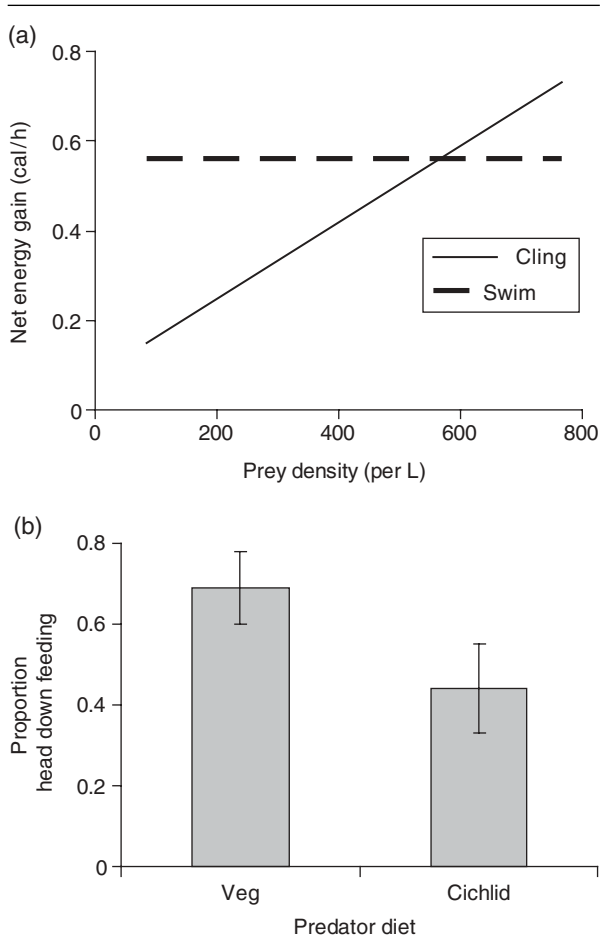


**Figure 5.6.** Trading costs against benefits of foraging mode. (a) Potential net energy gain in relation to prey density in small juvenile lumpfish foraging either by clinging to the substratum (solid line) or by swimming (dashed line). Adapted from Killen *et al*. 2007. (b) Mean (±SE) proportion of head down foraging attempts (directed to a horizontal food patch) by juvenile cichlids exposed to water containing larger cichlids previously fed either a vegetable diet (Veg) or a diet of juvenile cichlids (Cichlid). Adapted from Foam *et al*. 2005.

that juvenile lumpfish are more vulnerable to predation when actively searching for prey than when waiting in ambush and they spend more time clinging to the substrate in the presence of a predator (Killen *et al*. 2007). Likewise, juvenile convict cichlids (*Archocentrus nigrofasciatus*) exposed to the odour of a larger conspecific that have been feeding on small fish as opposed to a vegetable diet (and hence represent a greater threat) switch from feeding on

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food on the substrate to feeding on food presented on a vertical surface (Figure 5.6b). The head down position that the fish use when foraging on the substratum is more energetically efficient, but the head up foraging posture allows the fish to feed while maintaining vigilance (Foam *et al*. 2005).

### 5.5.4 Summary of functional aspects of foraging strategy

Different food types and foraging strategies vary in the benefits they generate, in terms of the quality and quantity of food acquired by the fish adopting them. Nutritional benefits are highest for animal diets, particularly so in the case of piscivory. Methods used for prey acquisition differ in probability of success and just how effective each is depends on the morphological adaptations of the fish concerned and the circumstances in which they are feeding. Different broad food types also impose different costs (anti-nutrients in plants and injury by animal prey, for example), as do different foraging strategies (in terms of time, energy and risk of predation, for example). How the costs and benefits of different foraging strategies are balanced is relatively little studied compared to the extensive research on diet choice (Chapter 6), but it is clear that fish can and do adjust their methods of food collection in response to changes in the costs and benefits of the options open to them. Cultured fish have the same capacity to make adaptive adjustments in foraging methods as do wild fish and this can be both problematic and beneficial for aquaculture.

## 5.6 IMPLICATIONS FOR AQUACULTURE

Cultured fish must be given food that meets their nutritional needs, in a form that they can detect and that they can and will ingest. Proper feeding and feed management are therefore essential to ensure good growth and successful breeding of the captive fish. The importance of the natural feeding behaviour of fish is perhaps most evident in the context of the dietary choices that cultured fish are given and how much feed is delivered and at what times, the subjects of Chapters 6 and 7. However the types of food that fish eat in nature and how these are gathered are also important. Although fish are flexible in what and how they eat, this only applies up to a point and problems can arise in culture if the natural feeding habits and foraging behaviours of the fish are ignored. Where fish are being reared for supplementation programmes or for reintroduction, one requirement during rearing is that they be fed in a manner that does not compromise their ability to forage effectively after they have been released. The conditions in which cultured fish develop may not equip them for foraging in the wild, at least for a short time immediately after release. In the following sections, some of the problems that can arise in culture from the natural foraging behaviour of fish are considered, including those relating to domestication and the influences of captive rearing on foraging. In addition, the ways in which an understanding of feeding biology can help in solving such problems are discussed. To interpret this information, it is necessary to know how cultured fish are fed in production systems, what food they are given, how this is packaged and delivered and how much food is provided at different times.

### 5.6.1 How cultured fish are fed

Table 5.2 summarises several aspects of feeding and feed management for the 10 spotlight species of cultured fish. Many high value food fish are carnivorous, often piscivorous; examples include salmonids, bass, bream, tuna and cod. The feeding habits of such species represents a challenge when in comes to providing appropriate food. However, other important cultured species such as tilapias and cyprinids (including the common carp, *Cyprinus carpio*) are omnivorous or herbivorous, making provision of appropriate food easier. Most ornamental fish are small, as are those commonly cultured for use in scientific research, such as zebrafish, medaka (*Oryzias latipes)* and goldfish (*Carassius auratus*). This means that they generally eat small food items, such as zooplankton or small benthic invertebrates. Feeding habits of fish cultured for conservation purposes cover the complete range of diets.

After the larval period, intensively farmed fish are usually given formulated feeds in the form of crumbs, flakes or pellets. These feeds differ in texture, appearance and often in taste and smell from the natural prey of the species concerned. When formulated feeds are not available, cultured fish may be provided with either frozen natural prey, with prey substitutes given either whole or chopped or with cultured live prey. Cleaner wrasse represent an exception in that they experience a range of natural food types when held in production systems. Thus wrasse held in net cages along with their clients feed on mucus, scales and ectoparasites from the client fish and on encrusting organisms that they remove from the walls of the net cages. Species that are cultured extensively, for example pond-reared carps and tilapias, usuallly feed on natural prey organisms present in the pond, but are often also given nutritionally-incomplete feeds as supplements. Feeding conditions for pond reared cyprinids and tilapias are sometimes enhanced by adding inorganic and organic fertilizers (human and livestock faeces or composted agricultural

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**Table 5.2.** Natural foraging mode and usual kind of food provided for cultured fish in the 10 spotlight fish species.

| | Natural foraging mode | | Usual feeding in culture | |
|---|---|---|---|---|
| | Type of food eaten | Food harvesting methods | Type of food provided | Method of delivery |
| Atlantic salmon | Carnivorous. Initially feed on zooplankton, expanding diet with size to include larger aquatic drift & some benthic prey. Sea run fish feed on pelagic crustaceans & small fish. | Juvenile sit and wait predators. Adults cruising predators. | Formulated feed in crumbs or pellet form. | At surface, pellets dispersed by hand or by automatic feeders. |
| Rainbow trout | Carnivorous. Initially feed on small zooplankton, later expanding diet to include small aquatic insects, then terrestrial insects & small fish. | Juvenile sit and wait predators. Adults cruising predators. | Formulated feed in crumbs or pellet form. | At surface, pellets dispersed by hand or by automatic feeders. |
| European seabass | Carnivorous. Fish take small crustaceans when young. Later take larger crustaceans, polychaetes, cephalopods & small fish. | Mainly active hunters. | Young fish fed on live food. Weaned onto formulated feed in crumb or pellet form. | At surface, pellets dispersed by hand or by automatic feeders. |
| Nile tilapia | Opportunistic omnivorous. Juveniles mainly carnivorous, feeding on zooplankton. Diet expanded later to include detritus & aquatic plants, plankton, small aquatic invertebrates & fish larvae. | Larger items taken individually by suction or ram feeding. Smaller organisms & detritus collected by suction feeding & filtering. | In extensive systems rely on natural algal growth enhanced by fertilisation of ponds. May receive supplementary grain etc. In intensive systems, fed floating formulated feeds. | Supplementary feed dumped on pond bottom. Pellets delivered at surface, by hand or by automatic feeders. |
| Pacific salmon | Carnivorous. Juveniles take small zooplankton & then insects, insect larvae & small fish. Larger salmon eat krill, squid & fish. | Juvenile sit and wait predators. Adults cruising predators. | Juveniles may be fed moist feed. Mainly fed formulated feed in crumb or pellets form. | At surface, pellets dispersed by hand or by automatic feeders. |
| Seahorses | Carnivorous. Feed on zooplankton, including small crustaceans & fish larvae. | Prey ambushed and captured by suction through elongated snout. | Juveniles reared on live feed (eg rotifers & brine shrimp). Older fish fed live food & frozen crustaceans. | Offered in suspension, hand delivered. |

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**Table 5.2.** *continued*

| | Natural foraging mode | | Usual feeding in culture | |
|---|---|---|---|---|
| | Type of food eaten | Food harvesting methods | Type of food provided | Method of delivery |
| Koi carp | Omnivorous. Young fish feed on zooplankton. Older fish eat a variety of live foods & detritus. | Bottom feeders. Suction feeding followed by filtering. | May take natural food, but usually fed formulated flake & pellets, supplemented with mixed animal & vegetable food.. | Usually delivered by hand at water surface. |
| Zebrafish | Carnivorous/omnivorous. Eat zooplankton, small insects (aquatic & terrestrial) & some plant material. Adults sometimes cannibalistic. | Larger items taken individually. Smaller items & detritus collected by suction feeding & filtering. | Fry fed small live prey e.g. ciliates. Adults fed flakes, frozen *Chironomid* larvae & live prey e.g. *Artemia* | By hand or automatically, at water surface. |
| Guppy | Omnivorous. Eat freshwater algae, insect larvae, small crustaceans, fish eggs & fish larvae. Adults sometimes cannibalistic. | Food taken from surface, water column & substratum, individually or by suction feeding & filtering. | Fry fed small live prey e.g. *Daphnia, Artemia*. Adults fed flakes, supplemented by e.g. frozen *Tubifex, Chironomid* larvae. | By hand or automatically, at water surface. |
| Clown-fish | Omnivorous. Eat algae, small molluscs & crustaceans. May take prey captured by anemone. | Active predators, engulfing prey by ram feeding. | Larvae given live feed in suspension e.g. rotifers. Older fish fed flakes, small pellets, & live or frozen zooplankton | By hand at the water surface. |

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by-products) to the water to promote productivity (Edwards *et al*. 1983; Le François *et al*. 2010). The food given to cultured fish is usually delivered from above and falls gradually through the water column to the bottom of the tank or pen. Movement of the food as it falls though the water column is imparted to it by the water currents.

### 5.6.2 Problems during production arising from natural foraging patterns

The expression of natural feeding behaviour under culture conditions can cause problems, both for the farmer and for the fish. All cultured fish must be reared to a size that is appropriate to the use to which they are to be put and some potential problems arising from the expression of natural feeding behaviours can be considered common across fish culture. Table 5.3 summarises such problems as they impact on production, welfare and environmental impact. In addition, some problems, including those arising from the effects of domestication and captive rearing on foraging, are mainly relevant for fish reared for release into the wild.

#### *Problems arising from the types of food that fish eat*

Whether a particular species of fish is carnivorous, herbivorous or omnivorous helps to determine its suitability as a species for aquaculture and the ease with which it can be farmed (Le François *et al*. 2010). For example, many carnivores, and especially piscivores, tend to grow large, have a high flesh yield and provide fillets of good nutritional quality, so they are preferred as food fish and are favoured species for aquaculture. However, provision of food with the appropriate nutritional content for carnivorous fish is one of the major challenges to sustainable aquaculture (Halver & Hardy 2002; Webster & Lim 2002; Jobling 2004, 2010). Smaller conspecifics represent high quality prey for piscivorous species, at least in terms of provision of the nutrients needed for growth; cannibalism is therefore a natural feeding strategy in some fish that are cultured. For example, cannibalism is common among red drum (*Sciaenops ocellatus*) larvae when held in captivity, with the larger larvae in a cohort often consuming all small larvae, but cannibalism becomes less common when all fish are greater than 1.8 cm in length (Liao & Chang 2002). Cannibalism is not always dependent on size differences; for example in larval perch, *Perca fluviatilis*, size heterogeneity does not increase the incidence of cannibalism (Mandiki *et al*. 2007). Whatever its developmental progression, the occurrence of cannibalism in fish culture can be a serious problem; since it can be the cause of much mortality and injury, it can have strong influences upon both production and welfare (Baras & Jobling 2002).

As well as posing problems, the natural foraging behaviour of fish can also be exploited in fish culture. For example, the ability of fish to learn using sensory inputs from contact with food (Suboski & Templeton 1989) can be exploited when training fish to operate self-feeding devices (Boujard & Leatherland 1992; Alanärä 1996). The natural feeding habits of fish can also be used to prevent fouling; goldsinny wrasse (*Ctenolabrus rupestris*) are effective at removing small blue mussels (*Mytilus edulis*) and other fouling organisms from the nets of salmon cages (Kvenseth 1996). Finally, killifish (*Fundulus heteroclitus*) can be used to control sea squirts (tunicates or ascidians) in clam (bivalve mollusc) trays (Costello 1996).

#### *Problems arising from the mechanisms used to detect food*

The sensory cues used to locate food are extremely important in determining whether cultured fish feed well. For many new and potential culture species, not enough is known about the cues that trigger and direct feeding to enable effective feeding programmes to be developed. This is especially the case at the transition from endogenous feeding on the yolk sac to exogeneous feeding, when mortality rates can be extemely high. In addition, it is increasingly recognised that fish in culture can be exposed to high levels of background noise (Wysocki *et al*. 2006) and it is possible that this may interfere with feeding, as might the quality of the water in the rearing units (Houlihan *et al*. 2001; Jobling 2004, 2010).

As described above, chemoreception plays an important role in the food searching behaviour of many fish species (Lamb 2001; Rust 2002; Kasumyan & Døving 2003) and a nutritionally balanced feed may not support good rates of growth if it is deficient in chemicals that induce food searching and capture. For many fish, visual cues are important for locating and identifying food. Poor visibility, in terms of food appearance and of the context in which it is viewed, compromises the ability of cultured fish to feed. Problems with prey detection can arise even when prey is present at relatively high densities. For example, larval Atlantic cod survive poorly when held at low light intensities even with abundant food, because they are unable to capture prey efficiently (Puvanendran & Brown 2002). Spectral quality is also important for fish that detect food visually and feeding success may be reduced under artificial lighting conditions that fail to match natural illumination. Atlantic cod, for example, grow less well under artificial than natural light (van der Meeren & Jørstadt 2001). Guppies forage on semi-transparent zooplankton less effectively when long wavelengths are filtered out of

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**Table 5.3.** Aspects of the natural foraging behaviour of cultured fish and some potential problems caused by these.

| Issue | Implications for production | Implications for welfare | Implications for the environment |
|---|---|---|---|
| Difficulties in supplying nutritionally appropriate feed, especially for piscivores | Poor nutrition can lead to lost production through reduced growth, ill health and increased mortality. | Inadequate or inappropriate nutrition can compromise the welfare of individual fish, both directly and indirectly, through consequent ill health. | More wasted food and less efficient food processing means more waste released into the environment.<br>More disease in farmed fish may mean more disease transfer to wild fish. |
| Failure to provide feed in a manner that stimulates natural feeding behaviour. Lack of natural cues for feeding | Poor intake of nutritionally adequate feed leads to lost production through reduced growth, ill health and increased mortality. | Failure to eat the right kind of food can compromise the welfare of individual fish, both directly and indirectly, through consequent ill health. | More disease in farmed fish may mean more disease transfer to wild fish. |
| Natural feeding responses in inappropriate conditions | Failure to capture food leads to lost production through reduced growth, ill health and increased mortality.<br>Injury during feeding attempts causes lost production. | Failure to eat sufficient food and injury during feeding can compromise the welfare of individual fish. | More disease in farmed fish may mean more disease transfer to wild fish.<br>Injury and disease may mean more wasted feed. |
| Cannibalism | Lost production arises through mortality, injury and stress and related diseases. | Stress, injury and mortality from cannibalistic attacks may compromise the welfare of the attacked fish. | More disease in farmed fish may mean more disease transfer to wild fish. High stress levels may mean more wasted feed. |

the light source, partly because contrast between prey and background is reduced, but pssibly also because motion detection is impaired (White *et al*. 2005). Larvae and small juveniles of many fish species feed on zooplankton and often localise their prey with the help of UV-sensitive visual pigments. If the artificial lighting within a fish hatchery is deficient in the UV part of the spectrum this could compromise the ability of start-feeding larvae and juvenile fish to detect the live prey organisms (zooplankton, rotifers, *Artemia*) that are used during the early phases of rearing.

Water turbidity may influence the ability of cultured fish to detect food items in the water column and is likely to be particularly relevant in relation to the feeding of larval fish on live prey, such as zooplankton. Turbidity sometimes compromises the ability of fish to detect and capture prey, but in other circumstances, the opposite is the case, with increased water turbidity promoting feeding and enhancing growth (Kestemont & Baras 2001; Shaw *et al*. 2006). This may result from a combination of factors, including reduced reflection of light from the walls of the rearing tanks, improved contrast leading to better visibility of food particles and changes in the spatial distributions of the fish within the tanks (Bristow *et al*. 1996; Shaw *et al*. 2006).

### *Problems arising from the mechanisms used to gather food*

The ways in which fish capture food once it has been detected also have potential implications for how easily a species can be farmed. The morphological and behavioural adaptations of fish to their natural diet mean that, for example, fish that take food from the substratum tend to be inefficient at feeding on prey in the water column, and the converse. The natural feeding behaviours displayed will determine how well fish are able to feed on pellets floating on the water surface, falling through the water column or

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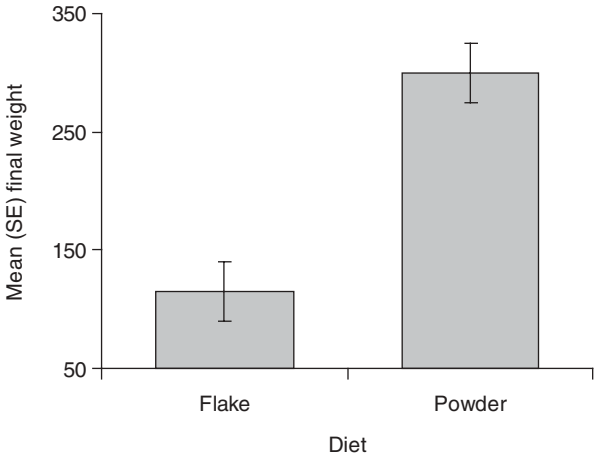


**Figure 5.7.** Allowing for foraging mode in fish culture. Mean (±SE) final weight (mg) in guppies fed either powdered or flaked food. Adapted with permission from Harpaz *et al.* 2005.

that have settled on the bottom. Farmed cod are sometimes unable to empty their swim baldder sufficiently fast when moving up through the water column to intercept feed delivered at the water surface, making it difficult for them to make accurate strikes at the food (Victoria Braithwaite, personal communication). In addition, fish for which the natural mode of prey capture is to chase and dart could acquire foraging-induced injury when confined in tanks.

Problems can also arise from the way in which cultured fish process their food. For example, gilthead seabream (*Sparus aurata*) feed naturally on hard bodied prey such as molluscs and crustaceans and have the powerful jaws and molariform teeth needed to crush such prey. While chewing dry feed pellets, they often spit out particles of food which may be washed away before they can be eaten, resulting in increased feed waste and poor feed conversion efficiency (Andrew *et al*. 2003, 2004). Guppy larvae grow faster when fed on powdered diets than when given the same formulations as flakes (Figure 5.7) and they also survive somewhat better. Powdered feed spreads over the water surface and then sinks slowly through the water column, whereas flakes remain intact and float on the surface for much longer. Guppies eat powdered food quicker than flake food, before there has been excessive leaching of nutrients into the water. In addition, a greater variablity in size in guppies fed flake food (approximately 40% as opposed to approximately 20%) may arise because dominant fish are able to defend flakes that are floating at the water surface (Harpaz *et al*. 2005. Chapter 9).

### 5.6.3 Effects of domestication and captive rearing

The effects of domestication of fish on their foraging strategy have been little studied, although laboratory-reared offspring of feral carp are more likely to eat free swimming prey, including other fish, than are the offspring of domesticated fish. This may be because they have more streamlined bodies and smaller heads and so are better at capturing such active prey (Matsuzaki *et al*. 2009). Differences between wild fish and fish reared in captivity until released have been described for a number of species. For example, cultured juvenile Atlantic salmon tend to feed lower in the water column and at lower current speeds than do wild fish (Orlov *et al*. 2006). During the first few days after being released, cultured 0+ cod feed mainly on non-evasive, invertebrate prey, whereas wild cod feed on mobile prey, including other fish (Nordeide & Salvanes 1991). When held in tanks, both cultured and wild caught cod chase small gobies when the gobies are active, but ignore them when static. Cultured cod tend to use a pursuit strategy, chasing the gobies to exhaustion, whereas wild cod used a lunge technique. Both techniques are effective and in both wild and reared cod foraging efficiency improves with experience, but the lunge strategy remains more energetically efficient (Steingrund & Fernö 1997). In Florida largemouth bass (*Micropterus salmoides floridanus*) cultured for stock enhancement survival after release is very poor (less than 1%) and this may be due to difficulties faced by the released fish in foraging on natural prey. When encountering live prey for the first time, bass reared in hatcheries on pelleted food use ram feeding as wild bass do, but are less adept at capturing live mosquitofish (which are agile and hard to catch), striking less and using less effective suction than do wild fish (Figure 5.8). Consequently, their capture success is lower, although after a few encounters with mosquitofish, the foraging technique of reared bass improves until it is similar to that of wild fish (Wintzer & Motta 2005).

A number of studies have compared trophic morphology and foraging strategies in fish of the same strain reared either in culture or in the wild. Any differences observed could be the result of captive rearing, though differential mortality by foraging phenotype could also influence the results of such studies (Cowx *et al*. 1998). Juvenile Masu salmon raised in hatcheries and fed exclusively on artificial feeds differ from wild caught fish in the structure of the skull and jaw. Cultured fish have a smaller buccal cavity and less well developed processes for the attachment of jaw muscles, perhaps reflecting the fact that natural prey is larger, more difficult to capture and requires a stronger bite than does artificial feed (Romanov 1984).

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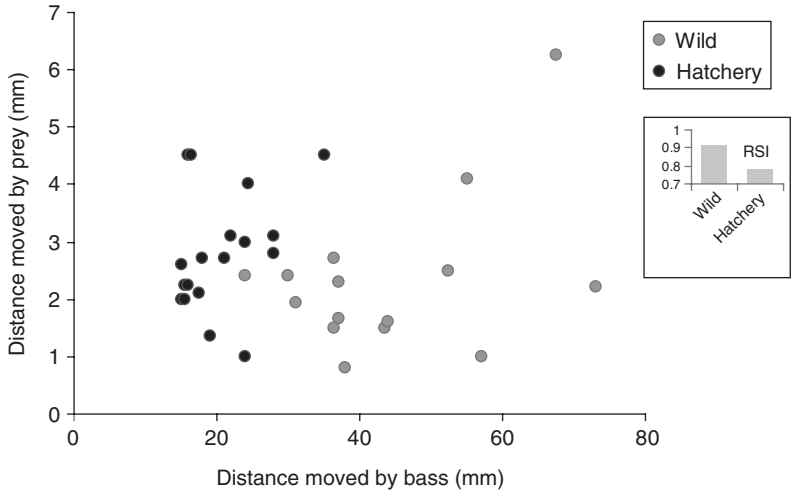


**Figure 5.8.** Differences between wild and captive reared fish. Distance moved during prey capture by wild (grey dots) and hatchery-reared (black dots) largemouth bass in relation to the distance moved by they prey (mosquitofish). Inset: Ram suction index (RSI) in wild and hatchery-reared fish. RSI = (distance moved by predator-distance moved by prey)/(distance moved by predator + distance moved by prey). Adapted with permission from Wintzer & Motta 2005.

When released into a stream as juveniles, the offspring of wild Honmasu salmon (*Oncorhynchus rhodurus* × *O. masou*) reared under hachery conditions on pelleted food start to eat natural prey within a day. Although their stomachs are initially less full than those of wild fish, stomach fullness gradually increases with time spent in the stream. These results suggest that Honmasu salmon that are reared in captivity have an inbuilt response to natural prey, that lack of experience makes them less effective than wild fish at capturing such prey, but that practice improves foraging efficiency (Munakata *et al*. 2000). Similar conclusions can be drawn from studies on the development of feeding in Atlantic salmon reared on dry pellets or on live natural prey (*Artemia* and *Daphnia*) of the same size. The development of capture movements is similar in the two groups of fish, but is slightly delayed in those reared on pellets. For example, on day 8 after the start of feeding pellet-fed fish tend to compress their mouth cavities later relative to mouth opening, which makes for less efficient suction; by day 12 they have shorter and more variable capture distances. The fish reared on pellets behave like younger wild fish, so feeding on artificial food causes a slight lag in the normal development of effective feeding (Coughlin 1991). Wild brown trout are quicker to attack a novel prey type (crickets) than are hatchery reared fish originating from the same river. Hatchery fish eat less, are slower to attack and are less efficient at eating crickets than wild trout, though both groups become more efficient with experience (Sundström & Johnnsson 2001).

An impaired ability of cultured fish to capture and process natural food, even if of short duration, could potentially reduce their chances of survival during the critical period just after release. This would compromise the aims for which such fish are being cultured, namely to supplement threatened populations or to reinstate extinct ones. It also raises welfare issues if large numbers of such fish fail to obtain sufficient food.

### 5.6.4 Solving problems arising from the natural feeding biology of cultured fish

The previous sections have shown that a number of problems can arise in fish culture as a result of the natural foraging patterns of the fish concerned. The general problem of meeting the nutritional requirements of fish that their natural diet dictates could be solved by judicious choice of species for culture (Le François *et al*. 2010). Providing an adequate, sustainable diet to omnivorous, herbivorous or detritivorous fish is much less challenging than providing such a diet to piscivores (Chapter 6). In species with trophic polymorphisms, it may be that one form is easier to culture than others; benthivores may be easier to farm than piscivores, for example. Where variable

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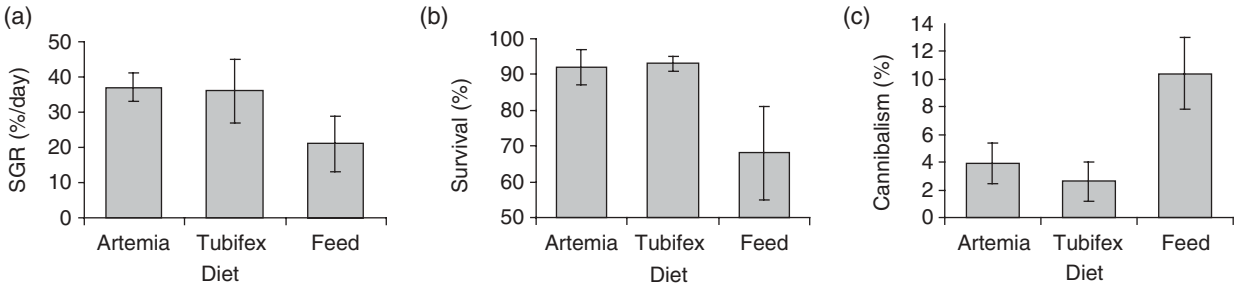


**Figure 5.9.** Importance of live feed. Mean (±SD) (a) specific growth rate (SGR%/day), (b) percentage survival and (c) percentage of mortalities due to cannibalism in larval Asian catfish fed to day 11 either on *Artemia* nauplii, or on chopped *Tubifex* worms or on trout starter feed. Plotted from data in Hung *et al*. 2005.

foraging modes are the result of experience, this could be managed by simply allowing (young) fish to adjust behaviourally and morphologically to the diet that is most convenient for the farmer. Where there is a genetic component to differences in feeding response, this would need to be taken into account in choice of broodstock.

Problems arising from lack of knowledge about feeding habits can only be solved by gathering more information. Problems arising from poor detection and uptake of food or from inefficient feeding by cultured fish can be solved by applying what is known about the mechanisms that fish use naturally in this context. Although what fish eat and how they capture food is broadly dictated by their phylogenetic history, fish may display a considerable degree of flexiblity, both during development and over shorter time scales. This offers scope for solving problems caused by domestication and captive rearing, especially in relation to improving the ability of released fish to forage effectively on natural prey.

### *Finding out about foraging in candidate culture species*

The transition from endogenous to exogenous feeding is a major bottleneck in fish culture and mass mortalities often occur at this point. There is therefore considerable value in collecting detailed behavioural and morphological information about fish larvae when looking at species that are candidates for culture, whether this be for food, for supplementation programmes, for the ornamental trade or for conservation (Le François *et al*. 2010). A complicating factor is that it is necessary not just to find sources of food on which young fish can survive and grow well, but also that these sources can be obtained in sufficient quantities for mass rearing to be feasible.

The Asian catfish (*Pangasius bocourti*) is cultured in south-east Asia, particularly in the Mekong delta. Culture of this species has experienced rapid growth and most of the farmed fish are sold for export. Culture is still often based on the capture of wild juveniles, but research is underway to develop effective methods for culture of larvae. Larvae fed on *Artemia* nauplii or on chopped tubifex worms for the first few days after hatching survive and grow well. Growth is slower and mortality higher in larvae fed on artificial starter feeds, partly because of high rates of cannibalism (Figure 5.9). Feed-fed larvae also grow poorly. Both survival and growth increase with the number of days larvae are fed *Artemia* nauplii before being weaned onto artificial feed. This study demonstrates the feasibility of using tubifex worms as a starter diet and suggests that 3 days of live feeding may be appropriate before weaning the fish onto artificial feed; this is somewhat earlier than for other species of catfish, in which the stomach develops later (Hung *et al*. 2002).

Seahorses are used in the aquarium trade and also for medicinal purposes; many seahorse species are endangered and much research is being directed at finding ways of mass rearing these fish in culture. Juvenile (1–2 months) pot bellied seahorses (*H. abdominalis*) are able to feed on non-living food (frozen or dried), but grow better on live prey (*Artemia* nauplii). Non-living prey such as frozen copepods remain in the water column for several hours under suitable water current conditions, so the fish have ample opportunity to eat them. The fish detect, approach and inspect such non-living prey just as they do live prey, but once inspected, non-living prey are usually rejected; this is in contrast to the high rate of attacks made on live *Artemia* nauplii. It may be that the dead copepods do not present the appropriate visual cues because they do not move in the same way as live prey. Juvenile seahorses can be weaned onto non-living food by a period of mixed feeding with live *Artemia* nauplii and frozen copepods, during which rates of striking at the non-living prey increase (Woods 2003).

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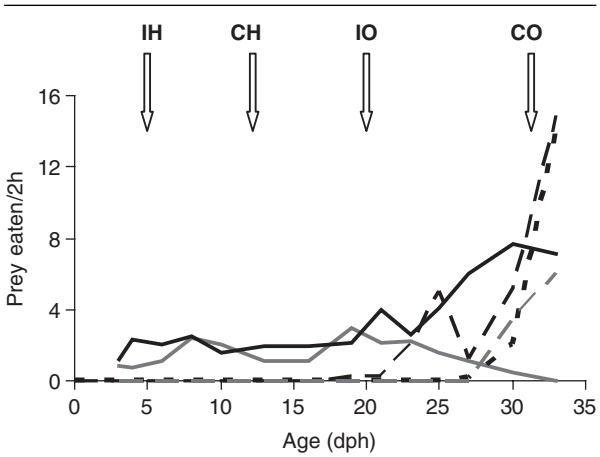


**Figure 5.10.** Changes in food type eaten in relation to morphological development. Number of prey of different kinds consumed by larval common snoop on successive days post hatching (dph) in relation to stage of development of the ingestive apparatus. Solid grey line = rotifers. Solid black line = small (35–90 μm) zooplankton. Long dashed black line = large (91–270 μm) zooplankton. Dashed grey line = large (48 h) *Artemia*. Short dashed black line = small (12 h) *Artemia*. IH = initial hyoid. CH = complete hyoid. IO = initial opercular. CO = complete opercular. Adapted with permission from Wittenrich *et al*. 2009.

The common snook is a tropical and sub-tropical esturine fish that supports major recreational fisheries; it is cultured for supplementation and as a food fish. Both larvae and adults use suction feeding to capture prey. Analysis of head development identified four ontogenetic stages (Figure 5.10). In the 'initial hyoid' stage, the feeding apparatus comprises cartilaginous elements of the lower jaw and hyoid apparatus. In the 'complete hyoid' stage (about 5 dph) the hyoid apparatus has expanded, the musculoskeletal links between the jaw and the cranium are well developed and the upper jaw is beginning to differentiate. By 20 dph, the larvae reach the 'initial opercular stage', in which ossification of the operculum has started, the suspension of the jaw from the skull is reinforced and all the bones involved in jaw suspension are ossified and capable of independent movement. Finally the 'complete opercular stage' (31 dph) is characterised by complete separation and almost complete ossification of all the skeletal elements of the jaw and the structures that suspend it, together with musculoskelatal links between the head and jaw; this allows cranial rotation, protrusion of the premaxilla and lateral expansion of the buccal cavity. Over this period, the number of teeth present in the jaw and pharynx increases, as does gape size. Over the same period, larval snook offered mixtures of zooplankton of different sizes take successively larger prey, though not the largest that they could potentially handle on the basis of jaw gape (Figure 5.10). The prey eaten are related to stage of head development, with larvae in the initial hyoid stage taking mostly small, non-elusive zooplankton and those in the complete hyoid stage taking mostly rotifers and larger zooplankton. Consumption of larger more elusive prey, including *Artemia*, increases as larvae approach the complete opercular stage. This analysis of how functional development of the feeding apparatus coincides with development of the ability to feed on prey that differ in size and agility suggests that stage-specific feed management systems could be developed to prevent the high mortality seen at first feeding in many species of cultured fish (Wittenrich *et al*. 2009)

### *Solving problems by knowing about the cues fish use to locate and capture food*

Understanding the relationship between feeding responses and the properties of potential food can contribute to the development of effective culture systems, particularly during larval rearing. The efficiency with which cultured fish feed can be increased by making sure that the food offered presents the cues that enable fish to detect and capture it. Chemical cues are known to be very important when fish detect food; ingestion of artifical diets by larval gilthead seabream increases markedly when the young fish are exposed to visual and chemical cues from *Artemia* (Koven *et al*. 2001; Chapter 6).

In terms of visual cues, larval seahorses survive and grow better when fed live food, partly because movement is an important cue in prey detection (Woods 2002) and visual cues provided by *Artemia* augment chemical cues in promoting the uptake of artificial feeds in larval sea bream (Koven *et al*. 2001). The same is true for the larvae of many species of fish; for example, the preference for live over dried tubifex shown by larval Asian catfish is probably due to movement of the live prey (Hung *et al*. 2002). The importance of visual cues in prey detection means that the lighting conditions to which fish are exposed are critical for good feeding. Larvae of the longsnout seahorse *Hippocampus reidi* survive and grow well when fed in a sequence that progresses from rotifers to *Artemia*, in combination with copepod nauplii. Both survival and growth are best in fish held on a 24 h light regime, which allows the fish maximum time for feeding (Olivotto *et al*. 2008).

Seahorses survive and grow well when held at light intensites of about 2000 lux, possibly because this

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stimulates activity and searching for food (Murugan *et al*. 2009), though the optimal intensity may change with age (Sheng *et al*. 2006). Larval Atlantic cod survive better when held at high light intensities, because they are able to capture prey more efficiently (Puvanendran & Brown 2002). One reason why high light intensities promote effective feeding is that the contrast between the prey and the background may be enhanced, which is important in food detection for many species of fish. Anything that enhances contrast will promote effective feeding; surprisingly perhaps, turbidity may promote prey detection by reducing reflection of light from the walls of the rearing tanks, improving contrast, increasing visibility of food particles and changing the spatial distributions of fish within the tanks (Bristow *et al*. 1996; Shaw *et al*. 2006).

Green-water techniques, whereby the water in which larvae are held is innoculated with phytoplankton, are beneficial in the larval culture of many species of marine fish. One possible reason for this may be that a background is created against which prey can be viewed, enhancing contrast (Muller-Feuga 2000). For example, survival is better and the incidence of feeding higher in rotifer-fed Atlantic cod larvae held in green as opposed to clear water at both high and low irradiance (van der Meeren *et al*. 2007). The spectral quality of light is relevant, as well as its intensity. Since many fish use UV light to detect zooplankton, ensuring that light sources are not deficient in the UV wavelengths will improve the ability of start-feeding larvae and juvenile fish to detect the live prey organisms (zooplankton, rotifers, *Artemia*) that are used during the early phases of rearing.

#### *Solving problems by knowing about how fish capture food*

Just as some problems arise from the natural foraging mechanisms of cultured fish, so knowing about this behaviour can help to solve these and other problems. For example, gilthead seabream fed soft-textured feed show less chewing and manipulation of feed than when fed harder, dry pellets and this increases consumption and reduces waste (Andrew *et al*. 2004). Further, knowing about the relationships between gape size of a would-be cannibal and the size of potential prey might open ways of reducing the development of cannibalism within captive populations of fish. Size grading is one common strategy used by farmers to reduce the incidence of cannibalism. For example, cannibalism is reduced and survival enhanced following size grading in yellowtail kingfish (*Seriola lalandi*; Moran 2007), but size-grading may be very labour intensive and may not always be particularly effective (Baras & Jobling 2002; Chapter 6). The known plasticity of jaw structure and function in small fish could potentially be used to reduce cannibalism; the predatory fish could be given prey of suitable size at the different stages of their development, thereby reducing the risk that they would attack conspecifics (Baras & Jobling 2002). When fish have the capacity to prey on smaller conspecifics, the likelihood of this happening might be reduced by manipulating the costs and benefits of this form of foraging. For example, in the culture of black sea bream *Sparus macrocephalus*, increasing the turbidity of the water through addition of the algae *Chlorella* reduces cannibalism, possibly by increasing the ease with which alternative prey can be captured (Chenshu *et al*. 1992).

### 5.6.5 Mitigating the effects of domestication and captive rearing

Effects of captive rearing on foraging behaviour have been reported for many cultured carnivorous species and a number of studies have shown how prey handling efficiency can be improved by a relatively short period of experience with natural prey. For example, Atlantic salmon given prior exposure to live prey show enhanced foraging performance, but only if the exposure takes place in a structurally complex environment (Figure 5.11; Brown *et al*. 2003). Such studies suggest that negative effects of captive rearing on foraging skills might be substantially reduced by relatively short exposure to more complex foraging conditions prior to release of fish intended for stock enhancement.

## 5.7 SYNOPSIS

Fish eat a wide range of foods and the cues used to detect food are also varied, although a prominant role for chemical and visual cues is common. Likewise, fish use a wide range of strategies to gain access to and capture prey, although once in contact with food most fish ingest it using some sort of suction or ram feeding. It is not uncommon to find subsets of fish populations that specialise, morphologically and behaviourally, on different types of food. What fish eat and how they harvest it is strongly reflected in their trophic apparatus, including jaws, teeth, gill rakers, stomach and intestine. The fish that are cultured for various purposes reflect most of this diversity in diet and foraging strategy. Changes in what fish eat and how they eat it take place during development in almost all species and these are especially dramatic in those that undergo changes in habitat during development. The period at which larvae shift from endogenous to exogenous feeding is a critical one for wild fish and represents a major bottleneck for the development of effective culture methods for many species. The diet and foraging methods

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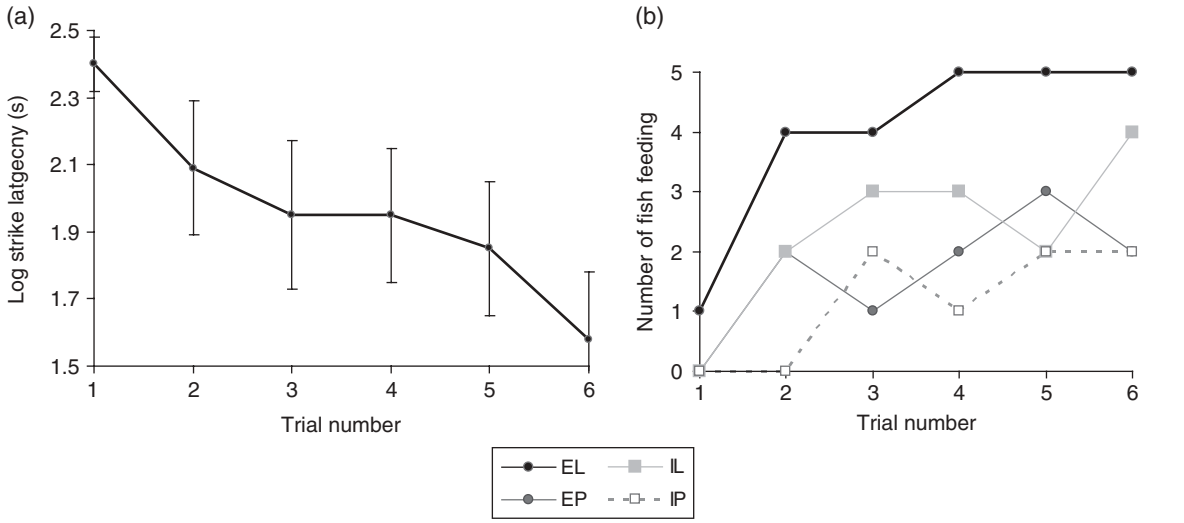


**Figure 5.11.** Effect of experience of live prey on foraging skills. (a) Mean (±SE) log strike latency of all fish and (b) the number of fish feeding in each of four experimental groups over successive exposures to a novel live prey (brine shrimp) in juvenile Atlantic salmon reared in simple and enhanced hatchery tanks, with and without prior experience of live prey (tubifex worms). EL = enriched environment and live food. EP = enriched environment and pellets. IL = impoverished environment and live food. IP = impoverished environment and pellets. Adapted with permission from Brown *et al.* 2003.

of fish are relatively hard wired, in the sense that fish reared without experience of their natural food will often try to feed on such food if they encounter it. Initial feeding attempts may be relatively inefficient, but with experience fish quickly become more effective at handling novel prey. Foraging in a particular way brings costs and benefits and exactly how fish gather food in any particular set of circumstances has been moulded by natural selection, costs and benefits being balanced in such a way as to promote individual fitness.

There is still a great deal to be learned about, and hence a strong research focus on, effective feeds and optimal feeding conditions for many potential culture species. However, it is clear that fish farmers face problems arising from the natural feeding behaviours of their fish; for example, the feed used on fish farms may not present the correct stimuli for to be detected and attacked, environmental conditions may interfere with the detectability of food and fish expressing their natural feeding behaviour may damage each other or themselves. In addition, the unnatural foraging conditions experienced by fish in culture may influence the chances that they will feed effectively if released into the wild. However, the examples given in the final sections of this chapter make it clear that effective solutions to these problems can be developed based on knowledge about the natural foraging behaivour of the fish concerned.

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# 6
# Nutrition and Diet Choice

*David Raubenheimer, Steve Simpson, Javier Sánchez-Vázquez, Felicity Huntingford, Sunil Kadri and Malcolm Jobling*

**Abstract:** This chapter starts with an account of the nutrients that fish require, the dietary choices that they make and the mechanisms that generate selective feeding. The sensory systems involved in diet choice in fish are considered, with particular reference to chemical cues, post-ingestive signals and the ability of fish to select nutritionally adequate diets from a range of macronutrients. Changes in dietary preferences with age are described, as are the ways in which inherited differences and experience interact to determine what fish choose to eat. The impact of diet on fitness is addressed with reference to optimal diet theory (emphasising rapid energy acquisition) and nutritional ecology (highlighting the capacities of fish to balance their macronutrient intake). The dietary choices experienced by cultured fish are considered, as are problems for aquaculture arising from their natural preferences and from the effects of domestication and captive rearing on diet choice. Some possible solutions to such problems based on current knowledge of the behavioural biology of foraging in wild fish are outlined. Finally, an account is given of how nutritional ecology can be used to identify diets for cultured fish that optimise production, welfare and environmental protection.

**Keywords:** cannibalism; macronutrients; micronutrients; nutritional ecology; ontogenetic dietary shifts; optimal diet theory; post-ingestive signals; selective feeding; taste preferences.

## 6.1 INTRODUCTION TO WHAT FISH EAT

Within the general foraging habits described in Chapter 5, such as herbivory, planktivory or piscivory, fish encounter a much wider range of food items than they actually eat; in other words, they feed selectively. Selective feeding is the topic of the present chapter, which looks at the mechanisms that underpin diet choice in fishes, how diet choice develops as fish grow and mature and the ways in which natural selection has moulded the decisions fish make when faced with a choice of food items. These issues can only be properly interpreted in the light of the nutritional requirements of fish and this chapter therefore starts with a brief overview of the topic (for reviews see Halver & Hardy 2002; Webster & Lim 2002; Jobling 2004) and continues to explore the interface between nutrition and behaviour. It is obviously of critical importance that cultured fish are offered, and that they eat, food containing the nutrients required for growth and, where appropriate, reproduction. The implications of the biology of diet choice for fish culture are addressed explicitly in the final sections of this chapter.

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### 6.1.1 What fish need from the foods they eat

In common with all other animals, fish are heterotrophic, meaning that they are unable to synthesise organic compounds from inorganic substrates. They therefore require organic sources of carbon and nitrogen, among other substances, as starting materials for the biosynthesis of the molecules that make up their body tissues and provide the energy needed to sustain their bodily functions. The major nutrients (carbohydrates, proteins and lipids) can all be used as metabolic fuels, but these different types of organic compound are not equally well suited for tissue biosynthesis, cellular proliferation and growth. For example, an adequate supply of dietary protein is needed if fish are to thrive and grow well, whereas they have no such specific requirement for carbohydrate. Substances needed for maintenance, growth and reproduction are defined as nutrients and are classified as macronutrients (proteins, lipids and carbohydrates) or micronutrients (vitamins and minerals), depending upon the amounts required. Growth and other metabolic processes rely upon fish obtaining adequate supplies of certain essential nutrients that cannot be synthesised *de novo* and must be present in the diet. If the diet lacks, or has insufficient amounts of, one or more of the essential nutrients, the fish will display deficiency symptoms. Such symptoms may include reduced feed intake and growth, metabolic disturbances, abnormal development and body colour and the display of abnormal behaviour.

Proteins are the most abundant organic molecules within cells and the proportion of protein in the fish body is usually within the range 15–19% of the wet body mass. As a group, the proteins have great diversity in their biological function. Many proteins are enzymes, catalysing a wide range of chemical reactions. Some proteins have roles as structural elements; for example, collagen is a fibrous protein with structural functions in connective tissue and bone. Other proteins have an essential function in muscle contraction, and some serve to transport specific molecules either across cell membranes or in the bloodstream. For example, the haemoglobin in vertebrate red blood cells binds to and transports oxygen. Proteins all contain combinations of the same set of 20 amino acids, most of which have little or no intrinsic biological activity in their free form. Of the 20 amino acids found in proteins, 9 (in some species 10) are not synthesised by animals and so must be acquired via the diet. In addition to their roles as constituents of proteins, amino acids act as precursors for the synthesis of other biologically active compounds. For example, the amino acid tyrosine is the precursor for thyroid hormones and catecholamines, while tryptophan is the precursor for the hormone melatonin and the brain bioamine serotonin.

Along with proteins, lipids and their constituent fatty acids are major organic constituents of fish. The fatty acids in lipids can be oxidised to provide energy and also play important roles as precursors for the synthesis of many hormones and in the formation of cell membranes. Lipids and fatty acids can also be deposited in adipose tissue and used as a source of energy at a later date. Particularly important in the diets of fish are the *n*-3 and *n*-6 series of unsaturated fatty acids (named ‘omega 3’ and ‘omega 6’), which are synthesised by bacteria, algae and plants, but not by animals. Carbohydrates, the third main organic constituent of animals, are present in the body of fish in small quantities. This class of macronutrient includes sugars (for example, glucose) and their polymers (for example, glycogen). Fish can synthesise carbohydrates from amino acids and fatty acids, so they are not essential nutrients. Glycogen is the major energy source for fish white muscle, but little glycogen is stored in the muscle. Liver glycogen is mobilised as an energy source during starvation in fish.

Among micronutrients, vitamins are complex organic compounds that are required in small amounts and deficiency symptoms will occur if a single vitamin is omitted from the diet of a species that requires it. Several of the vitamins act as coenzymes, providing and transporting chemical groups during enzymatic reactions, but others do not have a single role and may play a part in several vital functions. The vitamins have been divided into two groups based upon their solubility characteristics, namely the water-soluble vitamins (vitamins B and C) and the fat-soluble vitamins (vitamins A, D, E and K). The solubility characteristics of the two groups of vitamins affect their distributions in the different chemical fractions of foods and feedstuffs and also influence the ways in which the different types of vitamins are absorbed from the gastrointestinal tract, are transported and are stored in the body tissues.

Minerals fulfil a variety of functions within an animal’s body. Some are incorporated into bone, others have a major function in acid–base balance and in the maintenance of cell homeostasis and yet others act as cofactors, non-protein chemicals that bind to enzymes and influence their structure and function. Major minerals that are required by fish in relatively large quantities include calcium, sodium, potassium, magnesium, phosphorus, chlorine and sulphur. Trace minerals that are required in lesser amounts include iron, iodine, manganese, copper, cobalt, zinc, selenium, molybdenum, chromium and fluorine. These minerals are dissolved in the water in which fish swim, so not all of the minerals required by fish need to be supplied via the diet, though the concentrations of dissolved minerals and their availability depends on environmental conditions.

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### 6.1.2 What fish choose to eat

In nature, the nutrients that fishes need (both macro- and micronutrients) come packaged within particular food items, most of which on their own do not provide a balanced diet, having a surfeit of some nutrients and a dearth of others. This means, for example, that to achieve a balanced diet, a fish that feeds on a food source rich in carbohydrate but poor in protein will also have to eat other food sources that are rich in protein relative to carbohydrate. In other words, since nutrient availability and requirements often do not coincide, most fish consume a variety of foods in order to get the nutrients they need. Wild fish select from among a wide variety of food items, so that their gut contents rarely resemble a random sample of all available foods (Kaiser & Hughes 1993). For example, juvenile flounder (*Platichthys flesus*) in nursery areas in the Duoro estuary feed preferentially on amphipods and bivalves, with polychaetes and prawns being underrepresented in their stomach contents (Figure 6.1). As fish grow, their diet gradually changes to favour larger prey, including polychaetes (Vinagre *et al*. 2008). Several *Tilapia* species undergo an ontogenetic dietary shift from visually guided selective capture of the protein-rich zooplankton needed to sustain early growth to consumption of less-nutritious phytoplankton or detritus (Beveridge & Baird 2000).

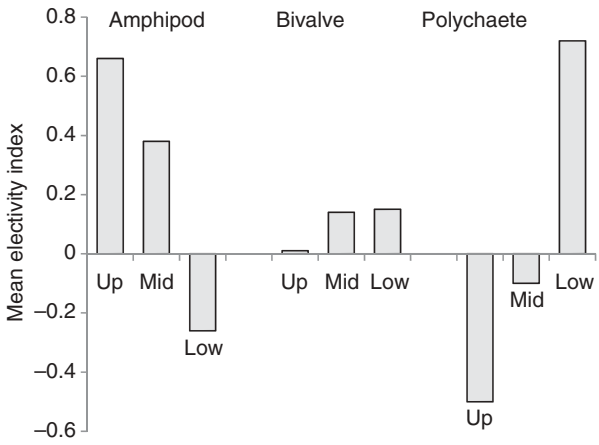


**Figure 6.1.** Non-random feeding in juvenile flounder on a natural nursery ground. Mean electivity index (a measure of preferential feeding in relation to prey availability) for juvenile flounder for amphipods, bivalves and polychaetes at different points in the Duoro estuary, from upstream (Up) to the sea (Low). Inset are the mean lengths for flounder at these points in the estuary. Adapted from Vinagre *et al*. 2008.

## 6.2 MECHANISMS

### 6.2.1 Mechanisms for selective foraging

A number of mechanisms could explain how fish feed non-randomly on the food types available to them. In the first place, selection may be passive, in the sense that some types of prey may be more accessible or more conspicuous than others. For example, walleye pollock (*Theragra chalcogramma*) foraging in the dark feed on large prey items, primarily because they have higher encounter rates with such prey (Ryer *et al*. 2002). Newly settled winter flounder (*Pseudopleuronectes americanus*) show a preference for the copepod *Eurytemora affinis* over *Acartia hudsonica*, also a copepod, though both species are abundant and both are readily eaten. The preference may arise because *E. affinis* is more visible than *A. hudsonica* on account of its erratic movements, but may also result from the fact that *A. hudsonica* move away from the substratum when they detect predators foraging on the bottom (Shaheen *et al*. 2001). Juvenile flounder (*Platichthys flesus*) take fewer prawns than the abundance of this prey type might suggest, because prawns are active prey and are better at escaping than more sedentary, benthic animals (Vinagre *et al*. 2008).

Selective feeding may also be the result of morphological constraints, diet choice often being a function of the relative size of the forager and its potential food items. For example, piscivores often swallow their prey whole, taking them head first, so whether or not a given prey type can be swallowed depends on the jaw gape and the size of the gullet of the predator in relation to the body depth of

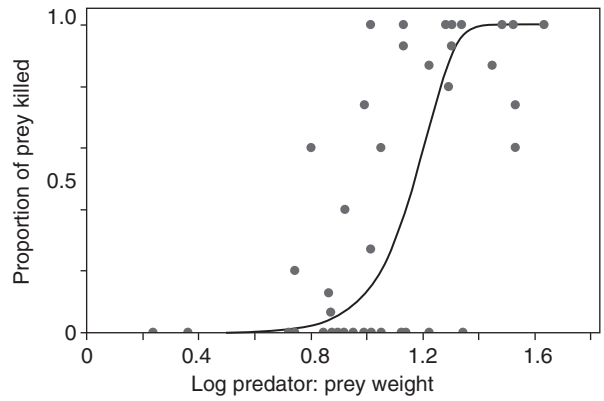


**Figure 6.2.** Morphological constraints on diet selection in fish. The probability of cannibalism in Nile Tilapia in relation to the relative weight of the potential cannibal and its potential prey. Reproduced with permission from Fessehaye *et al*. 2006.

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the prey. As a result, whether or not prey of a particular size is eaten depends on the relative body size of predator and prey. For example, in juvenile Nile tilapia (*Oreochromis niloticus*), a commonly-cultured omnivorous freshwater species, the probability of a cannibalistic attack is dependent on the size of the cannibal in relation to its potential prey (Figure 6.2; Fessehaye *et al*. 2006).

In other cases, constraints arise from the fine morphology of the trophic apparatus. For example, juvenile cichlids (*Haplochromis piceatus*) of less than 4 cm in length do not feed on chironomid pupae, a prey type favoured by larger fish. This arises because maximum prey size is constrained by the ability of fish to hold prey in the buccal cavity (Galis & de Jong 1988) and by the ability of the pharyngeal teeth to pierce the exoskeleton of the prey (Galis 1992). Small pumpkinseed sunfish (*Lepomis gibbosus*) feed on soft-bodied littoral invertebrates, being unable to feed on molluscs until their pharyngeal teeth and associated muscles have developed sufficiently to allow them to crush mollusc shells (Osenberg & Mittelbach 1989). Molluscs are favoured as prey by large pumpkinseed sunfish.

Finally, selective feeding may be the result of active choice, whereby a forager faced with different prey types that are equally accessible, detectable and capable of being consumed elects to feed on a limited selection of prey types. For example, cleaner fish (*Labroides dimidiatus*) prefer the mucus of parrotfish to the mucus of snapper when these are presented in equal concentrations (Grutter & Bshary 2004). Pike-perch, or zander (*Stizostedion lucioperca*), offered roach (*Rutilus rutilus*) and rudd (*Scardinius erythrophthalmus*) of a range of sizes feed selectively on smaller prey. This is not due to differential encounter rates or capture success or to faster satiation in fish taking large prey; rather it is primarily the result of active choice, the pike-perch being more likely to attack and eat a small than a large prey once they have approached it (Turesson *et al*. 2002; Figure 6.3).

### 6.2.2 Sensory inputs to diet choice

The ability of fish to detect and assess potential prey underlies several facets of selective feeding, and the senses that are used to detect food (Chapters 2 and 5) are also used to distinguish among potential food items. Food may be rejected before being taken into the mouth on the basis of cues detected from a distance (visual, chemical, mechanical or electrical). However, once a given food item has been located and grasped, whether or not a fish will ingest and swallow it is determined by sensory systems within the mouth (Hara 2006). The gustatory system provides the final evaluation in the feeding process, but mechanosensory stimuli, giving information about the hardness of an item for example, may supplement evaluations made on the basis of chemical signals. This section considers these different aspects of the sensory basis of diet choice, with special reference to the role of chemical cues.

#### *Vision, mechanoreception and* electro*reception*

Visual cues are important in the search for and location of food and also play a role in food choice. For example, juvenile Atlantic salmon (*Salmo salar*) differentiate between food items visually on the basis of size. The salmon are more likely to fixate on and capture prey measuring about 2.5% of the salmon body length than prey that are either larger or smaller (Wañkowski 1981; Wañkowski & Thorpe 1979). The salmon also differentiate food items on the basis of shape and colour, preferring those that are long and thin to those that are short and round (Stradmeyer *et al*. 1988),

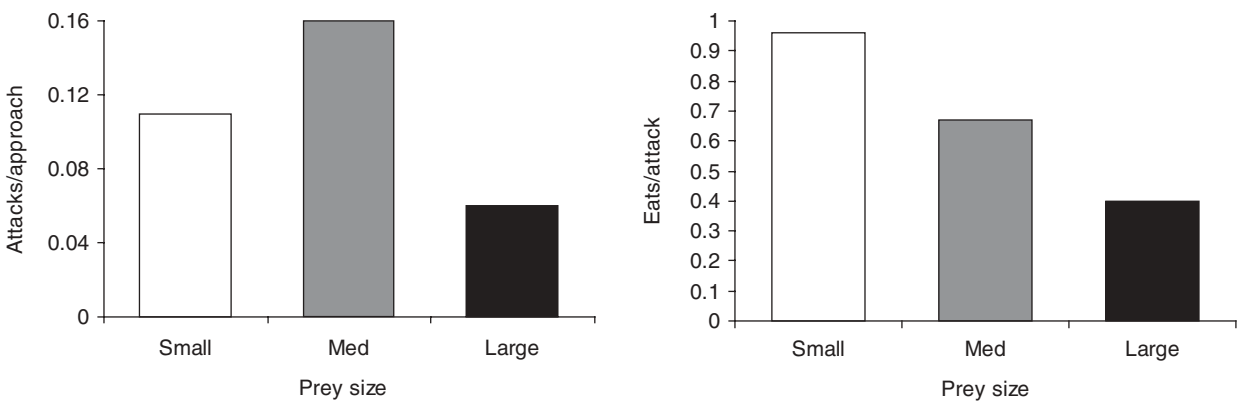


**Figure 6.3.** Active prey choice in fish. The ratio of attacks per approach and of eating per attack in pike-perch feeding on prey fish of different sizes. Adapted with permission from Turesson *et al.* 2002.

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**Box 6.1** General classification of the mode of action of chemical cues that influence feeding in fish

**Incitants:** promote searching for and capture of potential food items, via stimulation of the olfactory (smell) or extraoral gustatory (taste) systems
**Suppressants:** decrease the rate at which potential food items are grasped and taken into the mouth, acting via the extraoral gustatory system
**Stimulants:** induce rapid ingestion of food items, acting via the intraoral gustatory system
**Deterrents:** curtail feeding, evoke rejection and inhibit recapture of potential food items, acting via the intraoral gustatory system
**Enhancers or potentiators:** do not act as stimulants, but increase ingestion of food by accentuating the existing flavours, acting via the intraoral gustatory system
**Detractors:** do not act as deterrents, but diminish the positive effects of stimulant chemicals, acting via the intraoral gustatory system
**Indifferent substances:** do not exert any influence upon feeding responses, either being undetected by the olfactory and gustatory systems, or not serving a role related to feeding.

and seem to prefer red prey above those of other colours. Walleye pollock are able to capture food in the dark using mechanosensory cues, encountering large prey more frequently and favouring such prey as a consequence (Ryer *et al*. 2002). *Aplocheilus lineatus* uses its complex head lateral line canal system to detect insects by vibrations on the water surface; the fish can distinguish between different prey types on the basis of the patterns of vibration that they produce (Vogel & Bleckmann 1997). Fish can also use electrical cues in prey detection, location and selection; for example, both cartilaginous fishes and paddlefish can detect and locate food using the electric cues generated inadvertently by their prey (Wilkens & Hofmann 2007). Visual, mechanical and electrical cues can provide information about some features of potential prey, but they provide no direct information about its nutrient composition. This is in contrast to chemoreceptor input, which can provide such information; hence the importance of chemical cues in diet choice.

### *Behavioural effects of chemical cues*

Chemicals can be classified according to how they influence the probability that potential food items will be captured or ignored, swallowed or rejected and also how much of the particular food item is consumed (Box 6.1; Mackie & Mitchell 1985; Kasumyan & Døving 2003). It should be noted that a chemical that acts in a particular way for one species of fish may act in a different way for another species (Hara 2006; Yamashita *et al*. 2006).

### *General taste preferences in fish*

Dietary preferences in fish have been assessed in terms of the classical tastes identified subjectively by humans, namely sweet, sour, bitter and salt. As far as compounds associated with sweet tastes for humans are concerned, sucrose is usually either an indifferent taste substance for fish or evokes positive behavioural responses. Herbivorous and omnivorous fish may use sugars in palatability assessment, with sugars having stimulant properties. Highly acidic foods that have a sour taste are generally rejected by fish, though mildly acidic feeds are readily accepted by salmonids (Kasumyan & Døving 2003). Among acidic-tasting chemicals, citric acid (which may be added to commercial fish feeds as a preservative) has stimulant properties for some species, but for others it acts as an indifferent compound or as a feeding deterrent. Quinine and other bitter-tasting compounds appear to be highly deterrent substances for all fish species (Lamb 2001) and are widely used by both plants and animals as chemical defences (Hoffmann *et al*. 2006; Paul *et al*. 2006; Tripathi & Mishra 2007). As far as salts are concerned, calcium chloride has a bitter and astringent taste for humans, but appears to be an indifferent taste substance for many fish species. Sodium chloride is generally either an indifferent taste substance or acts as a feeding stimulant at low concentrations; high concentrations of sodium chloride make food items unpalatable to fish.

### *Effects of specific chemicals*

Acceptance or rejection of food by fish is also determined by specific substances that are present in natural foods, particularly amino acids, which may have incitant, stimulant or deterrent effects (Kasumyan & Døving 2003). Most prey animals and plants eaten by fish contain high concentrations of free amino acids. Some fish (for example,

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**Box 6.2** Some constituents of food that influence diet choice in fish

**Betaine** (glycine-betaine, trimethylglycine), found in many prey species, is a feeding stimulant or potentiator (flavour enhancer) for many fish species, including some flatfish, but is an indifferent chemical in others, including some salmonids and sturgeons (Mackie & Mitchell, 1985; Kasumyan & Døving, 2003; Yamashita *et al*. 2006)
**Nucleosides** (the repeating units in nucleic acids) and their derivatives can have taste properties (Mackie & Mitchell, 1985). For example, breakdown products of ATP are feeding stimulants for several species of flatfish and potentiators in many other species.
**Biogenic amines** are formed as a result of the degradation of amino acids by microbial action, may be present at relatively high concentrations in fish meals prepared from stale fish (Jobling, 2004) and may act as olfactory stimulants leading to the initiation of food search (Hara, 2006). At high concentrations may act as feeding suppressants, via the gustatory system.
**Fatty acid oxidation products** and their derivatives (alcohols and aldehydes) may promote feeding at low concentrations (Jobling, 2004), but extensive oxidation of fatty acids leads to rancidity, which reduces consumption.

ictalurids) detect and respond to many amino acids, whereas others (for example, salmonids) respond to just a few (Yamashita *et al*. 2006). The amino acids alanine, cysteine, serine, glutamine, glycine and proline seem to act most frequently as feeding stimulants, either separately or when included in amino acid mixtures. Deterrent effects on feeding have been recorded for valine, arginine, histidine, phenylalanine and methionine. Arginine, histidine, phenylalanine and methionine are all essential (indispensable) amino acids and their potential to act as feeding deterrents underpins the lack of any relationship between the ability of an amino acid to stimulate feeding and its status as an essential dietary component (Kasumyan & Døving 2003). A few of the many other constituents of the natural foods of fish that influence diet choice are presented in Box 6.2.

### *Defensive chemicals*

Many plants and animals (particularly sessile and slow-moving ones) use chemical defence as protection against potential predators (Hoffmann *et al*. 2006; Long & Hay 2006; Paul *et al*. 2006). The chemicals may be toxic or may act as feeding deterrents, or both, and tend to be effective against a wide range of foragers. Chemical defences are rare in animals that are at low risk of being consumed. Within the vertebrates, larger species are less likely to use chemical protection than are smaller species, and chemical protection is more common in species that live longer (Blanco & Sherman 2005). Chemical defences are widespread amongst non-vertebrate animals, being found in sponges, ascidians, soft corals, bryozoans, polychaete and oligochaete worms, insects and molluscs. Some species obtain their defensive chemicals via their food, but many can synthesise these substances. Defensive compounds span a range of biochemical compositions and include terpenes (components of the aromatic oils of terrestrial plants), flavonoids (also common plant products) and various amino acid derivatives (Hoffmann *et al*. 2006; Long & Hay 2006; Paul *et al*. 2006; Sotka *et al*. 2009). A number of the metabolites produced by cyanobacteria or algae may act as feeding deterrents, imparting odours or flavours that are undesirable to animals that might consume them (Watson 2003).

In the nutritional literature the defensive compounds of both plants and animals are sometimes included within the broad category of antinutritional factors. An antinutritional factor is a substance that reduces the nutritional value of a feed or feedstuff by influencing ingestion or by interference with the digestion, absorption or metabolism of nutrients. Thus, in addition to acting as feeding deterrents, various anti-nutritional factors may interfere with protein digestion and utilisation, bind to minerals and reduce their bioavailability, act as antivitamins or interfere with metabolic pathways via endocrine-disrupting mechanisms (Acamovic & Brooker 2005; Tripathi & Mishra 2007). For example, isoflavones such as genistein, which is found in soybeans, can interfere with steroid biosynthesis and metabolism, including the pathways by which sex steroid hormones are metabolised (Ng *et al*. 2006). Clearly the existence and action of substances that reduce the nutritional value of feedstuffs is of considerable importance in aquaculture.

### 6.2.3 Post-ingestive signals and diet choice

Chemical stimuli from the food once it is in the mouth are critical in the evaluation of its nutritional content and hence in the dietary choices that fish make. However, diet choice is also influenced by previous experience of the positive and negative consequences of ingesting particular prey types. Thus fish will choose a certain food based on its beneficial metabolic and physiological effects and will

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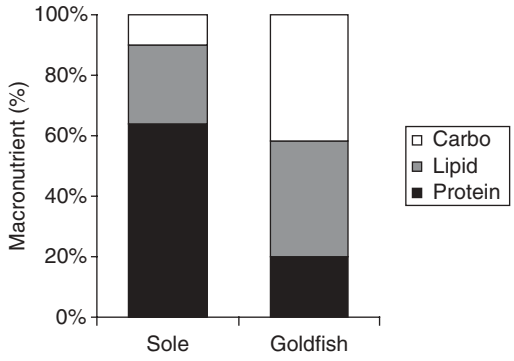


**Figure 6.4.** Self selection of macronutrient diets in fish. The percentage of energy taken in as carbohydrate (carbo), lipid and protein by sole and goldfish using self-feeders delivering these three macronutrients in pure form. Adapted from Sanchez-Vasquez *et al.* 1998 and Rubio *et al.* 2009.

avoid those with harmful or less positive consequences. For example, the diet of wild *Girella tricuspidata* contains 65% non-algal food during winter, but only 34% non-algal food in the summer. The fish adjust their intake and utilisation of algae so that they gain similar amounts of protein regardless of the species on which they are feeding (Raubenheimer *et al*. 2005). Such nutritional wisdom appears to be a basic attribute of animals, which make dietary selections that ensure an adequate intake of essential nutrients (Simpson & Raubenheimer 2001).

The ability of fish to select nutritionally-appropriate diets, based in part on previous experience, is demonstrated by studies of macronutrient self-selection. When offered three separate diets, each providing a single macronutrient (protein, lipid and carbohydrate), fish of various species soon learn to compose a diet that reflects their natural feeding habits. For example, carnivorous species, such as rainbow trout (*Oncorhynchus mykiss*; Sánchez-Vázquez *et al*. 1999) and European sea bass (*Dicentrarchus labrax*; Aranda *et al*. 2000) select diets composed predominantly of protein (about 64% and 57% protein respectively). Sole (*Solea senegalensis*) also compose a protein-rich diet from feeds consisting of protein, lipid and carbohydrate (Figure 6.4; Rubio *et al*. 2009). In contrast, goldfish select a diet comprising, in terms of digestible energy, 22% protein, 32% lipid and 46% carbohydrate, reflecting their omnivorous character (Figure 6.4. Sánchez-Vázquez *et al*. 1998). Nile tilapia (*Oreochromis niloticus*) are able to make dietary self-selections based on the food oil source (Fortes-Silva *et al*. 2010a) or the supplementation of exogenous phytase, an enzyme that hydrolyses non-digestible phytate and improves the nutritional value of a plant-based diet (Fortes-Silva *et al*. 2010b).

Sole are also able to adjust their diet to compensate for protein dilution, as is also the case for the omnivorous sharpsnout sea bream (*Puntazzo puntazzo*). The latter responds to dietary protein dilution (diluted with 50% of cellulose) by consuming double the amount of the diluted diet without increasing intake of diets containing lipid and carbohydrate. In this way, they can compensate for protein dilution to sustain both energy intake and the relative proportions of macronutrients (Vivas *et al*. 2006). So long as the fish are given the possibility of discriminating between the different single-nutrient diets (protein, lipid and carbohydrate), dietary adjustments can be made on the basis of post-ingestional cues in the absence of oral stimuli. For example, diets can be packaged into taste-free, colour-coded gelatine capsules that mask both texture and chemosensory properties (Ruohonen *et al*. 1997). Sea bass and sharpsnout sea bream continue to regulate their macronutrient intake when fed such encapsulated diets (Rubio *et al*. 2003; Almaida-Pagán *et al*. 2006).

### 6.2.4 Modulation of diet choice

The fact that fish can make adjustments when self-selecting diets shows that choices are made flexibly according to nutritional needs. The balance of macronutrients selected may vary over the year, even when fish are held under constant conditions. For example, sea bass held at a constant temperature and photoperiod favour a protein-rich diet in the spring, but select more fat in late summer (Figure 6.5; Rubio *et al*. 2008). Gender differences in diet are also common; for example, in the cleaner goby (*Elacatinus evelynae*) the number of items derived from cleaning client fish (fish scales and ectoparasites) is greater for females than males, perhaps because of the greater nutritional requirements of females (Whiteman & Côté 2002). Fish also adjust their choices in response to changes in their external environment. For example, juvenile Atlantic salmon are more likely to attack inedible items when foraging under a perceived predation risk than when foraging without disturbance (Metcalfe *et al*. 1987). The presence of competitors can also cause shifts in diet choice in fish, as when three-spined sticklebacks (*Gasterosteus aculeatus*) switch to smaller, less profitable prey when foraging in the presence of better competitors of the same species (Milinski 1982).

### 6.2.5 Overview of the mechanisms controlling diet choice in fish

Given a range of potential food items, fish are selective in what they eat. Such selectivity may be the result of

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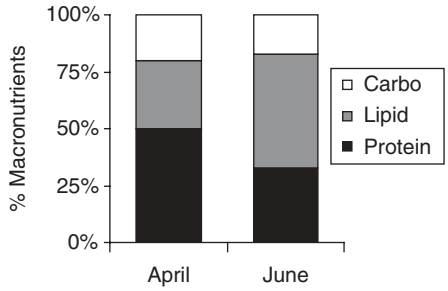


**Figure 6.5.** Changes in self-selected diet with season. The percentage of energy taken in as carbohydrate (carbo), lipid and protein in April and in June by sea bass using self-feeders delivering these three macronutrients in pure form. Adapted from Rubio *et al.* 2009.

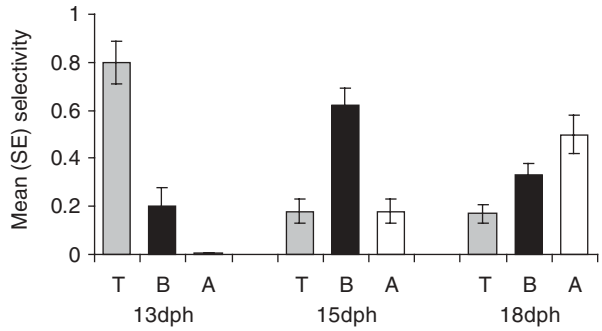


**Figure 6.6.** Age-related changes in diet. Mean (+SE) selectivity index (a measure of preferential prey selection) in greenback flounder of 3 different ages (13, 15 and 18 days post hatching, dph) fed a diet consisting of two rotifer species (*Brachionus plicatilis*, B, and *Testudinella* spp. T) and *Artemia* (A) in equal numbers. Adapted from Shaw *et al.* 2003.

differential accessibility or detectability of different kinds of prey, of mechanical constraints on the types of food that can be ingested efficiently or of active choices. Fish use cues in various sensory modalities for assessing food from a distance, but cues detected at close quarters and in the mouth play a key role in eventual acceptance or rejection of potential food. Mechanical and, particularly, chemical cues are critical in this context, since these provide fish with direct information about the nutrient properties of ingested food. Fish are able to assess many different chemical properties of food while it is in the mouth; these include its quality with respect to the four classical tastes of sweet, sour, bitter and salt, as well as specific nutrients or antinutrients that it may contain. In addition, experience of post-ingestive signals, specifically detection of macronutrients or their digestive products by gastrointestinal receptors, influences subsequent diet selection. Together, these mechanisms enable fish to select diets on the basis of their nutritional properties. Diet choice in fish is modulated by nutritional status and needs and also by immediate circumstances, such as the presence of potential predators and competitors. To the extent that they dictate what fish will and will not eat, these mechanisms clearly have important implications for feed management in aquaculture.

## 6.3 DEVELOPMENT

Not surprisingly, what fish can eat and choose to eat alters as they grow, particularly when their life history includes a change in habitat at metamorphosis. Larval rearing and weaning onto artificial feeds is a recognised bottleneck in fish culture. In addition, the ability of larger fish to choose an appropriate diet is critical to the success of supplementation programmes in which captive-reared fish are released into the wild. For these reasons, it is important to know how diet choice changes with age and maturity in cultured species and how it is influenced by interacting genetic and environmental effects.

### 6.3.1 Ontogeny of diet choice

Age-related changes in diet choice are widespread among fish. For example, species such as the Nile tilapia and common carp (*Cyprinus carpio*), in which the adults are omnivores or herbivores, start life as zooplanktivores. Shortly after hatching, greenback flounder (*Rhombosolea tapirina*) feed preferentially on small rotifers (*Testudinella* spp.), at about 15 days post hatching, they switch to larger rotifers (*Brachionus* sp.) and then at day 18 to *Artemia* (Figure 6.6). Thus, as they grow the young flounder eat prey of increasing size, probably reflecting changes in sensory systems, in jaw gape and in prey handling ability, as well as active preference for certain prey types (Shaw *et al*. 2003). In catfish (*Clariallabes longicauda*) the proportion of large prey in the diet, the size of the largest prey consumed, the proportions of hard and soft prey types and the proportions of evasive prey consumed all change with growth of the fish from 100 to 250 mm in length (Wyckmans *et al*. 2007).

#### *Development of sensory systems*

Some age-related changes in diet are the result of changes in sensory systems. For example, visual acuity increases with age in fish and particularly rapid changes occur in salmonids at the time of emergence from the redd, and in mouth-brooding cichlids at the time of independence from

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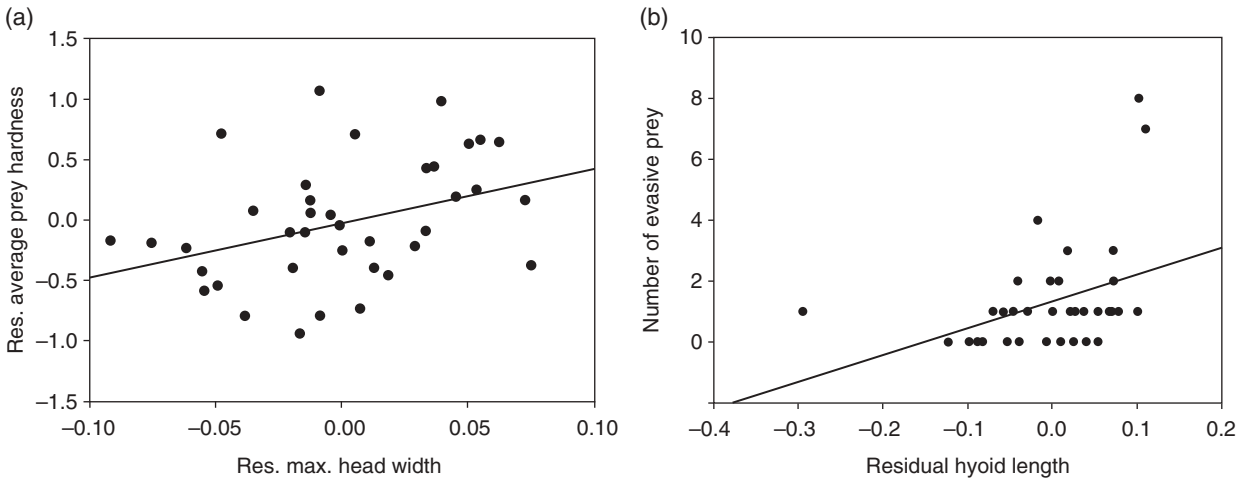


**Figure 6.7.** Parallel ontogenetic changes in diet and trophic morphology in fishes. (a) Average prey hardness in relation to maximum head width (corrected for body length by regression analysis) and (b) number of evasive prey captured in relation to hyoid length (corrrected for body length by regression analysis) in juvenile catfish. Reproduced with permission from Wyckmans *et al.* 2007).

their parents. In both cases, the sensory developments coincide with the transition to feeding on exogenous food (Noakes & Godin 1988). Development of the ability to discriminate between food items on the basis of taste corresponds with the development of taste receptors, which may develop before the start of exogenous feeding. For example, in sturgeon (*Acipenser* spp.) the number of substances that stimulate feeding increase with age, as taste buds appear on the barbels and in the mouth. First-feeding sturgeon show the same pattern of responsiveness to some chemicals, such as sucrose, as seen in older juveniles; however, unlike older fish, they do not respond to amino acids (Kasumyan & Døving 2003).

### *Development of the trophic apparatus*

Changes in diet choice can often be ascribed to the development of the structures needed to feed effectively on different types of food. This may be the result of an increase in body size and with this in jaw gape. For example, in pike-perch the capacity to feed on *Daphnia* peaks when the fish are 66 mm in length, and shortly thereafter they switch to feeding on other fish (Persson & Brönmark 2002). Once the transition to piscivory has taken place, there is a positive linear relationship between prey body depth and length on the one hand and predator gape width on the other (Dörner *et al.* 2007).

In addition to the effects of increasing size, diet choice in young fish is influenced by the development of components of the trophic apparatus. For example, the switch in the diet of young tilapines from zooplankton captured individually to suction-based feeding on phytoplankton is associated with an increase in the number of cells that produce mucus, which is needed to retain phytoplankton in the buccal cavity (Northcott & Beveridge 1988). The dietary changes with age observed in catfish (*Clariallabes longicauda*) depend both on size-dependent and on size-independent effects. There is allometric (disproportionate) growth in length of several of the bones that make up the jaw, in the muscles that close the jaw and in head length and width. When corrections are made for fish size, the relative length of the hyoid bone predicts the proportion of evasive prey eaten and relative head width predicts prey hardness and the proportion of large prey eaten (Figure 6.7; Wyckmans *et al.* 2007). In sea bream (*Sparus aurata*), rapid changes in the shape of the head, body and trophic apparatus are reflected in ontogenetic dietary shifts. In this case, dietary shifts are probably caused by size-related changes in morphology and, in particular, by enlargement of gape (Russo *et al.* 2007). It is also possible that dietary shifts can act as initiators of changes in trophic morphology. For example, young Chinese hook snout carp (*Opsariichthys bidens*) eat zooplankton, but as they grow they switch diet to benthic macroinvertebrates and then to fish. These changes in diet are associated with, and possibly cause, changes in body shape (from shallow to deep bodied), in mouth position (from upward pointing to downward pointing) and in jaw shape (taking on the odd 'zig-zag' form that is typical of this species; Johansson *et al.* 2006).

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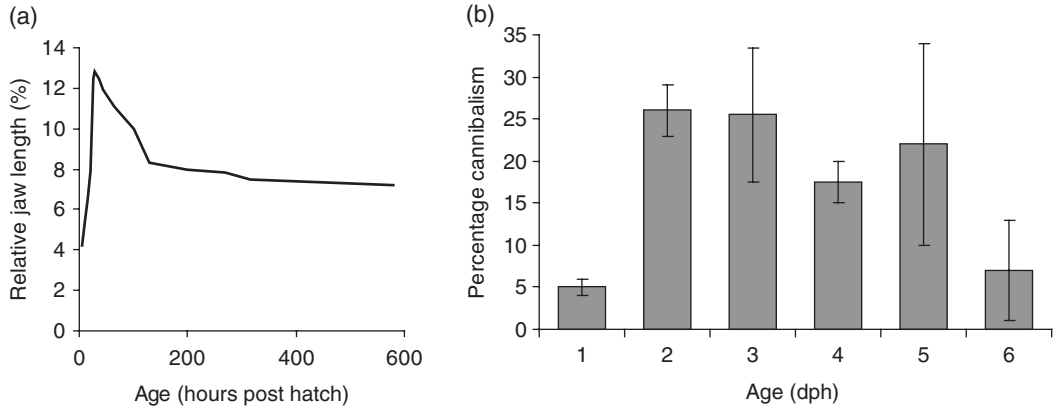


**Figure 6.8.** Ontogeny of cannibalism in *Brycon moorei*. (a) Relative jaw length in relation to age (hours post hatching). (b) The incidence of cannibalism in relation to age (days post hatching, dph). Adapted with permission from Vandewalle *et al*. 2005.

### *Ontogenetic diet shifts and the development of cannibalism*

Ontogenetic shifts in diet based on changes in the ability to capture prey of different sizes has been particularly well characterised in the case of cannibalism, which is common in fishes, including many that are cultured (Baras & Jobling 2002). Young-of-the-year pike-perch initially feed on planktonic microcrustaceans, but as they grow, they switch to feeding on larger invertebrate prey and at a certain size to feeding on other fish, including conspecifics (Specziár 2005). Above a certain size, some Arctic charr may change from feeding on invertebrates to feeding on smaller, younger conspecifics (Amundsen *et al*. 1995). In both species, the fish that become cannibalistic seem to maintain this feeding strategy throughout life. In other cases, including cod (*Gadus morhua*) and catfish (*Clarias gariepinus, Pangasianodon hypothalamus*), there is a limited period during early development when cannibalism within a cohort is common, after which it declines, but some adults can cannibalise smaller and younger conspecifics (Baras & Jobling 2002; Baras & d'Almeida 2001).

The dorada (*Brycon moorei*) is a Latin American characid that has supported an inland fishery and is currently cultured both for supplementation and for food. Intense cannibalism appears in this species within 1 day of hatching, 40% of fish being cannibalised during their first day of life and 98% during the first week. In the first few hours after hatching, the jaw enlarges at a rapid rate (Figure 6.8a) and sharp jaw teeth develop. These are feeding structures that are needed for piscivory and allow a young fish to capture and retain a prey that is larger than itself (Baras *et al*. 2000a,b). As fish are particularly nutritious, cannibals grow rapidly and quickly become larger than their prey. In general, small and deformed fish are targeted as prey. Cannibalism becomes less frequent as the fish grow older (Figure 6.8b).

### 6.3.2 Inherited differences in diet choice

Recently hatched fish and fish reared without experience of natural food may show species-typical dietary preferences. For example, hatchery-reared juvenile Atlantic salmon and brown trout display species-typical preferences for particular cues even though they have never encountered live prey (Stradmeyer *et al*. 1988). Young rainbow trout prefer live, moving prey to dead, immobile prey regardless of previous experience (Irvine & Northcote 1983). Arctic charr reared in the laboratory with no experience of fish as prey readily take up cannibalism, both when offered small conspecifics as food and when released into a lake (Amundsen *et al*. 1995; Svenning & Borgstrøm 2005).

Such observations are suggestive of inherited prey preferences, as are cases in which natural differences in prey choice persist in fish reared under standard conditions. For example, Arctic charr from some landlocked populations show higher rates of cannibalism than do fish from anadromous populations when reared in a common environment (Amundsen *et al*. 1999). Hatchery-reared juvenile Arctic charr belonging to sympatric morphs specialising on benthic or plankton prey show morph-specific prey choices even though they have never experienced live prey (Adams & Huntingford 2002). In some cases, crossing experiments have confirmed the existence of inherited feeding-related

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responses. For example, hybrid offspring of crosses between a female goldfish (which find citric acid and proline aversive) and a male common carp (to which these two substances are attractive) show preferences that are similar to those of their father, suggesting that these taste preferences are inherited through the paternal line (Kasumyan & Døving 2003). Inherited differences in the propensity for cannibalism are indicated by the fact that hybrids between a cannibalistic species (*Poeciliopsis monacha*) and a non-cannibalistic species (*P. lucida)* show levels of cannibalism intermediate to those of their parents (Thibault 1974).

### 6.3.3 Experience and diet choice

Although there is evidence for inherited differences in diet choice, feeding is also often flexible, enabling fish to eat a variety of food types should the need and the opportunity arise. Such flexibility is based on a number of processes, ranging from environmental influences on growth (and hence nutritional needs), through effects of novel diets on trophic morphology, prey handling and digestive capacity to learning from previous experience of eating particular types of food (Warburton 2003; Long & Hay 2006; Skelhorn & Rowe 2006).

#### *Experience, growth rates and diet*

At a general level, since fish size is a determinant of diet choice, anything that influences growth may influence the occurrence of ontogenetic changes in diet. In pike-perch, for example, the timing of the switch from eating zooplankton to eating fish is influenced by the availability of zooplankton, which determines how quickly pike-perch pass the optimal size for feeding on such prey, and the density of prey fish species, which determines energetic returns from piscivory (Persson & Brönmark 2002). In the specific case of cannibalism, anything that promotes differential growth in a potentially cannibalistic species will favour the development of cannibals from among the few 'lottery winners' that gain a size advantage over their companions (Baras & Jobling 2002). In small juvenile red drum (*Sciaenops ocellatus)*, an economically important species cultured for stock enhancement, a size disparity of 1:3 may result in the initiation of sibling cannibalism (Chang & Liao 2003a).

#### *Experience and digestive capacity*

Fish have the capacity to adapt digestive processes such as enzyme secretion and nutrient transport and absorption to match changes in diet (Kapoor *et al*. 1975; Hofer, 1979a,b; Buddington *et al*. 1987, 1997; Gawlicka & Horn 2006). Macronutrient composition of the food may influence the production of digestive enzymes and the density of cell membrane nutrient transporters, resulting in changes in digestive and absorptive capacity (Kapoor *et al*. 1975; Buddington *et al*. 1987, 1997; Ferraris & Diamond 1989; Hirst 1993; German *et al*. 2004; Gawlicka & Horn 2006). The ability to match the profile of digestive enzymes and nutrient transporters to diet seems to vary amongst species. Carnivores, for example, appear to have a limited capacity to alter digestive and nutrient transport functions, whereas omnivores display a much greater ability to match their digestive and absorptive physiology to changes in dietary composition (Buddington *et al*. 1987, 1997; Krogdahl *et al*. 2005).

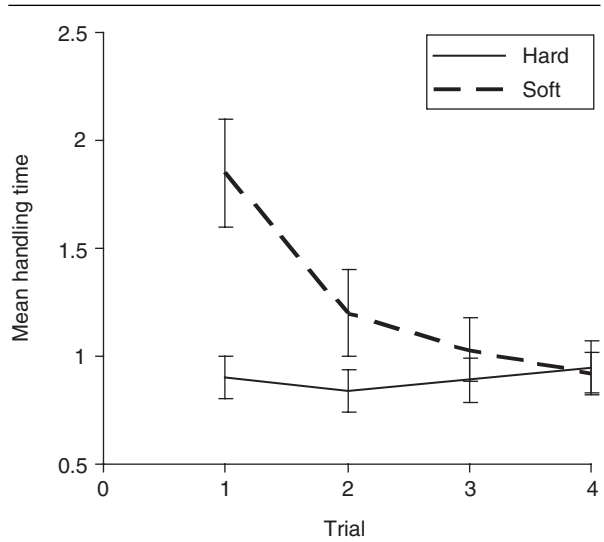


**Figure 6.9.** Effects of diet on prey handling. Mean (+SE) log handling time (sec) for hard food items in red drum previously fed either hard (solid line) or soft (dashed line) food. Adapted from Ruehl & De Witt 2007.

#### *Experience and trophic morphology*

Juvenile red drum reared on a diet of hard food develop heads that are deeper in the region of the pharyngeal jaws, larger feeding muscles and more anterodorsally positioned eyes than do those fed on soft food. Initially, they also feed faster on hard food compared to fish reared on soft food, but this effect disappears quickly, as fish reared on soft food learn how to handle hard food (Figure 6.9; Ruehl & DeWitt 2007). This example shows that early dietary experiences can induce changes in the trophic apparatus, with consequent effects on the ease with which fish can exploit different foods, but that learning from experience of handling different prey types can also be important.

#### *Learning and diet choice*

Effects of experience on prey handling and prey preferences are well documented. For example, cichlids

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(*Labrochromis ishmaeli*) that are used to eating snails work their pharyngeal jaw apparatus using a specific muscle activity pattern when ingesting these prey, which are hard and broad. On first encountering a novel prey type, specifically *Chaoborus* larvae, which are soft, elongated and narrow, the fish show the same pattern of muscle activity, but after several larvae have been eaten, a new pattern emerges, involving the same muscles contracting with different timing and also recruitment of new muscles. As a consequence, the pharyngeal jaws move in a different way, which increases in the efficiency with which the soft larvae are eaten (Galis *et al*. 1994).

Although there may be plasticity in prey choice, fish often prefer familiar foods and may be reluctant to add new prey types or food items to their diet; in other words, they display dietary neophobia (Warburton 2003). For example, in grass carp (*Ctenopharyngodon idella*) raised for 6 months either on plants (duckweed and lettuce) or animal prey (mosquito larvae), fish of both groups prefer extracts of the foods on which they have been raised (Kasumyan & Døving 2003). Familiarity with prey of a particular size may also be important, with fish sometimes having a tendency to avoid, or reject, novel food types. This may have adaptive significance, in that it prevents the consumption of large amounts of food when the consequences of intake are unknown.

Forming an association between the appearance or tastes of potential foods and their post-ingestive effects is important not only in the development of prey choice in young fish, but also in updating prey choice in adults. Such learning enables fish to amend their feeding habits in response to changes in food availability and to maintain a nutritionally sound diet over time. Chemical cues have particular relevance in this context; for example, the rejection of foods with a particular taste (taste aversion) may relate to avoidance of a gustatory stimulus that has previously been associated with noxious or unpleasant post-ingestive effects (Warburton 2003; Long & Hay 2006). If an animal ingests a toxic food it will develop a conditioned aversion to its flavour, whereas if the post-ingestive effects are positive the animal will acquire a preference for its flavour. The establishment of a clear dietary preference may take some time, as the fish learn to associate consuming a particular food with its post-ingestion effects (Rubio *et al*. 2003).

### 6.3.4 Summary of the development of diet choice

Dietary preferences change as a fish grows and its trophic apparatus develops; there is often a change from smaller to larger food items and to food that is more difficult to capture, but this is far from being universal. In some species, young fish go through a transient stage of intense cannibalism, whereas in other species, cannibalism emerges as a feeding specialisation as the fish grow. Some of the observed differences in diet choice between and within species are the result of genetic differences, with preferences for particular chemical stimuli being particularly conservative. However, other differences in diet choice arise as the result of experience. These include general effects, for example those mediated through differences in growth rate, as well as experience-mediated changes to trophic morphology and behavioural effects of experience of feeding on particular prey types. As a consequence of these various processes, while fish are generally conservative in their broad dietary choices, they are also flexible in the details of what they eat. This allows dietary adjustment to the availability of different prey types and current nutrient needs. It is important to take account of such conservatism and such flexibility when it comes to making decisions about the types and nutrient compositions of feeds to be given to cultured fish.

## 6.4 FUNCTIONS

In general, what fish choose to eat serves the purpose of ensuring that they obtain a diet appropriate for their species-specific and stage-specific needs. The question of exactly how and how much selecting a particular food type promotes fitness is more difficult to answer. Behavioural ecologists have adopted optimal diet theory as one approach to the problem. This focuses on how choosing particular foods influences the rate at which foragers accumulate energy. An alternative approach, rooted in both nutritional physiology and behavioural ecology, focuses on the effects of foraging decisions on the rate of acquisition of particular macronutrients and the consequences for growth and fitness. This approach is sometimes called nutritional ecology, defined as the study of how animals relate to their environment through nutritional interactions (Parker 2003; Raubenheimer *et al*. 2009). Both approaches can contribute to explaining the dietary choices that fish make, their effects on growth and survival and how the natural behaviour of fish can be used to promote effective fish culture.

### 6.4.1 The behavioural ecology of energy-based diet choice

Optimal diet theory in its simplest form is based on the assumption that the fitness consequences of eating particular foods depend on the energy content of a given type of food (irrespective of nutrient composition) and the time taken to harvest it. The aim is to identify choices that maximize the rate of energy gain when foragers are exposed to different food types. According to what is often called the

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basic prey model, each food yields a certain energetic return, requires a certain time for processing (handling time) and hence has a certain profitability, defined as the rate at which units of energy are harvested. Large food items may take a long time to handle, so the larger of two items is not necessarily the most profitable. Several predictions can be derived from this simple model: thus foragers should either feed exclusively on the most profitable prey type and ignore less profitable prey (in other words, they should act as specialists), or they should take all prey types whenever encountered (acting as generalists). There should be no partial preferences and the switch from specialist to generalist should depend on the abundance of the most profitable prey type, occurring abruptly at a particular threshold.

### *Testing optimal diet theory in fish*

Fish have often been used to test the predictions of optimal diet theory and the results show that they do tend to select diets that favour fast growth. For example, juvenile Atlantic salmon offered food pellets of different sizes prefer the size (2–2.5% of their own length) on which they grow fastest (Wañkowski & Thorpe 1979). Bluegill sunfish (*Lepomis macrochirus*) foraging in ponds also behave as predicted, expanding their diet to include less profitable prey as the abundance of the most profitable prey type is reduced (Werner & Hall 1974). In the cichlid *Haplochromis piceatus* the rate of energy gain for fish feeding on *Daphnia* and *Chaoborus* larvae increases with fish size, but the slope is steeper for *Chaoborus* larvae (Galis & de Jong 1988). The rate of energy return from feeding on *Chaoborus* is generally greater than that for *Daphnia,* but when the fish are small *Daphnia* are slightly more profitable. Theory predicts that small fish should feed on *Daphnia*, whereas large fish should specialize on *Chaoborus* and this is more or less what the fish do when offered a mixture of prey, although large fish do not totally exclude *Daphnia* from their diet (Figure 6.10).

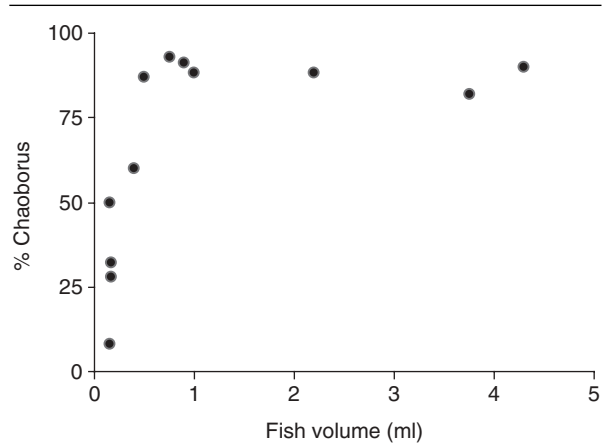


**Figure 6.10.** Testing optimal diet theory. Percentage of *Chaoborus* larvae ingested by the cichlid *Haplochromis piceatus* of different sizes when offered a choice of *Chaoborus* larvae and *Daphnia*. Adapted from Galis & de Jong 1988.

### *Cannibalism as optimal prey choice*

Cannibalism is profitable because eating food that has the same body composition as the consumer will provide nutritionally rich food that is ideally suited for growth (Baras *et al*. 2003), although it may not serve equally well in terms of providing fuel for energy metabolism (Raubenheimer *et al*. 2009). In addition, in many cases, cannibals select the smallest prey available, due to the costs of feeding on large conspecifics. These costs include low capture success, long handling times (Finstad *et al*. 2006), risk of suffocation (Hseu *et al*. 2007), risk of injury, risk of predation by larger fish while subduing prey (Nilsson & Brönmark 2000) and risk of contracting disease (Pfennig *et al.* 1998). The decision as to whether or not to eat a given conspecific depends on the balance of these costs and benefits. In the orange-spotted grouper (*Epinephelus coioides*) cannibals prefer small prey even though they can ingest larger fish; the energetic costs of pursuing and handling large prey and the fact that large prey are more likely to escape makes them less profitable (Hseu 2006).

### *Deviations from the basic prey choice model*

Studies with fish have also demonstrated that the basic diet model does not fully capture the fitness consequences of diet choice. For example, rather than being fixed for a given species and size of fish, the profitability of a given type of food may fall during a meal as the stomach fills and increase with experience as fish learn how to deal efficiently with particular prey types (Hughes 1996). As an example, juvenile roach feed on progressively smaller *Daphnia* as a feeding bout progresses and stomach fullness increases. During a short initial period the rate of energy acquisition is maximized, but then the fish switch to prey that minimizes foraging time, possibly because this allows them to watch for predators or rivals (Mikheev & Wanzenböck 1999). Feeding responses of many species of fish are influenced by the danger of predation, as when juvenile Atlantic salmon fail to distinguish between edible and inedible items when foraging under predation risk (Metcalfe *et al*. 1987). The presence of competitors can influence diet choice. For example, in young-of-the-year Arctic charr an ontogenetic change in diet from benthic cladocerans and chironomids to zooplankton occurs earlier when charr densities are high, presumably due to reduced availability of benthic food (Byström *et al*. 2004).

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### 6.4.2 The nutritional ecology of diet choice

#### *The principles of nutritional ecology*

Optimal diet theory assumes that the relative energy content of different foods is the key nutritional determinant of the fitness consequences of choosing a particular diet. This is a convenient approximation that can be used to answer some questions relating to diet choice; however, ignoring the nutrient content of food oversimplifies the issue. Nutritional ecology involves an integrative approach, taking account of features of the foraging animal, the environment in which it feeds and the interplay between them. Because it addresses how much fish eat of the various diets available to them, it is clearly relevant to the control of appetite (Chapter 7) as well as to diet choice.

Nutritional ecology is aimed at understanding the interactions between animals, which have nutritional requirements, and their environment, which contains the food that, once consumed, digested and assimilated, can fulfil these requirements. Homeostatic mechanisms governing both behaviour and physiology lead to reductions in any differences between an animal's current state and its optimal state. Knowing where an animal is in terms of nutrition (its current nutritional state) relative to its optimal nutritional state allows predictions to be made about both behavioural responses (food choices, for example) and physiological responses (levels of nutrient excretion, for example). Patterns of feeding and nutrient utilisation determine life history variables, including growth rate, longevity, size and reproductive output. These, in turn, determine evolutionary fitness and so are subject to Darwinian natural selection. Animals that interact effectively with their nutritional environment leave more offspring and, as a consequence, the gene variants involved in effective regulatory mechanisms spread at a faster rate than do less effective variants. Thus, nutritional ecology deals with the consequences of nutrition for the fitness of an animal. The aim of the following section is to provide an introduction to the methods used by nutritional ecologists to understand an animal's diet choices and behaviour (for more detail see Raubenheimer *et al*. 2009). An application to fish culture is considered at the end of this chapter.

#### *Constructing an integrated geometrical model*

The first step in constructing a geometric nutritional model is to decide which nutrients will be involved. This can be a difficult task, given that animals need, and many foods contain, over 40 nutrients. However, in many nutritional interactions the macronutrients protein, carbohydrate and lipids dominate, and in some contexts models can be reduced to contain just two of these, namely protein and non-protein macronutrients. Wild carnivorous fish, for example, eat very little carbohydrate and such fish can be used to illustrate the approach. For the purposes of modelling, the arena in which the fish conduct their nutritional interactions can be depicted as a two-dimensional *nutrient space*, the axes of which are proteins and lipids (Figure 6.11a). Current nutritional state and the optimal state (the *intake target*) are each represented by a point in this space. The amount of lipid and protein that the fish must eat to move from its current state to the intake target is represented by the arrow. Providing the costs of doing so are not too high, the fish should move along the arrow, thereby achieving its optimal state.

A particular type of prey can be depicted as a point in the same two-dimensional space, reflecting the amount of protein and lipid it contains (Figure 6.11b). A line joining this point to the origin of the graph (called the food rail) reflects the balance of prey nutrients and represents the amounts of lipid and protein that a fish gains by eating increasing amounts of this food. Thus, a fish moves through nutrient space by feeding, gaining protein and lipid in the same proportion as they are present in the food; the distance moved is proportional to the amount the fish eats. Two behavioural decisions therefore allow the fish to approach its intake target; which food it eats determines the direction of movement in nutrient space and how much of it is eaten will determine the distance moved in a given direction.

#### *Modelling the effects of nutritionally balanced and unbalanced foods*

When a fish has access to food containing an optimal balance of nutrients (in other words, when the food rail passes through the intake target), all it needs to do to meet its intake target is increase the rate at which it eats the food (Figure 6.11b). This provides the rationale behind the formulation of feeds for cultured fish. If a fish does not have access to a single nutritionally balanced food, it can reach its intake target by eating appropriate amounts of two food types that are nutritionally imbalanced (Figure 6.12a). The combinations of nutritionally imbalanced foods that enable fish to satisfy their nutrient needs are known as *nutritionally complementary* foods. In extensive aquaculture systems, the supplementary feeding of fish that are expected to forage on natural prey could be considered as an example of this situation.

A more challenging situation arises when a fish has access to a single nutritionally-imbalanced food, for example one that includes much more protein than lipid. The fish could refuse to eat, but a more likely outcome is one that is imperfect, but nonetheless better than starvation. The fish might make one of three different compromises (Figure 6.12b). First, it may satisfy its needs for protein, but at the cost of a lipid shortfall. Second, it could feed to the point at which it achieves its needs for lipids, but at the cost of

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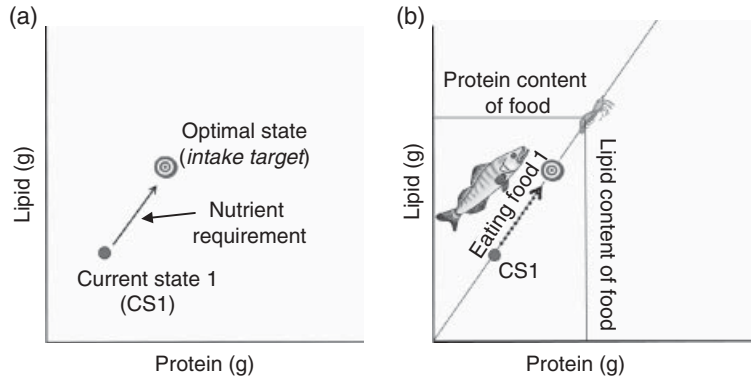


**Figure 6.11.** (a) Graphical representation of the central components of the Geometric Framework model for an animal consuming two nutrients, lipid and protein, over a specified time. This figure displays the current nutritional state of the animal (CS1) and an intake target, the optimal nutritional state for that animal (concentric circles). The animal changes its nutritional state by eating, travelling along the vector (solid arrow), which represents the integrated nutritional requirements for the animal. (b) A schematic depiction of the consequences of feeding on a balanced diet. The animal's current nutritional state is represented at CS1. By consuming the food item (Food 1), the animal travels along the vector (dashed arrow), directly towards its optimal nutritional state (the intake target). This is displayed by the food rail (Food 1) which intersects both the animal's current nutritional state (CS1) and the intake target (concentric circles).

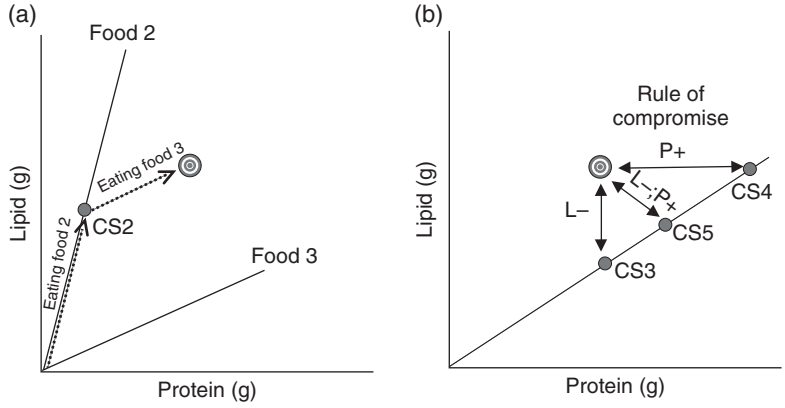


**Figure 6.12.** (a) Graphical representation of the consequences of feeding on two nutritionally unbalanced foods, Food 2 and Food 3, where food 2 is a high lipid:low protein food and food 3 is a high protein: low lipid food. In order for the animal to achieve its optimal nutritional state, it must consume the correct balance of the two foods. The animal achieves its intake target (concentric circles) by initially consuming food 2 to reach a state where it has almost consumed its total requirement for lipid, but where it is deficient in protein (CS2). The animal then makes up for the imbalance by consuming a quantity of food 3, so moving along a trajectory parallel to the nutritional rail for this food and approaching the intake target. In this way the fish mixes the two imbalanced foods to achieve a balanced nutritional state. (b) Graphical representation of the options available to an animal confined to feeding on a nutritionally imbalanced food, displayed as CS3, CS4 and CS5. At CS3 the animal has stopped feeding having satisfied its need for protein, but with a deficit in lipid. At CS4 the animal has satisfies its need for lipid, but suffers an excess of protein. However, at CS5 the animal has a protein excess and lipid deficit, but this is not as severe as the other two situations. This balancing of nutrient excesses and deficits, or rule of compromise, represents the decision made by an animal consuming an imbalanced food source.

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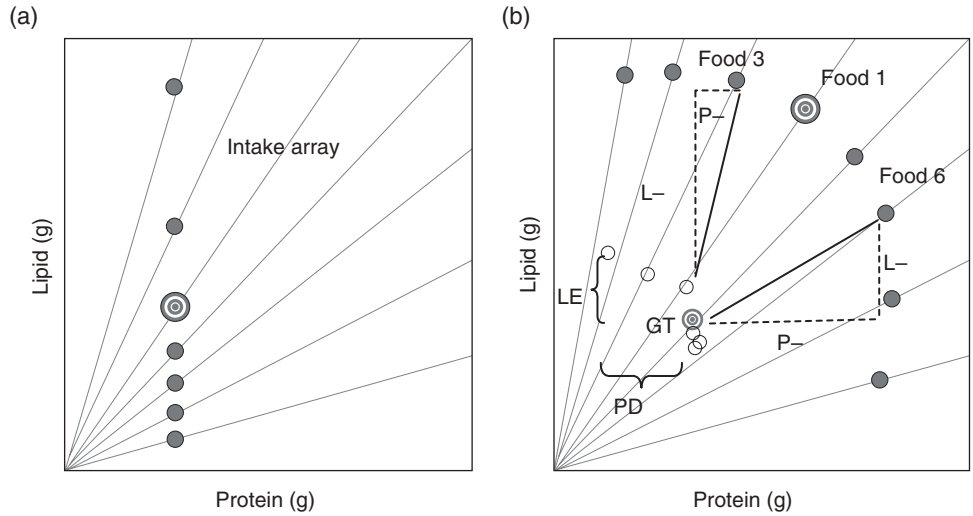


**Figure 6.13.** (a) Graphical representation of the rule of compromise displayed by animals confined to one of a range of nutritionally imbalanced diets, but allowed to feed to their own chosen point on each diet. In each case in this example the animals feed to a point where their protein needs are satisfied, regardless of whether they suffer an excess or deficit of lipid. Thus, the animals appear to compromise their lipid intake and preferentially satisfy their need for protein. (b) Graphical representation of the geometric framework model for two nutrients, lipid and protein, which incorporates the physiological regulatory processes of the animal under study. Displayed is an array of intake points (solid circles) and growth (hollow circles) points for animals confined to one ofa range of foods, which differ in their protein:lipid ratio. The growth target (GT) is the point at which optimal allocation of nutrients to growth is achieved, analogous to the intake target (IT), which represents the optimal nutrient intake. Dashed lines represent the amount of protein and lipid eaten for a particular diet, but not converted to growth. PD: body protein deficit. LE: body lipid excess. The figure shows that while animals which achieve their intake target readily achieve their growth target, animals receiving imbalanced diets can also come close to achieving their growth target by differential use of the two nutrients. For example animals consuming the lipid-rich diet, Food 3, convert most of their protein intake to growth, losing only the amount of protein represented by P–, but much of the lipid taken in by fish on this diet is lost as L–.

eating excess protein. Third, it could settle on some intermediate point, at which it suffers a shortfall of lipid and an excess of protein, neither of which are as extreme as in the other two compromise options. The compromises that fish make when unable to achieve their nutritional optimum (their *rules of compromise*) are an important component of the regulatory toolkit of animals that encounter variability in the foods they eat. To understand the nutritional ecology of such animals, knowledge is needed about these compromises and how they may be depicted.

How can we measure such rules of compromise? The best way to do so is using an experiment like that modelled in Figure 13a, where there are several groups of animals each allocated to one of a range of foods that are graded in their nutrient balance. The *intake points* of these groups would jointly form an intake array, and the shape of this array would provide a comprehensive description of the rule of compromise. In the specific case modelled in Figure 13a, the rule of compromise is "eat to the point on the nutritional rail where the protein requirement is met, regardless of whether this involves incurring an excess or shortfall of lipid". There are many other possibilities, another of which is shown 13b. A real example from aquaculture will be given in Section 6.5.6 (Fig. 20).

### *Integrating the effects of nutrition into models of Darwinian fitness*

Fish can reduce the costs of eating nutritionally imbalanced foods by avoiding them, by mixing them with complementary foods or by regulating the excesses and deficits of the nutrients they ingest. Another possible response is to deal physiologically with the excesses and deficits that result from eating imbalanced foods, storing or excreting excesses and increasing the efficiency with

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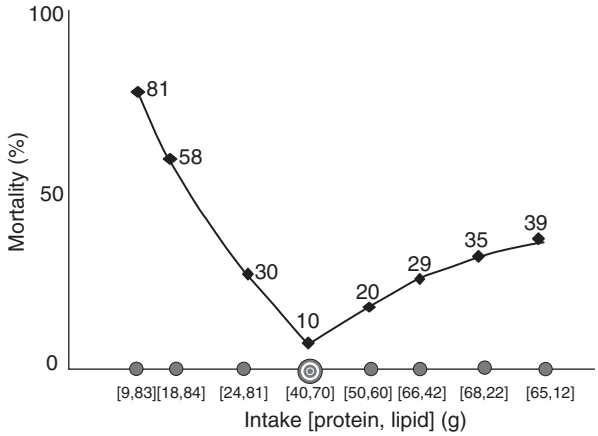


**Figure 6.14.** Graphical representation relating Darwinian fitness to diet by exploration of the relationships between nutrient intake and mortality for a given animal. The percentage mortality is displayed for a range of nutrient intake points for a series of diets, ranging from low protein: high lipid, to high protein: low lipid. A diet of 40 g protein and 70 g lipid maximises survival. Concentric circles represent the intake target.

which limiting nutrients are retained; these are post-ingestive regulatory processes. Such responses can be incorporated into a nutritional model by depicting growth targets, the optimum allocation of different nutrients to growth. Figure 6.13b illustrates this when the behavioural rule of compromise is 'eat to the point that takes you as close as possible to the intake target'. Several important points emerge. First, the distance separating the intake point and growth point indicates the amount of each nutrient that is lost, for example through excretion. Second, similar growth rates can be attained with different patterns of nutrient intake, by altering the amounts of nutrient lost from the body. There is, in other words, target-like regulation of growth in the same way as there is for nutrient intake. However, there are limits (differing between diets) because animals provided with extreme diets do not attain the growth target.

A complete analysis of the nutritional ecology of diet choice requires consideration of the fitness related outcomes of consuming particular diets. One way of doing this, given that fitness measures need to be mapped onto an existing two-dimensional space defined by lipid and protein levels, is to collapse the two intake dimensions into a single dimension that represents combinations of lipid and protein. For example, in Figure 6.14 mortality rate of whitefish (*Coregonus lavaretus*) is plotted against the macronutrient composition of their diet. Mortality rates are lowest for fish feeding on a 40 protein:70 lipid diet.

### 6.4.3 Summary of functional approaches to diet choice

Acquiring an appropriate diet is important for survival, growth and reproduction. Fish display many behavioural and physiological adaptations that ensure that the food they eat provides the nutrients they need. For example, choices among prey items are moulded by the need to acquire energy rapidly, as predicted by optimal foraging theory, while at the same time foraging fish should (and do) attempt to avoid injury, predation and disease. Nutritional ecology highlights the capacities of fish to adjust foraging behaviour so that their diet is balanced with respect to the major macronutrients, thereby ensuring that growth and survival are not severely compromised when only sub-optimal foods are available. The insights gained from both these approaches have important applications in fish culture, because they help to explain how farmed fish respond to the food they are offered.

## 6.5 IMPLICATIONS FOR AQUACULTURE

In nature, dietary choices can have profound effects on growth, survival and reproduction, and the mechanisms that determine what fish choose to eat have been strongly moulded by natural selection. Fish bring these mechanisms with them into culture, where they can cause problems, in terms of production, welfare and environmental impact. Some of these problems arise from the nutritional needs of the fish; others arise from the behavioural responses shown during feeding. Nutritional needs and natural feeding preferences vary both between and within fish species, so problems in culture and solutions to them are specific to the species and, for example, age of the fish concerned. Effective solutions could come as a result of integrating behavioural and nutritional approaches and examples are given to illustrate how knowledge about fish nutrition, behaviour and nutritional ecology can be integrated and applied in the context of fish culture.

### 6.5.1 The kinds of diet that cultured fish receive

Table 6.1 provides information on the kinds of dietary choices available to cultured fish from the 10 spotlight species. Long-established cultured species that are farmed intensively, such as salmonids, are usually provided with feeds formulated to contain sufficient nutrients to meet all their known requirements. Ideally, these are species- and age-specific and change with life history and season (Webster & Lim 2002; Le François *et al*. 2010). In theory, fish cultured in this way have neither the need nor the opportunity to be selective about their food. However, there

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**Table 6.1.** Natural diet and usual mode of feed delivery for cultured fish in the 10 spotlight fish species.

| | Natural diet | Opportunity for choice in culture |
|---|---|---|
| Atlantic salmon | Carnivorous. Initially fry feed on zooplankton, expanding diet with size to include larger aquatic drift & some benthic prey. Sea run fish feed on pelagic crustaceans & small fish. | Formulated diet at all stages. Fry fed meal, followed by crumble then pellets. Little scope for selecting among food types, except by small size differences. |
| Rainbow trout | Carnivorous. Initially feed on small zooplankton, later expanding diet to include small aquatic insects & then terrestrial insects & small fish. Opportunistic. | Formulated diet at all stages. Fry fed a meal diet, followed by crumble then pellets. Little scope for selecting among food types, except by small size differences. |
| European sea bass | Carnivorous. Fish take small crustaceans when young and larger crustaceans, polychaetes, cephalopods & small fish later. | Larvae fed live rotifers then enriched brine shrimp. After larval feeding, formulated diet offers little scope for selecting among food types, except by small size differences. |
| Nile tilapia | Omnivorous. Juveniles mainly carnivorous. Diet expanded later to include detritus & aquatic plants, plankton, small aquatic invertebrates & fish larvae. Opportunistic. | When reared intensively on pelleted feed, little scope for selecting among food types, except by size differences. When reared semi-intensively or extensively, opportunity to select from a range of prey types. |
| Pacific salmon | Carnivorous. Juveniles take small zooplankton & then insects, insect larvae & (in lakes) small fish. Larger salmon eat krill, squid & fish. | Fry fed a meal diet, followed by crumble then pellets. After larval feeding, little scope for selecting among food types, except by size differences. |
| Seahorses | Carnivorous. Feed on zooplankton, including small crustaceans & fish larvae. Opportunistic, feeding mainly on the most abundant prey. | Larvae fed a mixture of live rotifers & brine shrimp. Feed selectively by rotifer species. Adults typically fed a mixture of live and frozen zooplankton. Opportunity for selecting among feed types. Live diet preferred over frozen. |
| Koi carp | Omnivorous. Fry & fingerling need diet of live free-living protozoa, rotifers & larger plankton (cladocerans & copepods) during fry & fingerling stages. Older fish feed opportunistically on a variety of live food & detritus. | Usually fed formulated flakes and pellets, supplemented with mixed animal & vegetable food, offering some opportunity for selecting among several food types. |
| Zebrafish | Carnivorous/Omnivorous. Eat zooplankton, small insects (aquatic & terrestrial) & some plant material. Adults sometimes cannibalistic. | Fry fed live ciliates then rotifers & brine shrimp. Adults fed formulated flakes supplemented by frozen *Tubifex* & chironomids as well as live prey, offering opportunity for selecting among several food types. |
| Guppy | Omnivorous. Eat freshwater algae, insect larvae, small crustaceans & fish eggs & larvae. Adults sometimes cannibalistic. | Fry fed live *Daphnia*, rotifers & brine shrimp. Adults fed formulated flakes supplemented by frozen *Tubifex* & chironomid lavae & live prey, offering opportunity for selecting among several food types. |
| Clownfish | Omnivorous. Feed on algae, small molluscs & crustaceans. May feed on prey captured by anemone. Opportunistic. | Fry fed live rotifers & brine shrimp. Adults fed formulated flakes or pellets supplemented by frozen *Tubifex* & live prey e.g. mysids, offering opportunity for selecting among several food types. |

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**Table 6.2.** Aspects of the natural dietary choices cultured fish and some potential problems for aquaculture caused by these.

| Issue | Implications for production | Implications for welfare | Implications for the environment |
|---|---|---|---|
| Fish have precise, species- & stage-specific nutritional needs | Poor nutrition can lead to lost production through reduced growth, ill health & increased mortality | Inadequate or inappropriate nutrition can compromise the welfare of individual fish, both directly through unmet dietary needs & indirectly, through consequent ill health | Provision of an inappropriate diet means more wasted food<br>Less efficient food processing means more waste released into the environment<br>More disease in farmed fish may mean more disease transfer to wild fish<br>Provision of appropriate feed for piscivorous fish may deplete natural stocks of prey species |
| Fish have species- & stage specific preferences for food presenting particular stimuli | Failure to package food to meet the natural dietary choices of fish may lead to lost production through reduced growth, ill health & increased mortality | Lack of access to favoured food types can compromise the welfare of individual fish, both directly & indirectly, through consequent ill health | Failure to eat formulated feed pellets means more waste released into the environment<br>More disease in farmed fish may mean more disease transfer to wild fish |
| Cannibalism represents a special case of dietary preferences | Cannibalism can cause lost production through mortality, injury & stress and related diseases | Stress, injury & mortality from cannibalistic attacks compromise the welfare of the attacked fish | |



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are a number of reasons why an ideal situation is rarely achieved. In the first place, even for well established species, knowledge about requirements is incomplete. Second, devising optimal feeds for fish of all ages, raised in different environments (with respect to temperature, light regimes and water quality, for example) and that differ in status with respect to maturation and disease may simply not be possible. In addition, the capacity to provide what is known to be ideal may be compromised by problems of the sustainable supply of potential feed ingredients. For all these reasons, cultured fish may well be given food that is imperfect, with the feed formulation representing a compromise involving nutritional requirements, processing and economic and environmental constraints (Webster & Lim 2002; Jobling 2004, 2010; Le François *et al*. 2010).

In spite of the availability of formulated feeds, established, intensively cultured fish sometimes experience circumstances that offer them dietary choice; for example, the presence of natural prey in ponds, pens or sea cages can offer the fish a range of food choices in addition to that provided by the farmer. In extensive fish culture, it is not uncommon for pond-raised fish such as tilapias and cyprinids to be given incomplete feeds, under the expectation that any nutritional deficits will be compensated for and possibly corrected via consumption of natural prey organisms present in the pond. Finally, for many species of fish that are candidates for culture, including new food species, ornamental fish and fish reared for stock enhancement and conservation-based reintroduction, there is insufficient information about their nutritional requirements to enable complete, species-specific feeds to be formulated. Both feeding captive fish on suboptimal foods and the availability of dietary choices for such fish can lead to a number of problems in aquaculture, in terms of production, welfare and environmental impact (Table 6.2).

### 6.5.2 Problems arising from the nutritional needs of cultured fish

Where pond-raised fish are given incomplete feeds and alternative food sources are in short supply, the fish may experience a nutritional inadequacy. When fish are farmed under intensive conditions, the formulation of their feed may not be ideal, leading to a mismatch between the nutritional requirements and food preferences of the fish and the food provided. For example, the composition of diets self-selected by European sea bass (51–57% protein, 27–34% fat and 12–16% carbohydrate; Aranda *et al*. 2000) differs from that of feeds currently used in seabass aquaculture, which contain proportionally more fat and less protein and carbohydrate than the self-selected diet. When a single feed formulation is used throughout most of the production cycle, this may be unbalanced for fish in some physiological states (during rapid growth or maturation, for example) or when they are exposed to certain environmental conditions, such as at extreme temperatures or when water quality deteriorates. As a consequence, there are many examples of deficiency diseases in cultured fish. To give just one example, Atlantic salmon fed on low-phosphorus diets have reduced mineralization of the spine due to reduced calcium:phosphorus ratios in the body and also have higher body fat than do fish given high-phosphorus diets (Helland *et al*. 2005).

The fact that farmed fish require a number of essential (indispensable) amino acids and fatty acids can create difficulties for feed manufacturers when they seek to find suitable feed ingredients (Jobling 2004, 2010). Finding feed ingredients that are appropriate sources of essential amino acids and fatty acids in a time of declining fish stocks can be difficult. Fish-meal is well-balanced with respect to the proportions of amino acids it contains and has been the preferred protein source in feeds for farmed fish, particularly the carnivorous species. In contrast, protein sources of plant origin, such as oilseed meals and cereals, contain lower proportions of protein than fish-meal and plant proteins are also often deficient in some of the indispensable amino acids. Cereal proteins contain insufficient lysine and tryptophan, whereas oilseed meals are deficient in methionine and lysine. As discussed in Section 6.2.2, plants also often contain antinutritional factors of various kinds, and these can have adverse effects on the fish (Sotka *et al*. 2009); for example, some complex carbohydrates, such as non-starch polysaccharides may cause inflammation of the intestine. Marine fish oils are a rich source of the *n*-3 highly unsaturated fatty acids that are an essential dietary component for many species of fish. Plant oils often contain 18C *n*-3 fatty acids, but are devoid of *n*-3 highly unsaturated fatty acids, so can not be used as the main lipid source in the feeds formulated for many cultured species, particularly carnivorous marine fish. In this regard the nutritional requirements of individual species set the standards for feed formulation and inadequate feeds will impact both production and fish welfare (Jobling 2004, 2010).

### 6.5.3 Problems arising from natural dietary choices in cultured fish

In addition to the nutritional composition of the feed, several other important criteria must be taken into account in feeding captive fish. These include the physical dimensions of food items and their sensory properties.

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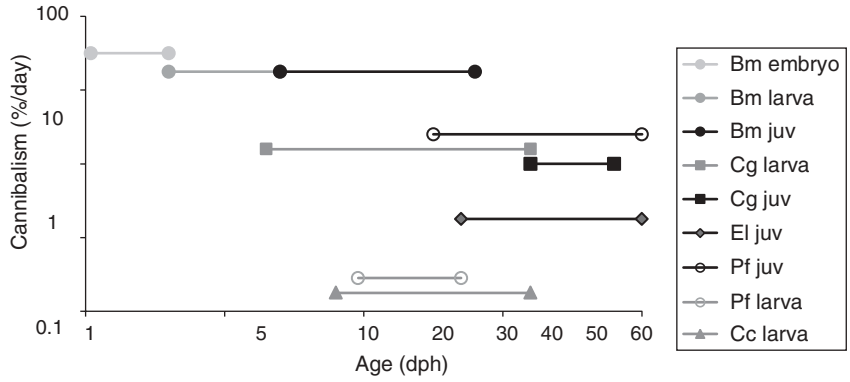


**Figure 6.15.** Ontogenetic incidence of cannibalism in cultured fish. Mean intensity of cannibalism (%/day) over the period during which cannibalism is observed by species and by developmental stage. Pale grey = embryos. Mid grey = larvae. Black = juveniles. *Cyprinus carpio* (Cc. non-predatory); *Perca fluviatilis* (Pf. predatory); *Esox lucius* (El. predatory); *Brycon moorei* (Bm. predatory). Adapted with permission from Baras & Jobling 2002.

### *Physical dimensions*

Food that is well-balanced nutritionally may be packaged in such a way that it fails to meet the natural preferences of the fish, in which case it may be ignored or rejected. For example, one week old common carp have small mouths (<200 µm) and are unable to consume cladocerans, but can handle rotifers (Khadka & Rao 1986). Adult salmon respond strongly to large pellets, but are more likely to reject them than smaller pellets, so if fish are offered pellets of incorrect size, fewer will be eaten (Smith *et al*. 1995). If cultured fish are offered food that they are unable or reluctant to eat, there are likely to be production and welfare problems. For example, non-acceptance of artificial feeds is a large cause of mortality in the rearing of marine fish larvae (Kasumyan & Døving 2003). Further, failure to take account of natural preferences of the fish can lead to high levels feed waste; an estimated 10–15% of the food delivered to intensively-managed tilapia cages is wasted (Beveridge & McAndrew 2000).

### *The special case of chemical cues*

Since chemical cues are particularly important in determining whether or not a fish captures and ingests a food (see above), many chemical additives could influence the palatability of formulated feed. Plant parts such as fruits and seeds are commonly included in fish feeds and these may contain secondary metabolites with feeding deterrent properties; this may also be the case for feedstuffs prepared from animal tissues. Other chemicals that can influence the attractiveness of commercial feeds are added during feed production. Citric acid, which is sometimes added to commercial fish feeds as a preservative, has stimulant properties in some species, acts as an indifferent compound in others; in others is a strong feeding deterrent. When feeds given to farmed fish are prepared from ensiled fish or fish waste they will contain lactic acid, formic acid and/or sulphuric acid, which may affect palatability and acceptance (Jobling 2004). Calcium chloride has a bitter and astringent taste for humans, but appears to be an indifferent taste substance for many fish species. This finding is of interest since treatment with a solution of calcium chloride may be used to increase the efficacy of the alginates that are frequently used as binding agents in moist fish feeds (Jobling 2004).

### *Cannibalism*

As discussed above and in Chapter 5, choosing to feed on smaller conspecifics is a natural aspect of diet selection in many fish and cultured fish are no exception (Baras & Jobling 2002; Kestemont *et al*. 2003; Figure 6.15). Cannibalism often occurs during a short phase early in development, as in the dorada (Baras *et al*. 2000a, b), but in some species cannibalism develops in older fish, with conspecifics remaining favoured prey throughout life. For example, cannibalism among cultured pike (*Esox lucius*) larvae begins when the fish reach a length of approximately 19 mm and is then maintained at a frequency that makes cultivation of this species impractical and uneconomic (Žiliukienė & Žiliukas 2006). Many husbandry practices designed to increase production in intensive aquaculture, such as high stocking densities (Li & Mathias 1982; Baras *et al*. 2000a, b) and temporal variation in food availability (Katavić *et al*. 1989), can increase the potential for cannibalism. Although the cannibals grow rapidly, the occurrence of cannibalism among cultured fish poses both

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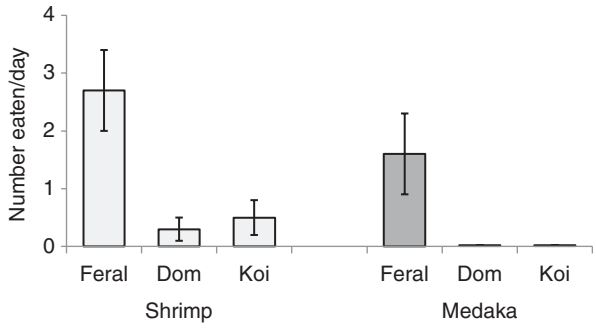


**Figure 6.16.** Domestication and diet choice. Number of two types of free-swimming prey (shrimp and medaka) consumed per day by laboratory-reared common carp from a feral strain, a domesticated strain (dom) and a koi carp strain. Adapted with permission from Matsuzaki *et al.* 2009.

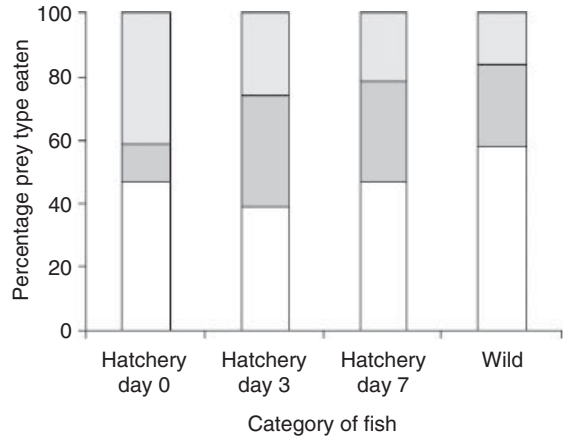


**Figure 6.17.** Diet choice in wild and hatchery-reared juvenile Atlantic salmon. Percentage of amphipods (Light grey), trichopteran larvae (Dark grey) and ephemoptera nymphs (Unshaded) among the prey eaten by wild juvenile Atlantic salmon and by hatchery reared fish of the same stock sampled on different days after exposure to live prey. Adapted with permission from Rierez *et al.* 1998.

production and welfare problems, through injury to and mortality of the victims.

### 6.5.4 Problems arising from domestication and captive rearing

If fish cultured for release into the wild fail to select appropriate food, whether through inherited effects of domestication or through the experience of captive rearing, this will compromise their growth and survival. A number of studies have compared diet choice in cultured and wild fish, although not always in a way that makes it possible to distinguish between genetic effects of domestication selection, maternal effects and experiential effects of the culture environment. When offered a choice of prey types, laboratory-reared carp from a feral strain are more likely to eat larger free-swimming prey than are domesticated fish, which show a preference for zooplankton (Figure 6.16; Matsuzaki *et al*. 2009). Compared to resident wild fish, juvenile salmon released from a hatchery may eat more benthic invertebrates and less drift, as well as ingesting more poor quality food and making more false feeding attempts (Orlov *et al*. 2006). In the first weeks after release into a river, cultured honmasu salmon (*Onchorhynchus rhodurus* × *O. masou*) are more likely than wild fish to have eaten non-food material such as stones and leaves, but by two months after release the diet of the cultured fish converges with that of the wild fish (Munakata *et al*. 2000). Wild caught brown trout (*Salmo trutta*), which have experienced a variety of prey types, are much more likely than hatchery-reared fish originating from the same river to accept novel prey and they handle such prey more efficiently (Sundström & Johnsson 2001).

A number of comparisons of diet choice in fish from the same stock reared either in the wild or in the laboratory have identified effects of captive rearing. During a first encounter with live prey, hatchery-reared juvenile Atlantic salmon show preferences that differ from those of wild counterparts, taking a relatively high proportion of amphipods and a relatively low proportion of trichoptera larvae. Lack of opportunity to learn about wild prey seems to influence prey choice in hatchery-reared fish, but there are rapid changes as the fish gain experience with natural prey (Figure 6.17; Reiriz *et al*. 1998).

### 6.5.5 Solutions to nutritional and behavioural problems relating to diet choice in cultured fish

The examples given in the previous section document a variety of problems experienced in fish culture that arise from the dietary needs of fish, their preferences and abilities to process different types of food. This section describes some possible solutions, informed by both nutritional physiology and behavioural biology.

#### *Improving the attractiveness of feeds*

Given the importance of using readily-available, cheap, and sustainable feed ingredients in feed formulation and the constraints imposed by feed manufacture and processing (Webster & Lim 2002; Jobling 2004, 2010), it is often

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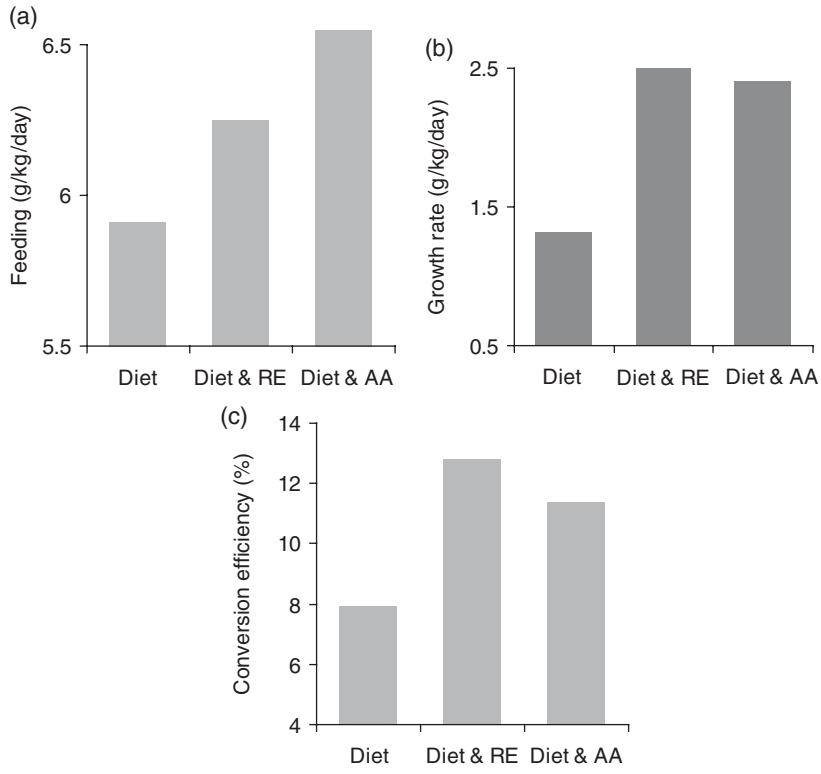


**Figure 6.18.** Effects of feeding stimulants on food intake and growth in glass eels. (a) Food intake (g/kg/day); (b) growth rate (g/kg/day) and (c) energy conversion efficiency (%) in glass eels fed either a commercial crumb diet (Diet), crumb diet with extract of cod roe (RE) or diet with added amino acids (alanine, glycine, histidine and proline. Diet & AA). Adapted from Heinsbroek & Kreuger 1992.

necessary to offer cultured fish food that does not meet their natural preferences. Food that is nutritionally appropriate may acquire negative properties either through the addition of chemicals during manufacture and processing or by the destruction or chemical alteration of some feed components (Halver & Hardy 2002; Jobling 2004, 2010). The negative effects of such substances on ingestion may, at least to some extent, be ameliorated by including in the feed chemicals with stimulant properties (Hertrampf & Piedad-Pascual 2000; Yamada and Yone 1986). For example, feeding of glass eels (*Anguilla anguilla*) on trout-fry crumble can be improved by adding a mixture of amino acids (alanine, glycine, histidine and proline) and this results in improved growth and feed conversion efficiency (Kamstra & Heinsbroek 1991; Heinsbroek & Kreuger 1992; Figure 6.18). Similarly, addition of a mixture of amino acids increases feed intake and growth in European seabass fed on plant-protein based feeds (Dias *et al.* 1997). Muscle extract from the blue mussel (*Mytilus edulis*) is an effective feeding stimulant for gilthead seabream (*Sparus aurata*; Tandler *et al.* 1982) and extracts of squid may act as feeding stimulants for salmonids, gadoids and some other species. In addition, the inclusion in feeds of krill meal or of by-products from processing wastes of crustaceans such as crabs and prawns may result increased ingestion in a range of cultured fish species (Webster & Lim 2002; Jobling 2004).

Knowledge about the non-chemical stimuli that elicit feeding and about optimal prey size can be applied directly to the design of formulated feeds. For example, the optimal pellet size for Arctic charr is about 2% of the fish's length (Linnér and Brännäs 1994), similar to that of several other salmonids. For a range of fish species the optimal feed size appears to be 25–50% of the mouth width (Wañkowski 1979; Wañkowski & Thorpe 1979; Tabachek 1988). It appears, however, that fish can adjust to some deviation from the optimal pellet size without suffering significant negative effects on growth. For example, Atlantic salmon suffer only a slight loss of growth when fed pellets that are

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either larger or smaller than recommended by feed manufacturers (Bailey *et al*. 2003). Other physical attributes of feed pellets that can have an important influence upon whether they are detected, attacked, accepted and ingested by farmed fish are colour (and contrast with the background), movement and the rate at which the pellets sink through the water column, and texture (soft and moist or hard and dry). These feed characteristics and attributes will interact with a wide range of biotic and abiotic factors to determine whether or not a fish will ultimately ingest a particular feed (Houlihan *et al*. 2001; Jobling 2010).

### *Reducing the incidence of cannibalism*

One strategy for reducing levels of cannibalism in fish culture could be to focus on those species or strains in which this behaviour is either not present or has low prevalence. For example, where there is inherited variation in the tendency to develop cannibalism, as in Arctic charr (Amundsen *et al*. 1999) and *Poeciliopsis* species (Thibault 1974), cultured stock might be selected from the less-cannibalistic end of the spectrum. Other approaches for existing culture species are to find ways of preventing the development of cannibalism and to alter the balance of costs and benefits so this diet becomes unprofitable.

In terms of developmental processes, variable age of metamorphosis in summer flounder (*Paralichthys dentatus*) can lead to cannibalism by larger, early metamorphosing fish (Chapter 4) and this problem is currently addressed by frequent grading. Exposing late-larval flounder to reduced salinity (one of the triggers for metamorphosis in this species) serves to reduce variability in developmental stage at settling, which can reduce cannibalistic tendency (Gavlik & Specker 2004). Careful management of the weaning of larval fish onto artificial feeds can also reduce the incidence of cannibalism. For example, weaning age influences the incidence of cannibalism in pike-perch, with the highest rates of cannibalism occurring in fish weaned at 19 (as opposed to 12 and 26) days posthatch (Kestemont *et al*. 2007). In addition, larger fish seem to learn more rapidly to accept dry feed than do their smaller counterparts, on which they subsequently prey (Bódis *et al*. 2007). Further, given that the consumption of large prey may influence jaw development in young fish, including sunfish (Mittelbach *et al*. 1999), perch (Hjelm *et al*. 2001) and Arctic charr (Adams & Huntingford 2004), feeding fish with small food particles during certain critical periods may reduce the development of the jaw structures necessary for cannibalism.

In terms of costs and benefits, one obvious solution to the problem of cannibalism in fish culture is to provide adequate quantities of alternative prey of appropriate size. As predicted by optimal diet theory, reducing the attractiveness and/or relative profitability of conspecifics as prey can lower the incidence of cannibalism in production systems. For example, increasing the availability of alternative sources of high quality food cuts down cannibalism in Nile tilapia fingerlings (Abdel-Tawwab *et al*. 2006) and juvenile African catfish, *Clarias gariepinus* (Al-Hafedh & Ali 2004). Availability of alternative prey is also important for the development and expression of cannibalism in dorada, which show less cannibalism when provided with alternative large prey (larvae of another fish. Baras *et al*. 2000a, b). The profitability of feeding on conspecifics can be reduced by a decrease in size differential among cultured fish, because in this way handling time is increased. For example, reducing size heterogeneity lowers the incidence of cannibalism in sharptoothed catfish (*Clarias gariepinus,* Figure 6.19a; Baras & d'Almeida 2001), in Nile tilapia (Fessehaye *et al*. 2006) and in fat snook (Corrêa & Cerqueira 2007). In red drum, there is a size-dependent threshold disparity at which cannibalism can be prevented (Chang & Liao 2003b; Figure 6.19b) and in dorada provisioning larvae with *Artemia* nauplia for a few hours before the teeth develop makes the size distribution more homogeneous and reduces cannibalism (Baras *et al*. 2000a, b). Reducing the visibility and availability of smaller conspecifics by the provision of cover can also tip the cost-benefit balance away from cannibalism by increasing searching costs. Thus, provision of shelter reduces cannibalism in Nile tilapia fingerlings (Abdel-Tawwab *et al*. 2006), in vundu (Coulibaly *et al*. 2007) and in barramundi (Qin *et al*. 2004).

### *Mitigating the effects of domestication and captive rearing*

The fact that some species-specific prey preferences are relatively hardwired means that cultured fish are potentially able to select an appropriate diet when released into their natural habitat. Nevertheless, they do not always do so and this may contribute to the high mortalities often observed in cultured fish during the first few days after release. Released hatchery-reared red drum may not fare as well as their wild counterparts, and some attempts have been made to alleviate problems relating to low post-release survival. Feeding hatchery-reared red drum on hard feed leads to the fish developing relatively large jaw muscles, which may enable them to feed on a wide range of prey types when they are released in to the wild. In addition to morphological effects, red drum given prior experience of several prey types are quick to make behavioural adjustments to novel food items (Ruehl & DeWitt 2007). Similarly, although the feeding responses of hatchery-reared Atlantic salmon

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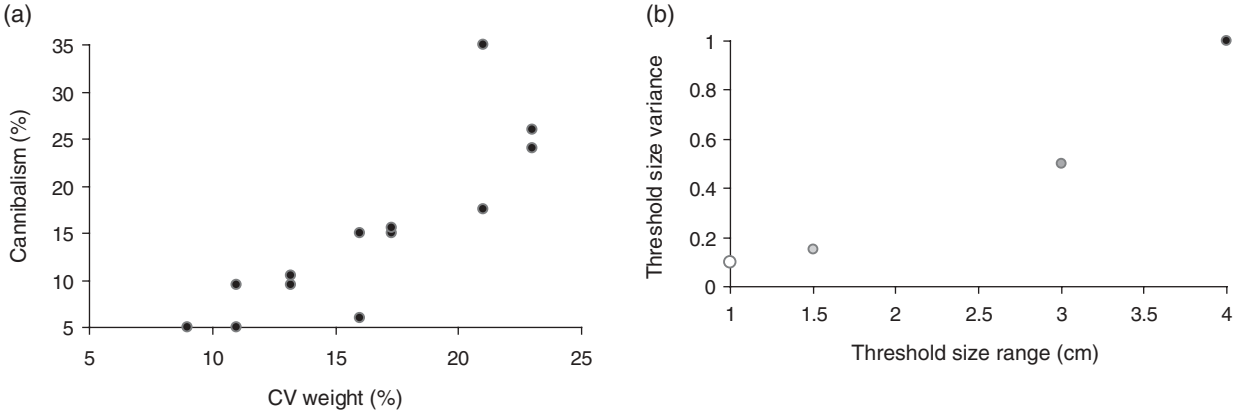


**Figure 6.19.** Reducing cannibalism. (a) Incidence of cannibalism (percentage of fish dying from cannibalism from 3–15 dph) in larval sharptoothed catfish in relation to the coefficient of variation in weight in 3 dph larvae. Adapted from Baras & d'Almeida 2001. (b) Threshold size disparity (cm) and size variance below which cannibalism does not occur in red drum of different ages (dph. White circle=<3 dph. Pale grey circle=3–6 dpg. Dark grey circle=6–10 dpg. Black circle=>10 dph). Adapted from Chang & Liao 2003b.

differ from those of their wild counterparts, the differences in responses to prey disappear following a short period of experience with the new prey type (Reiriz *et al*. 1998). This means that the feeding responses of cultured fish intended for release can be improved by giving them the opportunity to feed on a range of natural prey types, or by giving them the opportunity to observe companions feeding on a range of prey types (Brown & Laland 2001, 2003). For example, hatchery-reared Atlantic salmon given prior experience of a live prey item (chironomid larvae) are quicker to feed when presented with a novel live prey (brine shrimp) than are fish fed on pellets. The greatest improvement in response to novel live prey is obtained by combining an enriched habitat with exposure to live prey; offering this combination could improve post-release survival of the released fish (Brown *et al*. 2003).

### 6.5.6 Using nutritional ecology to solve problems in aquaculture

#### *The interface between nutritional ecology and aquaculture*

As discussed above, nutritional ecology is the study of how animals relate to their environment through nutritional interactions (Parker 2003). An animal's relationship with its nutritional environment involves a complex interplay between many different aspects of the environment (for example, the nature of the available food, temperature regimes and water quality) and of the animal (for example, feeding, digestion, excretion, growth and reproduction; Jobling 2010). For reasons of tractability, studies often concentrate on a small subset of such factors and it is important to use models that take into account several attributes both of the environment and of the animal. The geometrical models derived from nutritional ecology (see above) offer tools for doing this.

In this approach, the animal has defined optimal nutrient needs and is assumed to assess current nutritional state in relation to those needs. The behaviour and physiology of the animal are directed towards reducing differences between current nutritional state and optimal nutritional state. Effective fish culture is dependent on the nutritional elements that fish need, the behavioural mechanisms that they use to acquire these and the physiological systems that they use to process and assimilate the food once eaten. Therefore, the aims of nutritional ecology (to understand and predict the nutritional interactions of animals with their environment) and aquaculture (to manage these interactions for optimal outcomes) have much in common. Identifying the combination of nutrients that promotes growth and at the same time reduces mortality, excreted pollutants and the cost of production is most relevant to fish culture. The relationship between diet, longevity and lifetime reproduction is relevant when fish are reared as broodstock, for supplementation and reintroduction and, in some cases, for the ornamental trade and for scientific purposes.

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***Designing diets for cultured fish***

The use of nutritional ecology as a tool for identifying optimal dietary composition is illustrated by a study conducted on the European whitefish (*Coregonus lavaretus*; Ruohonen *et al*. 2007). There are several complications involved when trying to formulate feeds for animals in intensive production. Not only must the nutritional requirements of the animal be met, but these must also be balanced against a variety of economic, practical and environmental factors. With this in mind, the aims were to define the optimal macronutrient composition of a whitefish diet, to quantify the behavioural responses of fish to diets that departed from this composition and to optimise multiple performance criteria, taking account of economic, environmental and animal welfare concerns.

The problem can be broken down into five stages. The first step involves selecting the nutritional axes for modelling. Second a selection of diets for experimental testing is chosen. Third, intake and growth arrays are plotted and interpreted using the geometrical framework. Fourth, response variables are plotted onto the intake arrays, and finally multi-criterion optimisation is used to combine and weight relevant response variables. In the whitefish study, information about optimal nutrient needs was not collected directly from the fish, but they were estimated from the diets self-selected by other fish species, including salmonids (Sánchez-Vázquez *et al*. 1999; Rubio *et al*. 2003, 2005).

Considering first the selection of nutritional axes, the major macronutrients for carnivorous fish are protein and fat, with carbohydrate playing a lesser role, but for economic and manufacturing reasons it is desirable to include a proportion of carbohydrate in aquafeeds. The main feed ingredients used in the whitefish diets were fish meal, fish oil, corn starch and wheat meal (Vielma *et al*. 2003). Provided that dietary carbohydrate levels were below ~300 g $kg^{-1}$ (beyond which there were deleterious effects) there were no measurable effects (positive or negative) other than those relating to energy content; carbohydrate could therefore be combined with fat into a single non-protein energy dimension (Ruohonen *et al*. 2007). Having made this selection of nutritional axes, 15 diets, combining 12 ratios of protein to fat and carbohydrate, were selected for testing (Ruohonen & Kettunen 2004).

Figure 6.20 depicts the nutrient intake and growth arrays (step 3). Relative to the identified intake target (Sánchez-Vázquez *et al*. 1999; Rubio *et al*. 2003, 2005), it was found that, when confined to low protein diets, whitefish over-consumed non-protein energy in order to gain sufficient protein. On high protein diets, they over-consumed protein to gain non-protein energy, but to a much lesser extent. Thus, protein growth was more tightly regulated than lipid growth (reflected in the vertical elongation of the growth array in Figure 6.20). This meant that the flesh of the fish on low protein diets became increasingly fatty as they over-ate non-protein energy, whereas diets high in protein resulted in low levels of body fat as a result of the fish failing to substantially over-eat the high-protein diets.

The next step was to superimpose response variables onto the intake array, transformed into a straight line representing different combinations of protein and non-protein energy (Figure 6.21). Wet weight growth was consistent across the intake array, but growth comprised differing amounts of protein and fat, with flesh protein increasing as dietary protein increased. Feed efficiency and energy retention efficiency (the ratio of growth to feed consumption in g wet weight and kJ, respectively) showed little change across the intake array, but nitrogen waste (the difference between nitrogen eaten and nitrogen retained) rose with increasing dietary protein. Further, the commonly-used stress and welfare indicators, plasma glucose, plasma cortisol and liver glycogen fell as dietary protein increased.

The final step in the study was to optimise diet composition on the basis of multiple criteria, or in other words to choose a set of performance responses on which diet optimisation might be based and to normalise and scale these relative to one another. This involved making judgements as to which variables were relevant, what each was 'worth' and, for each variable, whether high or low values were more desirable. Fish and fish feed have market prices and there is usually a price premium for fish with high quality flesh. Environmental and welfare costs are harder to assess, but could be the target for taxes and licensing restrictions. Consequently, four scenarios were chosen for illustration, prioritising estimated production costs, flesh quality, environmental impact and animal welfare (Figure 6.22). The decision functions had different shapes, with maxima falling at different points along the diet composition axis. Were the fish to have chosen their own diet (grey vertical zones in Figure 6.22), they would have performed reasonably well under all four criteria, almost maximising production and welfare, but would have scored less well on flesh quality and environmental goals.

Nutritional ecology places the interactions of the animal with foods at the centre of diet optimisation decisions. Taking account of the pre- and post-ingestive regulatory responses of the animal can simplify problems related to identifying optimal diet formulations, and multi-criterion optimisation might be achieved by selecting and weighting responses of interest and then summing these to develop decision

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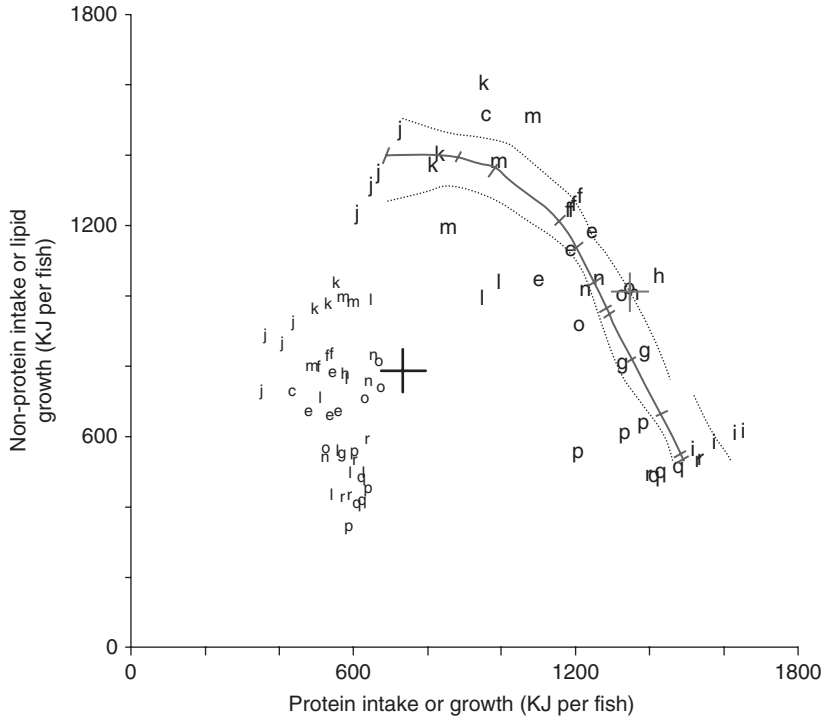


**Figure 6.20.** Nutrient intake and growth of European whitefish fed one of 15 experimental diets varying in macronutrient composition, represented in a nutrient space consisting of protein and non-protein energy. Diets are labelled with letters that correspond to formulations in Table 1 of Ruohonen *et al.* (2007). Larger sized letters denote intake and smaller sizes denote growth on the different diets, with duplicate letter representing intake and growth for replicate tanks of fish. A curve (intake array) has been fitted through the array of intake points, estimated using a cubic spline regression with 95% confidence limits (dashed lines). Tick marks along this line indicate the intersection points of the 15 diet treatments. The crosses indicate intake (grey) and growth (black) on diets that are estimated to be optimal for whitefish from self-selection data for species similar to the whitefish. Ratio of protein to lipid by diet: E = 2.96; G = 6.25; H = 2.65; I = 5.95; J = 1.13; K = 1.24; L = 2.62; M = 1.39; N = 2.90; P = 11.98.

functions. The results indicate that whitefish regulate protein growth more tightly than they regulate lipid growth, and that nitrogen waste increases and commonly used stress indicators fall as the percentage dietary protein increases. Additionally, if the fish had been allowed to choose their own diet they would have almost maximised human-defined production and welfare goals, while giving lower priority to goals relating to flesh quality and environmental protection.

## 6.6 SYNOPSIS

Obtaining an adequate, balanced diet is vital for wild fish and over evolutionary time natural selection has shaped their behavioural and physiological responses to the food they encounter and eat. As a consequence, wild fish have a remarkable ability to select from the wide range of food types available to them. They are able to compose a diet that is appropriate for their species, life history stage and gender; in other words, like other animals, fish are endowed with a high level of "nutritional wisdom". This is effected through differential responses to potential food items on the basis of cues detected from a distance, which may be visual, chemical, mechanosensory or electrical, and to contact cues detected once food has been acquired. Mechanosensory and chemical cues are of particular importance once food has been taken into the mouth, since they give fish direct information about the nature and quality of potential food. Some responses to food are hard-wired, in the sense that they do not depend on previous experience of particular prey types. Others are flexible and based on learned associations between particular kinds of food and the nutritional

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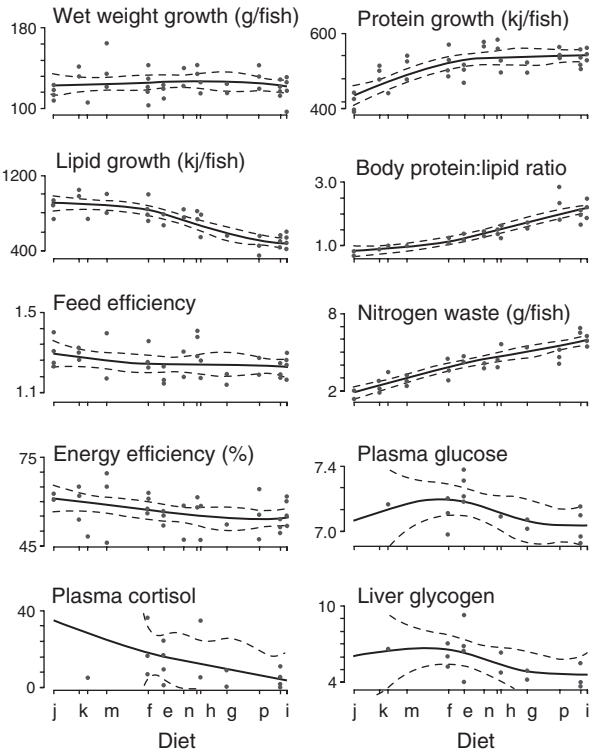


**Figure 6.21.** A selection of response variables superimposed onto the intake array in Figure 6.20 (from which the bi-coordinate intake points along the *x*-axes may be read at the tick marks along the fitted curve), laid out as flat strips. Dots denote the original observations and the line is the best-fitting function together with its 95% confidence limits (dashed lines), estimated using cubic spline regression.

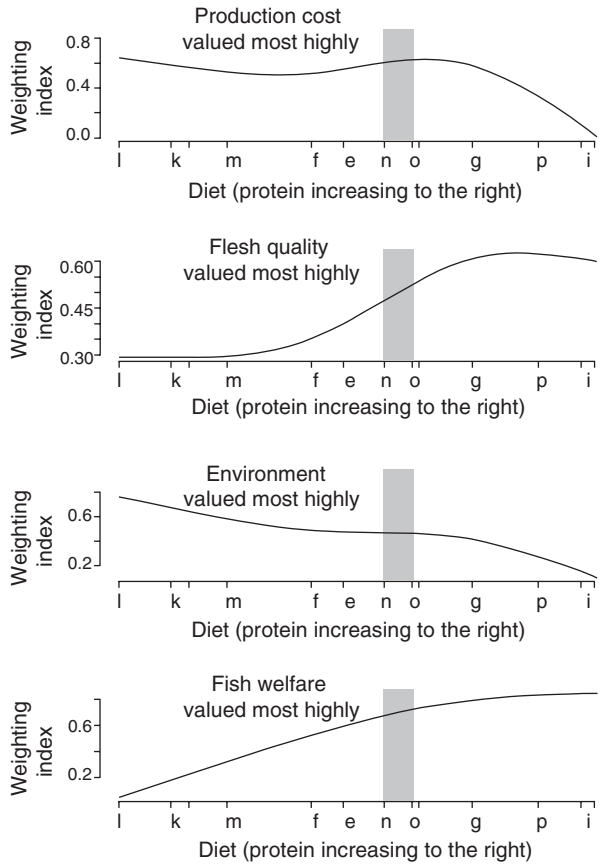


**Figure 6.22.** Decision functions for four diet optimisation goals with different emphasis. The functions on the *y*-axes (labelled 'weighting index') are the sums of predicted wet weight growth, feed efficiency, body protein:lipid ratio, nitrogen waste and blood cortisol (from Figure 6.21). These responses have first been normalised and then weighted with respect to each other according to one of four optimisation goals (see text).

consequences of eating such food. Thus dietary choice in fishes is sufficiently fixed to direct them towards the natural food type for their species, but sufficiently flexible to allow them to exploit the foods that are available to them in different locations and at different times.

The selective responses that in wild fish lead to effective diet choice can cause problems in aquaculture, for example restricting the range of ingredients that can be used for feed production and the forms in which feeds can be presented to fish. However, understanding the biology that underlies diet choice in fish can also suggest solutions. By way of example, feeding stimulants can be used to encourage fish to take otherwise unpalatable feed, while reducing the benefits and increasing the costs of feeding on conspecifics can be used to lower the incidence of cannibalism in several species. In addition, an understanding of the causes and consequences of diet choice in fish offers insights into and can be used to make predictions about a number of aspects of feeding biology in cultured fish. For example, the nutritional ecology models applied to whitefish predict that, as far as efficient growth and welfare are concerned, the interests of fish farmers and farmed fish are more or less the same. On the other hand, as far as flesh quality and environmental protection are concerned, farmers and regulators may be pulling in one direction, but the fish are pulling in another. Such insights could have application in the development of cost-effective, sustainable, environmentally sound fish culture.

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# 7
# Appetite and Feed Intake

*Malcolm Jobling, Anders Alanärä, Chris Noble, Javier Sánchez-Vázquez, Sunil Kadri and Felicity Huntingford*

**Abstract:** This chapter first describes changes in appetite that occur over different time scales in wild fish and the physiological mechanisms that generate these changes. It then gives an account of how food intake and appetite change as young fish develop and mature and the effects of genetic variation and differential experience on these processes. The costs of sustaining a high rate of food intake are then described, as is the way in which these are balanced against the obvious benefits of gaining a good supply of nutrients. The benefits gained by regular appetite cycles are also considered. The implications of natural appetite patterns for fish culture are then discussed, including problems arising from underfeeding and overfeeding and those resulting from failure to match feed delivery to current appetite. Underfeeding causes slow, uneven growth and high levels of aggression, as well as stress and mortality, while overfeeding may result in inefficient production and adverse environmental impact. Potential solutions to such problems are discussed, including the use of on-demand feeding systems that match delivery to appetite. The effects of domestication and captive rearing on feed intake are then considered, together with possible ways of mitigating such effects in fish that are cultured for release.

**Keywords:** adiposity signals; feed management; feeding rhythms; hypothalamus; insulin; leptin; nutritional regulation; overfeeding; stomach fullness; underfeeding.

## 7.1 INTRODUCTION

The previous two chapters have shown how fish gather food and how they select a balanced diet by choosing from an array of food items. Having located, or been presented with, suitable food, fish will not always eat it, because their motivation to feed is subject to change. Changes occur over a range of time scales, from minute to minute adjustments made during the course of ingesting a meal to the large changes in feed intake that may be associated with life history events such as maturation and the preparation for spawning. Changes in the propensity to feed may be irregular, for example occurring as the fish become sated during feeding bouts or as their nutrient reserves are depleted during a fast (Figure 7.1). Feeding is also modulated in relation to environmental conditions, and changes in appetite may also be rhythmic, adapting to environmental cycles with tidal, daily, lunar or annual periods (Jobling 1994; Houlihan *et al.* 2001; Lopez-Olmeda & Sánchez-Vázquez 2010).

Feed may represent up to 60% of the economic costs of farming fish for human consumption (Le François *et al.* 2010) and feed costs can also be significant when fish are

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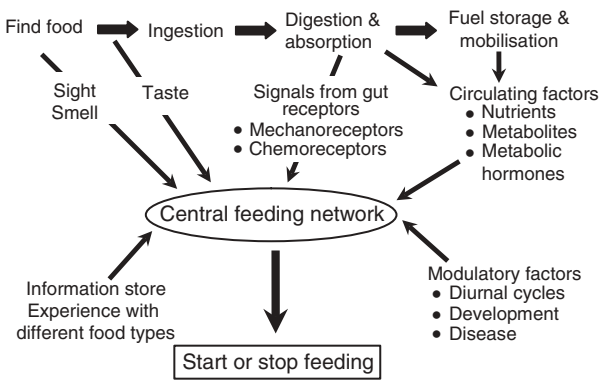


**Figure 7.1.** Schematic diagram of the processes that control food intake in fish.

farmed for other purposes. Consequently, knowledge about feeding patterns can help to promote efficient production in fish culture. Fish are an extremely diverse group, and their feeding patterns are varied, meaning that there is no single answer to the question of when and how much cultured fish should be fed. It is difficult to monitor feeding of wild fish, so much of what is known about feed intake and feeding patterns has been gained from studying fish held in captivity, in which feeding behaviour and feed intake can be monitored using a variety of techniques (Houlihan *et al*. 2001; Chapter 3).

### 7.1.1 Irregular changes in appetite

***Most fish eat distinct meals***

Fish do not feed continuously, but in distinct bouts or meals, although species that consume poor-quality food may need to forage for long periods to obtain the nutrients they need. In species that eat distinct meals, food intake generally increases in relation to the time elapsed since the fish last fed, as the processes of digestion and absorption take place (Figure 7.1). For example, over a time-span of a few hours to a day or two, feed intake almost invariably increases with time since the last meal in salmonids and other carnivorous species. Food intake is also influenced by longer periods of deprivation, due to depletion of nutrient reserves. For example, following extended periods of food deprivation fish may become hyperphagic, and maintain a high level of feeding until their nutrient reserves are restored (Jobling 1994, 2010a; Jobling & Johansen 1999). Thus, there may be considerable variation in both the timing and size of meals that a fish consumes, depending on size of stomach and rate of digestion of the food, among other factors. As such, feeding is extremely flexible, enabling meal patterns to be adapted to a wide array of environmental conditions and food types as well as to current metabolic demands (Reebs 2002; Rubio *et al*. 2005; Warburton 2003; Stubbs & Tolkamp 2006).

Changes in the morphology of the gastrointestinal (GI) tract may be induced by feeding experience in individual fish (Kapoor *et al*. 1975; Buddington *et al*. 1997). A commonly observed response to artificially imposed reductions in feeding frequency, in other words to a set number of 'meals' given each day, is an increase in meal size. The response is probably linked to an increase in gastric capacity and hypertrophy of gut tissues. For example, plaice (*Pleuronectes platessa*) fed every other day develop larger and more bag-like stomachs than do those fed more frequently, and infrequently fed fish also greatly increase their meal sizes (Jobling 1982). Hypertrophy of the GI tract may commence shortly after the imposition of such feeding regimes, but some days or weeks may be required before the changes in the relative size of the GI tract are complete. GI hypertrophy may also take place when fish are exposed to time-restricted feeding regimes and may also be reflected in the feeding response. Feeding activity and feed intake of fish fed according to time-restricted regimes increase with the passage of time and gradually approach those of conspecifics allowed continuous access to food (Alanärä 1992a; Boujard *et al*. 1996; Koskela *et al*. 1997).

In addition, feeding fish on high-roughage or nutrient-dilute diets tends to induce hypertrophy of the stomach and enlargement of the intestine. Such enlargement of the GI tract following feeding on foods of low nutrient density (Hilton *et al*. 1983; Ruohonen & Grove 1996; Grove *et al*. 2001) may represent one facet of the suite of adaptations that enable fish to maintain rates of nutrient and energy intake when provided with diluted feeds (Rozin & Mayer 1961; Grove *et al*. 1978, 2001; Vivas *et al*. 2006). Under such circumstances, varying the quantity consumed is the only mechanism available for controlling nutrient intake. This is a limitation compared to the natural situation where there may be a wide range of available prey (Galef 1996), and also differs from conditions where fish are given access to (and enabled to select from) feeds that differ in nutrient concentrations (Rubio *et al*. 2003, 2005; Vivas *et al*. 2006). In the short term, the regulation of feeding on diluted feeds is expected to be linked to gastric capacity and the filling of the stomach or intestinal-bulb, in relation to stomach emptying and to transfer of ingested food into the intestine. These factors are also expected to have a major influence upon feeding frequency in fish that are given unlimited access to feeds that differ in nutrient concentration; meal frequency increases when diluted feeds are provided.

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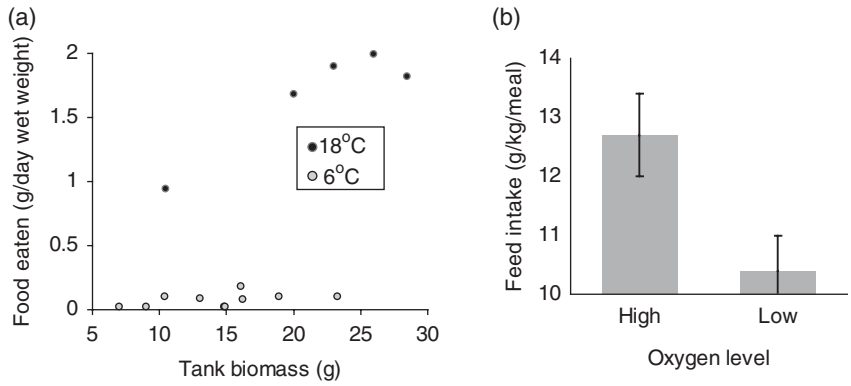


**Figure 7.2.** Effects of immediate environmental conditions of feeding rate in fish. (a) Food intake (g/day wet weight) in relation to tank biomass (g) at temperatures of 18°C and 6°C in juvenile seabass. Adapted from Russell *et al*. 1996. (b) Mean (±95% confidence intervals) morning feed intake (g/kg/meal) in Nile tilapia held at high (5.5 mg/l) and low (3 mg/l) dissolved oxygen. Adapted from Tran-Duy *et al*. 2008.

As a final example, the replacement of dry feeds by wet or moist feeds may induce stomach hypertrophy, meal size adaptations to feeds that differ in moisture content occurring gradually over time (Grove *et al*. 2001). When either a wet or a dry feed is given to turbot (*Scophthalmus maximus*) previously adapted to a dry feed, the amount (mass and volume) of feed consumed in a single daily meal is both greater and increases over time for the wet feed. Further, the amount of dry feed consumed is apparently regulated to enable the stomach to accommodate the expansion that occurs as the feed is moistened early in the digestive process; in other words, feeding is terminated before the stomach is filled to full capacity with the dry feed (Grove *et al*. 2001).

***Environmental modulation of feeding***

Even though a fish may be motivated to feed, it may not do so or it may eat little, because appetite is modulated by a variety of environmental conditions (Jobling 1994; Houlihan *et al*. 2001). For example, temperature has a strong influence on feed intake in ectotherms such as fish, due both to changes in rates of digestion and to changes in energetic requirements. In European sea bass (*Dicentrarchus labrax*) daily food consumption is higher at 18°C than at 6°C across a range of sizes (Figure 7.2a; Russell *et al*. 1996). Feed intake is reduced in fish exposed to hypoxic (low oxygen) conditions (Figure 7.2b; Tran-Duy *et al*. 2008), to high concentrations of dissolved ammonia (Ortega *et al*. 2005) and to potential risk of predation (Oswald & Robison 2008; Chapter 8). Since many of the conditions that reduce feeding in fish commonly occur in intensive fish culture, such effects are important for effective aquaculture (Le François *et al*. 2010).

### 7.1.2 Regular changes in appetite: feeding rhythms

A rhythm can be defined as a sequence of events that is repeated over time (Boujard & Leatherland 1992). Both plants and animals display rhythms on a variety of time scales. So-called ultradian rhythm (tidal rhythms, for example) have peaks that occur more than once every 24 h, daily or circadian rhythms have a cycle of around 24 h and infradian rhythms (lunar and circa-annual rhythms, for example) have less than one cycle per 24 h (Aschoff 1981). Feeding rhythms on all these time scales have been described in fish, including those that are cultured. For example, like many species of fish that inhabit shallow coastal waters, common goby (*Pomatoschistus microps*) feeding on estuarine marshes display tidal rhythms of activity, having more food in their stomachs, and hence presumably having fed more intensively, at high tide (Hampel & Cattrijsse 2004). Knowing about feeding rhythms is important in predicting when fish are most likely to feed (Houlihan *et al*. 2001; Lopez-Olmeda & Sánchez-Vázquez 2010).

***Circadian feeding rhythms***

Daily (or diel) rhythmicity is common in fish (Thorpe 1978; Ali 1992; Madrid *et al*. 2001) and interacts with deprivation to determine exactly how much a fish eats and when. For example, Senegalese sole (*Solea senegalensis*) feed nocturnally (Boluda Navarro *et al*. 2009), as do tench (*Tinca tinca*; Herrero *et al*. 2005) and European seabass (under certain conditions. Figure 7.3a; Madrid *et al*. 2001). In contrast, yellow tail (*Seriola quinqueradiata*) display rhythmic patterns of feeding in phase with the light-dark cycle (Figure 7.3b); in this case, there are peaks of feeding at dawn and dusk (Kadri *et al*. 1998). After

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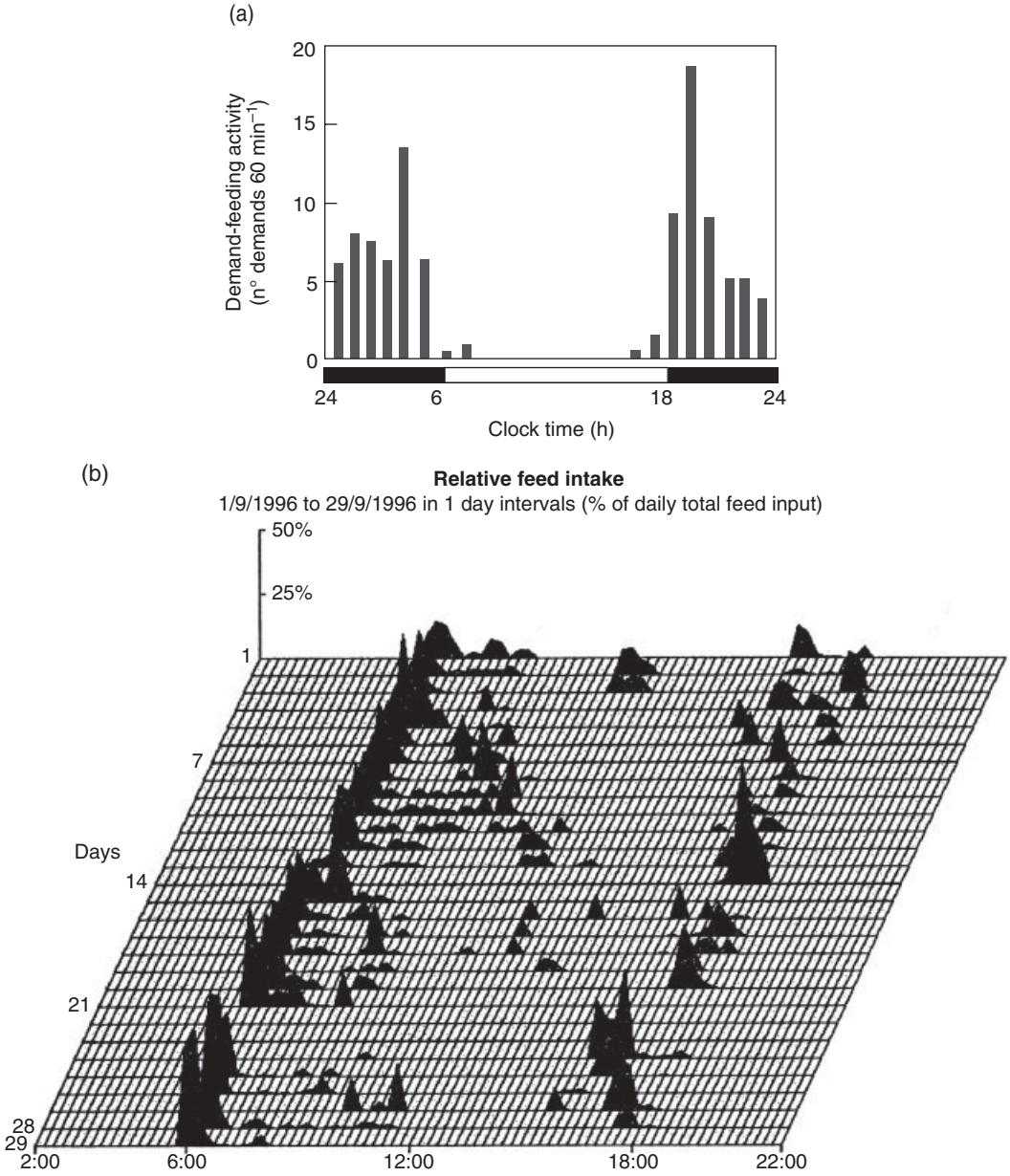


**Figure 7.3.** Appetite rhythms in fish. (a) Demand feeding activity (number of demands per h) in relation to time of day in seabass feeding in nocturnal mode. Horizontal solid bar: dark phase. Horizontal open bar: light phase. Adapted from Madrid *et al.* 2001. (b) Relative intake (% of total daily ration taken in each 15 min period) in relation to time of day in demand-fed yellow tail in production cages in late summer. Reproduced from *Suisan Zoshoku* (*Aquaculture Science*), courtesy of the Japanese Society for Aquaculture Research.

2 days of fasting, European sea bass increase feed intake without changing their daily feeding profile, but after 9 days of fasting the period during which the fish feed is extended (Rubio *et al*. 2010).

Despite the widespread occurrence of daily feeding rhythms, many species exhibit considerable flexibility in feeding times, depending on both abiotic factors such as the light-dark cycle and temperature and biotic factors

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such as food availability, predation risk and competition. For example, rainbow trout (*Oncorhynchus mykiss*) given unlimited access to food often show two clear peaks in activity during the day, one in the morning, associated with first light and one (often a more prominent peak) in the evening (Cuenca & de la Higuera 1994; Bolliet *et al*. 2001; Bailey & Alanärä 2006a), but they may also display only one major peak at first light (Alanärä & Brännäs 1997), or may feed during the night (Grove *et al*. 1978). European sea bass feed either diurnally or nocturnally (Sánchez-Vázquez *et al*. 1995) and individuals may change their phasing under constant laboratory conditions, without apparent changes in their environment. Variable daily feeding rhythms also appear in ornamental fishes, such as goldfish, which mostly feed during daytime, but may sometimes change to night-time feeding (Sánchez-Vázquez *et al*. 1996).

Variation in the daily pattern of feeding may be related to feed delivery rate, which influences whether fish can feed to satiation during a morning meal, and to temperature, which affects feeding activity, rates of food digestion and evacuation, and metabolic requirements. In addition, individual variation in feeding activity may reflect the position of a fish within a dominance hierarchy (Chapter 9). For example, under laboratory conditions, dominant brown trout (*Salmo trutta*) eat most of their food between dusk and midnight; when the temperature is raised, dominant fish increase the duration of their foraging, reducing the time available for subordinates to feed (Alanärä *et al*. 2001a). Similarly, in the giant kokopu (*Galaxias argenteus*), dominant fish feed primarily at night, whereas subordinate fish forage during the day; when food is limited dominant fish increase their activity and forage diurnally at the expense of subordinates (Hansen & Closs 2005).

#### *Infradian feeding rhythms*

Infradian feeding rhythms primarily refer to changes in food intake that are related to lunar and annual cycles. Changes in appetite according to the phases of the moon have been reported for rainbow trout and coho salmon (*Oncorhynchus kisutch*), with food intake peaking a few days before the new and the full moon (Leatherland *et al*. 1992). In nocturnal fish species, the influence of the lunar phase may be greater than in diurnal species, as lighting conditions may directly affect foraging behaviour and the risk of predation. In their natural environment, soleids, typically nocturnal feeders, have been reported to exhibit a lunar pattern of activity (and possibly feeding), with fish apparently less active at new moon than at full and quarter moon (Vinagre *et al*. 2006; Oliveira *et al*. 2009). Lunar and tidal rhythms can interact; for example, common goby (*Pomatoschistus microps*) foraging in a tidal marsh tend to feed by day during the spring tide, but feed by night at neap tide (Figure 7.4a; Hampel & Cattrijsse 2004). Fish living at high latitudes experience major seasonal changes in both feed requirements and availability and display marked seasonal changes in feeding activity. Seasonal effects on feed intake are well documented for salmonid species in both the wild and in culture. For example, anadromous Arctic charr (*Salvelinus alpinus*) feed intensely and grow rapidly during a short period of summer residence in the sea, returning to fresh water to spend the winter under ice, during which time they usually do not feed (Jørgensen *et al*. 1997). Seasonal changes in appetite have also been described for other species, such as yellowtail (*Seriola lalandi*), which show peaks of feeding activity in early summer and autumn (Figure 7.4b; Kohbara *et al*. 2003).

#### *Interactions between daily and annual feeding rhythms*

Annual cycles can affect not just how much fish eat, but also when during the day they feed. For example, in temperate regions some Atlantic salmon may display diurnal activity during the summer when water temperatures are high, but are predominantly nocturnal during the winter months when temperatures are low (Fraser *et al*. 1993, 1995; Fraser & Metcalfe 1997). In winter, rainbow trout often exhibit a peak in feeding activity around dawn, followed by a subsidiary peak 8 h later (Adron *et al*. 1973; Landless 1976), but may also show a completely nocturnal feeding pattern (Grove *et al*. 1978). The Arctic charr is generally nocturnal during the winter, but diurnal or crepuscular at other times of the year (Linnér *et al*. 1990) and this may also be the case in brown trout (*Salmo trutta*; Eriksson 1973). Phase inversions in feeding from diurnal in summer to nocturnal in winter are also known to occur in European sea bass (Sánchez-Vázquez *et al*. 1998).

### 7.1.3 Feeding in relation to life history events

Changes in appetite are often associated with life history events. For example, at the end of their first summer of life, a proportion of juvenile Atlantic salmon (those that have been growing slowly) show a gradual decline in appetite as winter approaches. These fish remain in a state of anorexia during winter, hidden in shelters under the gravel, until the following spring when they recommence feeding. Meanwhile faster-growing conspecifics continue feeding and growing during the winter and migrate to sea in the spring (Metcalfe *et al*. 1988). Appetite and migration seem to be linked in glass eels (*Anguilla anguilla*); juvenile fish collected in estuaries and classified as having a strong

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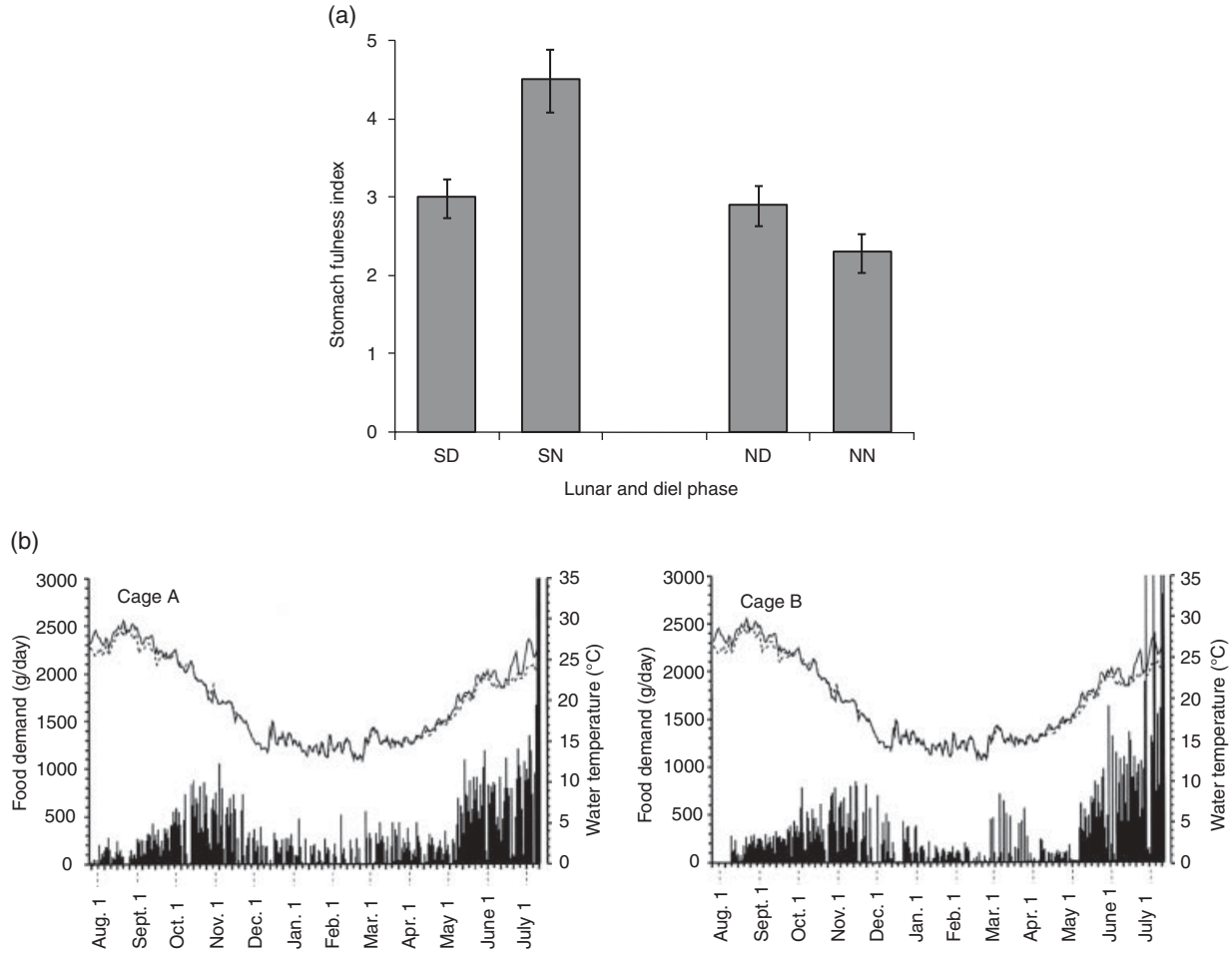


**Figure 7.4.** Infradian appetite rhythms. (a) Mean (±SE) stomach fullness index in gobies by day and night during the spring and neap phases of the tidal cycle. SD: spring tide, daytime. SN: spring tide nightime. ND: neap tide daytime. NN: neap tide nightime. Adapted from Hamel & Cattrijsse 2004. (b) Food demanded per day in one group of yellow tail over one annual cycle, with daily average water temperature at 0.5 m (solid line) and 4 m (dotted line). Reproduced with permission from Kohbara *et al.* 2003.

tendency to migrate, on the basis of moving out of shelter into a current at dusk, have a higher feeding rate and gain more weight than do individuals with a low migration tendency, which stay in shelter (Bureau du Colombier *et al*. 2008). Gonadal maturation and reproduction are often accompanied by changes in appetite, the precise timing depending on species. For example, maturing adult Atlantic salmon held in sea cages cease feeding in late spring and early summer, several months prior to spawning (Kadri *et al*. 1995, 1996) and maturing Arctic charr reduce their feed intake during late summer and virtually cease feeding a few weeks prior to spawning (Tveiten *et al*. 1996). By contrast, some fish species cultured in the Mediterranean, such as the European sea bass and sea bream (*Sparus aurata*), mature during late-winter and spring. They continue to feed whilst their gonads are maturing, even though weight gain is reduced, possibly as a result of a sex-steroid induced appetite reduction (Leal *et al*. 2009).

### 7.1.4 Feeding by diseased fish

Infection, disease and infestation by parasites are commonly associated with changes in appetite in fish. For example, 20 days after exposure to infectious pancreatic necrosis, a viral disease, Atlantic salmon show reduced

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appetite and growth (Damsgård *et al*. 1998). Bacterial diseases can also cause reduced appetite, for example in Nile tilapia (*Oreochromis niloticus*) suffering from a piscirickettsiosis-like condition (Mauel *et al*. 2007) and in Atlantic salmon suffering from vibriosis (Damsgård *et al*. 2004). Rainbow trout may cease feeding about 3 weeks after infection with the haemoflagellate parasite *Cryptobia salmositica* (Chin *et al*. 2004). Ectoparasitic infections can also influence appetite; for example, heavy infestation with the sea louse (*Caligus orientalis*) causes appetite reduction in rainbow trout (Nagasawa 2004).

## 7.2 MECHANISMS

### 7.2.1 Mechanisms underlying meal-based changes in appetite

#### *Nutritional regulation*

Irregular, short-term changes in food intake are the result of interplay between physiological and behavioural mechanisms (Figure 7.1) that allow fish to regulate their nutrient reserves in the longer-term (Houlihan *et al*. 2001; Kulczykowska & Sánchez-Vázquez 2010). Animals face the challenge of acquiring sufficient nutrients to support body maintenance, growth and reproduction, usually in the face of food resources that are heterogeneous mixtures of essential and non-essential nutrients (Chapter 6). Differential ingestion is the key to maintaining balanced nutrient intake under these conditions and this necessitates internal control over the acquisition, incorporation and release of nutrients and their metabolites. Regulation of nutrient intake in this way requires an animal to monitor its nutritional status, in terms of both stored reserves and recently ingested food, to assess the nutrient composition of the food available to them and to activate behavioural mechanisms for ingesting the correct types of food in the amounts required to redress any nutrient deficits (Figure 7.5).

As far as matching food intake to nutrient requirements is concerned, this may be based on visual and chemical (olfactory and gustatory) cues arising from the food, which give some information about its chemical composition (Galef 1996; Chapter 6). There is also a contribution from post-ingestive processes (Gietzen & Rogers 2006; He *et al*. 2006; Nelson & Sheridan 2006; Stubbs & Tolkamp 2006; Dockray 2010), as well as interactions between the pre- and post-ingestive sensory systems. For example, taste aversion involves the avoidance of a food with a taste that has previously been associated with noxious post-ingestive effects or unpleasant visceral stimuli; in other words, a gustatory stimulus previously associated with gastrointestinal (GI) discomfort is avoided (see Chapter 6).

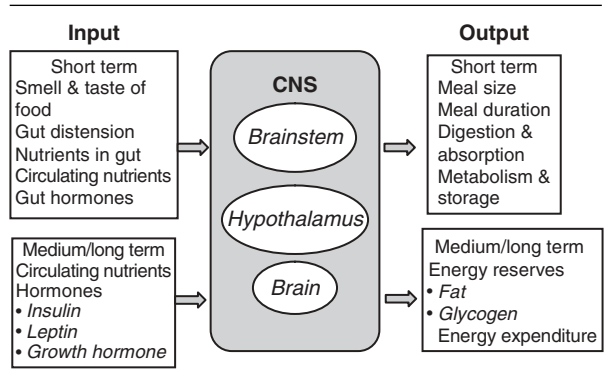


**Figure 7.5.** Schematic representation of signals from the periphery (Input) to the central nervous system (CNS) that influence feed intake and energy balance (Output) on different time scales.

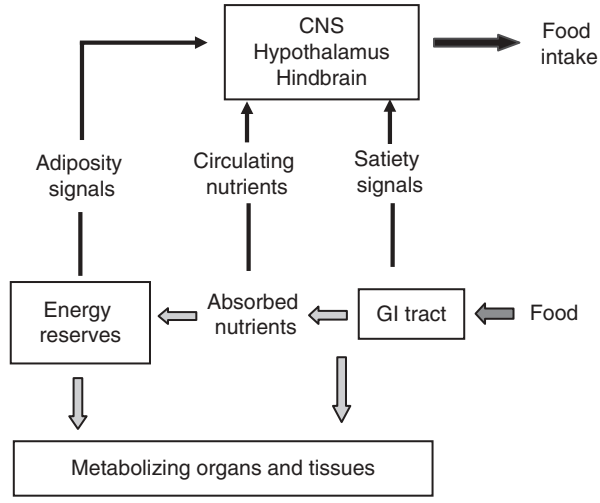


**Figure 7.6.** Schematic diagram of the sources of hunger and satiety signals and the routes through which these influence food intake.

A variety of cues can indicate whether a fish has been fasting, including an empty GI tract, reduced concentrations of absorbed nutrients in the blood and low energy reserves; all of these can act as hunger signals that promote feeding. Another set of cues indicates that a meal has been consumed and is being processed, including the presence of food in the GI tract, high concentrations of circulating blood nutrients and adequate energy stores; these can act as satiety signals that suppress feeding. Such hunger and satiety cues act on various systems within the central nervous system (CNS), activating and inactivating species-typical feeding responses (Figure 7.6; Dockray 2010).

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**Box 7.1** Some of the hormones and neurotransmitters implicated in the control of feeding and energy balance

**Cholecystokinin (CCK):** A gastrointestinal peptide released from cells in the duodenal mucosa in response to the presence of components of gastric chyme. Also present in neurons in the peripheral and central nervous system. CCK inhibits gastric emptying and the secretion of gastric acid, stimulates gall bladder contraction and pancreatic enzyme secretion and is implicated in the central regulation of food intake, acting as a 'satiety hormone'.

**Corticotropin-releasing factor/hormone (CRF/CRH):** A peptide synthesised in the hypothalamus with neuromodulatory actions that acts on the anterior pituitary leading to release of adrenocorticotropic hormone. Implicated in the regulation of energy balance via suppression of food intake.

**Galanin:** A peptide produced by cells in both the gastrointestinal tract and central nervous system. Central administration of galanin stimulates feeding.

**Ghrelin:** A peptide hormone secreted mostly in the stomach, but also in the kidney, pituitary and hypothalamus. A potent stimulus for secretion of growth hormone. Also acts as a regulator of feeding, increasing food intake, and may be a signal for meal initiation.

**Insulin:** A pancreatic polypeptide hormone important in regulating blood glucose concentrations, reducing blood levels of glucose and fatty acids and promoting their storage. Its action is antagonistic to that of glucagon, glucocorticoids and adrenaline. Implicated in long-term energy balance, acting as a signal of stored energy reserves.

**Leptin (*ob* protein):** A protein synthesised in and secreted by cells of the white adipose tissue, liver, spleen, thymus, stomach and some other tissues. Implicated in the regulation of food intake, energy expenditure, energy balance, reproduction and immune functions.

**Melanocyte-stimulating hormone (MSH):** A peptide of the hypothalamus and pituitary with both neuromodulatory and hormonal actions, implicated in the regulation of energy balance via supression of food intake and increasing energy expenditure.

**Neuropeptide Y (NPY):** A peptide in the central and autonomic nervous system implicated in the regulation of food intake and energy expenditure. Central administration results in increased food intake.

**Opioids:** Any of a class of compounds mimicking the effects of opium (morphine) in the brain. Several peptides found in the brain have opiate activity and may stimulate feeding.

**Serotonin (5-hydroxytryptamine or 5-HT):** A biogenic amine derived from tryptophan that acts as a neurotransmitter within the central nervous system and may suppress feeding.

### *Monitoring energy reserves*

The nutritional status of a fish at any particular time is intimately linked to stored energy reserves, largely in the form of body fat. That these reserves influence how much a fish eats has been demonstrated in studies showing increased food intake following a period of feed deprivation, and those where feed intake has been shown to decrease as body fat stores increase (Jobling 1994; Jobling & Johansen 1999; Ali *et al*. 2001; Johansen *et al*. 2001, 2002, 2003). Several signalling molecules, including hormones (endocrines), paracrines, neuroendocrine factors and neurotransmitters, interact and, in combination, provide the CNS with information about feeding state and nutritional status (Box 7.1).

Signals that reflect the size of the energy stores in mammals include adiposity signals, hormones secreted into the blood in proportion to the amount of stored body fat. The two best-known and widely studied adiposity signals in mammals are insulin and leptin (Volkoff 2006; Nelson & Sheridan 2006). Insulin is secreted from the pancreas and circulating concentrations of insulin bear a relation to amounts of body fat. Leptin is produced in adipose tissue (Masuzaki *et al*. 1995), circulates in proportion to body fat reserves (Maffei *et al*. 1995) and provides an endocrine message to the brain about the size of fat stores (Friedman 2009). Leptin has a number of functions (Robertson *et al*. 2008), one of which is in the regulation of long-term energy balance (Speakman *et al*. 2002; Friedman 2009). DNA sequences encoding for leptin have been identified in several fish species, including pufferfish (*Takifugu rubripes;* Kurokawa *et al*. 2005; Yacobovitz *et al*. 2008), common carp (*Cyprinus carpio*; Huising *et al*. 2006), rainbow trout (*Oncorhynchus mykiss*; Murashita *et al*. 2008), grass carp (*Ctenopharyngodon idella*; Li *et al*. 2010), zebrafish (*Danio rerio*; Gorissen *et al*. 2009) and Arctic charr (*Salvelinus alpinus*; Frøiland *et al*. 2010). The

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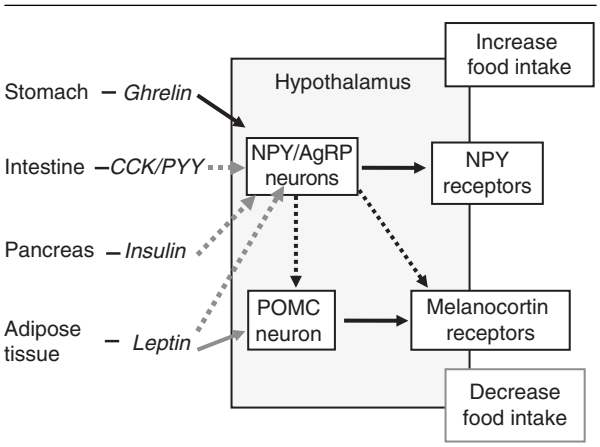


**Figure 7.7.** Biochemicals that influence food intake in fish and the neurochemicals with which they interact in the hypothalamus. NPY = Neuropeptide Y. AgRP = agouti-related peptide. POMC = Pro-opiomelanocortin. αMSH = α Melanocyte-stimulating hormone. Solid arrows indicate stimulatory effects. Dotted arrows = inhibitory effects.

amino acid sequences of fish leptins differ from those of mammalian leptins. In addition, although leptin is produced by fish adipocytes (Vegusdal *et al*. 2003), the liver seems to be the major leptin-producing organ in fish, along with the thymus and spleen in some species (Huising *et al*. 2006; Murashita *et al*. 2008; Gorissen *et al*. 2009; Kurokawa & Murashita 2009; Pfundt *et al*. 2009). Several of the functions of leptin in fish seem to be similar to those reported in mammals (Volkoff *et al*. 2005; de Pedro *et al*. 2006; Volkoff 2006). Given the sites of synthesis and patterns of release of leptin and insulin, their circulating concentrations are expected to provide a good indication of the size of the body fat stores. Both insulin and leptin are able to enter the brain from the blood and stimulate receptors on neurons present within several brain regions, but most importantly receptors on hypothalamic neurons (Figure 7.7).

### *Monitoring recently ingested food*

In addition to long-term energy stores, nutritional status depends on ingested food that is undergoing digestion in the GI tract, and feed intake in fish is under GI influence (Figures 7.1 and 7.6). This is demonstrated by the fact that both meal frequency and meal size can be related to gastric distension and evacuation. For example, in dab (*Limanda limanda*) feeding frequency is significantly influenced by the time taken to empty the stomach (Gwyther & Grove 1981). A number of short-term signals arise as a consequence of eating and digesting a meal, and of absorbing and processing the nutrients it contains (Figure 7.6; Dockray 2010); these signals combine to regulate the onset and termination of feeding.

One category of signal arises from the passage of ingested and partially digested food through the GI tract; these include pre-gastric stimuli (such as the taste of the food in the mouth), gastric stimuli (such as distension of the stomach as food accumulates) and post-gastric stimuli (related to distension of and the presence of nutrients in the intestine). Another category of signal arises after nutrients have been absorbed into the bloodstream, where they circulate, together with their metabolites and meal-related hormones. Some of these signals (hunger signals) reflect a lack of food in the GI tract and trigger feeding. Others (satiety signals) reflect a full stomach, the presence of nutrients in the GI tract and circulating products of digestion, and these suppress feeding. Hunger signals (or orexigenic factors), such as ghrelin, trigger eating, and satiety signals (anorexigenic factors), such as cholecystokinin (CCK), inhibit feeding. Integration of the various signals that originate in peripheral organs and tissues, including the GI tract and associated organs, takes place through neuroendocrine mechanisms that are highly conserved across vertebrates (Table 7.1; Figure 7.7; de Pedro *et al*. 2006; Metz *et al*. 2006; Nelson & Sheridan 2006; Volkoff 2006; Volkoff *et al*. 2009).

### *Generating and controlling ingestive behaviour*

Short-term, meal-related signals arising from the GI tract and other systems are integrated with signals of long-term energy stores to control feeding behaviour and food intake (Figures. 7.1 and 7.5). The central neural network that regulates feeding comprises three major elements, a sensory element, involving reception of inputs received from the GI tract, adipose tissue and metabolizing tissues, an integrative component in which the sensory information is processed and an efferent element that diverges towards the periphery to regulate feeding and energy expenditure. The principal brain region involved in the regulation of feeding is the hypothalamus, but hindbrain neurocircuitry and other pathways are also important (Figure 7.8). The hypothalamus receives inputs relating to circulating nutrients and metabolites and from satiety and adiposity signals. Some of these chemical factors, insulin and leptin for example, are endocrines (hormones) that circulate in the blood and act on receptors within the hypothalamus. Others, for example CCK, interact with receptors on neurons that run from the GI tract to the hindbrain,

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**Table 7.1.** Some neurotransmitters implicated in the control of feeding, some of which (e.g. CCK) have endocrine and paracrine functions and act on a range of body organs and tissues.

| Stimulate feeding | Inhibit feeding |
|---|---|
| Neuropeptide Y (NPY) | Cholecystokinin (CCK) |
| Melanin concentrating hormone | Corticotropic releasing hormone (CRH) |
| Agouti-related peptide (AgRP) | α-Melanocyte-stimulating hormone |
| Galanin | Cocaine- & amphetamine-regulated transcript (CART) |
| Orexins | Glucagon-like peptides (GLP) |
| Opiods | Serotonin (5-HT) |
| γAminobutyric acid (GABA) | Neurotensin |

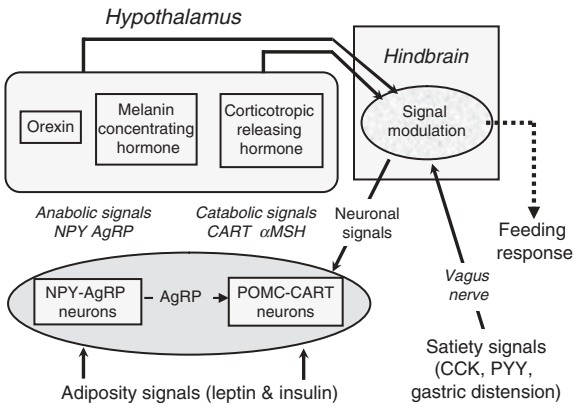


**Figure 7.8.** Neural mechanisms involved in the control of feeding in fish and their interaction with various hunger and satiety signals. NPY = Neuropeptide Y. AgRP = agouti-related peptide. POMC = Pro-opiomelanocortin. αMSH = α Melanocyte-stimulating hormone. CART = Cocaine & amphetamine regulated transcript. From Jobling (unpublished information).

especially those of the vagus nerve (Ritter 2004; Huda *et al*. 2006; Dockray 2010).

The central integration system generates two major types of effector signals modulated by a variety of neurotransmitter substances, specifically those that reduce food intake and those that increase it. Thus, the hypothalamus contains two key populations of neurons with opposite actions on food intake. One population expresses peptides (CART and MSHs – see Table 7.1) that suppress food intake when satiety signals predominate. The other population expresses peptides (neuropeptide Y (NPY) and AgRP. See Table 7.1) that stimulate feeding when hunger signals predominate. These hypothalamic neurons innervate a variety of targets within the hypothalamus and beyond that act as the first links in the effector pathways. It is, however, overly simplistic to reduce the control of feeding behaviour to a limited series of molecular interactions, since numerous sources of information are used by the central feeding network to regulate feeding responses and food intake. These include inputs relating to the abiotic environment, information acquired from conspecifics during social situations and physiological inputs such as stress and health status, all of which are known to have an impact on feeding activity and food intake (Figure 7.1).

### 7.2.2 Mechanisms that control circadian rhythms

#### *Endogenous and exogenous rhythms*

Activity rhythms can be broadly classified as exogenous (caused by a direct response to external periodic factors such as light or tidal cycles) or endogenous (driven by internal factors within the animal). Daily and, in some cases, annual rhythms of activity (including feeding) are often endogenous and depend on cyclic, internal molecular clocks. The exact timing of these rhythms may be fine-tuned by, or entrained to, a variety of stimuli, including regular meals (Reebs 2002; López-Olmeda & Sánchez-Vázquez 2010).

#### *Circadian rhythms*

When a regular daily pattern of feeding persists under constant conditions in the absence of external time cues, it is considered to be controlled by an endogenous circadian rhythm. Such endogenous, self-sustained rhythms persist without attenuation with a periodicity of about 24 h (hence 'circadian') when animals are held in a constant environment (Aschoff 1981). This contrasts with patterns that depend on hourglass-like processes, such as filling and emptying of the stomach, and that cease in the absence of external cues. For example, in European seabass trained to self-feed using a demand feeder, trigger activation

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continues, with fish demanding food at their preferred time of day even when the feeder is turned off; an hourglass mechanism would seem to be ruled out and endogenous control suggested (Madrid *et al*. 2001). In the amberjack (*Seriola dumerili*) feeding is mediated by an endogenous circadian oscillator, with feeding tending to occur between one and three hours after first light (Chen *et al*. 2007). Similarly an endogenous rhythm appears to control the feeding behaviour of the tench (*Tinca tinca*) a freshwater fish that feeds at night (Herrero *et al*. 2005).

### *Modulatory effects on daily feeding rhythms*

The precise timing of endogenously generated rhythms is often linked (or entrained) to external events occurring at approximately the same frequency as that of the free-running rhythm; such cyclic events are termed synchronizers or *zeitgebers* (time-givers). Light is often an important zeitgeber for resetting endogenous rhythms in fish, since the daily light–dark cycle and seasonal changes in photoperiod (hours of light and dark each day) provide reliable information about time of day and year (Eriksson & Alanärä 1992). The change in light intensity between the light and dark phase seems to be more important as a signal than absolute intensity or light wavelength (Gibson & Keenleyside 1966; Boujard & Leatherland 1992). Regular feed delivery can also act as a zeitgeber (Herrero *et al*. 2005); if food is provided at the same time each day, fish may synchronise their activity to meal-time. They may increase activity in anticipation of and a few hours prior to a meal (Figure 7.9; Vera *et al*. 2007a). Fish may maintain activity around their earlier meal-times even when not fed, which indicates the existence of an endogenous component to food anticipation (Sánchez-Vázquez & Madrid 2001).

Other cues, such as bouts of exercise (Valverde *et al*. 2005) and factors related to gastric evacuation (Houlihan *et al*. 2001), may influence the expression of circadian feeding rhythms. For example, if the time required for gastric evacuation and return of appetite is slightly more than 24 hours, as has been suggested for rainbow trout (Grove *et al*. 1978; Ruohonen *et al*. 1997), Atlantic salmon (*Salmo salar*) and Atlantic cod (*Gadus morhua.* Saunders 1963; Ramnarine *et al*. 1987; Storebakken *et al*. 1999), then feeding activity may show a 2 day period between peaks (Bailey & Alanärä 2006a).

### *Physiological mechanisms*

The circadian system of fish is composed of a central pacemaker within the brain and at least two peripheral oscillators located in the retina and the pineal organ (Figure 7.10). The pineal organ is a photoreceptor that

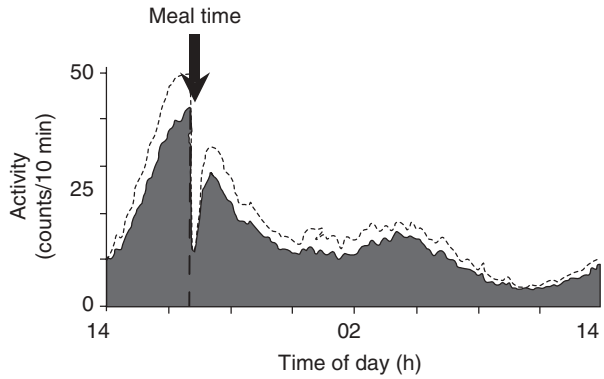


**Figure 7.9.** Feeding anticipation. Activity in relation to time of day and meal time (arrow) in goldfish. Grey zone delineates mean activity. Dotted line = standard error. Reproduced with permission from Vera *et al*. 2007a.

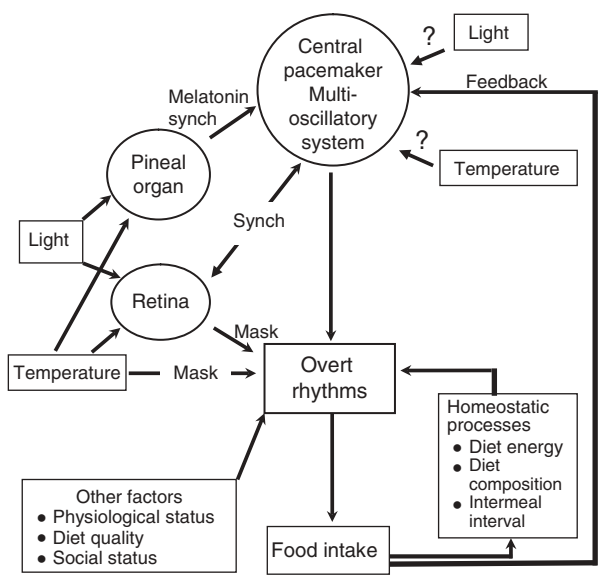


**Figure 7.10.** Schematic representation of the physiological control of circadian rhythms in fish.

contains a circadian oscillator controlling the rhythmic secretion of the hormone melatonin (Ekström & Meissl 1997). Melatonin is produced in and secreted from the pineal gland during hours of darkness, so melatonin rhythms codify the time of day. The fish pineal is highly sensitive to light; for example, in nocturnal fish such as tench and Senegalese sole (*Solea senegalensis*) a weak light pulse (intensity 0.3 lux) causes a decrease in plasma melatonin

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concentration similar to that experienced during daylight (Vera *et al*. 2005; Oliveira *et al*. 2007). The fact that such low light intensities exert an effect on the pineal point to a potential role of melatonin rhythms in mediating synchronisation to lunar as well as daily light–dark cycles (Rahman *et al*. 2004; Oliveira *et al*. 2010). Melatonin is directly involved in many rhythmic physiological processes and behaviours, including feeding, that are of central importance in aquaculture (Bromage *et al*. 2001; Falcón *et al*. 2010).

The pineal–melatonin system may represent a master central pacemaker that acts as a synchroniser of biological rhythms, but it has also been suggested that there are dispersed timing mechanisms, with each cell having its own functional circadian clock. Recent research using molecular techniques has revealed that such clocks are orchestrated by several highly conserved clock genes expressing transcription factors that modulate their own expression. For example, among the genes involved in the control of rhythms, clock (*clock*), cryptochrome (*cry*) and period (*per*) are homologous across the vertebrate lineage (Wager-Smith & Kay 2000) and are differentially expressed in relation to the light–dark cycle. For example, in zebrafish (*Danio rerio*), *period1* is maximally expressed at the beginning of the light phase, *period2* has its maximum 3 h into the light phase and the expression peak of *period3* occurs between 3 and 6 h after light onset. Furthermore, *period2* and *cry1a* are induced directly by exposure of the animal to light, whereas *period4* and *cry2b* show rhythmic expression in relation to temperature cycles (Lahiri *et al*. 2005). As such, light and temperature inputs may act to place the rhythmic expression of clock genes in phase with environmental cycles, thereby enabling fish to anticipate and cope with predictable changes in their environment.

### 7.2.3 Mechanisms underlying circannual changes in appetite

Seasonal variations in feeding often seem to be controlled by endogenous circannual rhythms that are under the influence of the seasonal photoperiodic cycle (Eriksson & Lundqvist 1982; Eriksson & Alanärä 1992). In general, in high latitude species increasing day-length in spring and early summer stimulates feeding, while the decreasing autumnal day-length has the opposite effect (Higgins & Talbot 1985). For temperate species such as salmonids, equinoxes (when day-length is changing most rapidly) and solistices (when the change in day-length switches direction) are often important environmental cues that influence feeding activity (Kadri *et al*. 1996). Melatonin rhythms in fish codify time of year in addition to time of day, because melatonin secretion varies in step with changes in photoperiod (Bromage *et al*. 2001; García-Allegue *et al*. 2001; Vera *et al*. 2007b). Circadian and circannual rhythms of feeding may be linked, in that gradual, progressive changes in photoperiod and water temperature are sometimes required to trigger a change from nocturnal to diurnal feeding and vice versa, as is the case in European sea bass (Sánchez-Vázquez *et al*. 1998).

Annual changes in feeding may be governed by a range of mechanisms. For example, one set of physiological triggers that lead to reduced feeding during the autumn seems to be related to the size of body fat depots, with fish reducing feeding once they have acquired sufficient energy reserves to survive the winter (Tveiten *et al*. 1996; Jørgensen *et al*. 1997; Jobling & Johansen 1999). Further, there may be an inverse relationship between body fat content and feed intake, which would partly explain the large increase in feed intake that often occurs in fish after a long winter, when energy reserves are depleted (Metcalfe & Thorpe 1992a; Jobling & Miglavs 1993; Shearer *et al*. 1997). For example, channel catfish (*Ictalurus punctatus*) display a feeding peak in April, corresponding to an increase in hypothalamic production of messenger RNA for NPY, which stimulates feeding (Silverstein 2002). Arctic charr feed avidly during the summer; feed intake then decreases during the autumn, remains very low throughout the winter and increases again in the spring. These changes are associated with marked seasonal changes in body fat and in expression of the genes encoding for the appetite-regulating peptides ghrelin and leptin (Figure 7.11; Frøiland *et al*. 2010).

### 7.2.4 Mechanisms underlying appetite changes in relation to life history events

There are strong reciprocal negative links between the mechanisms that control the onset of reproduction in seasonally-breeding fish (see Chapter 10) and those that control feeding. For example, in goldfish intraventricular injection of gonadotropin releasing hormone (GnRH), which stimulates the pituitary gland to release gonadotropic hormones and participates in initiation and maintenance of gonad development, decreases production of orexin in the hypothalamus, and results in a reduction in feeding. Conversely, injection of orexin at concentrations that promote feeding inhibits GnRH production and suppresses spawning (Hoskins *et al*. 2008). The changes in appetite shown by maturing fish may also be related to increases in plasma concentrations of sex steroid hormones and individual variation in the detailed timing of these events may depend on variation in nutrient reserves. For example, the onset of anorexia at the start of the breeding season in

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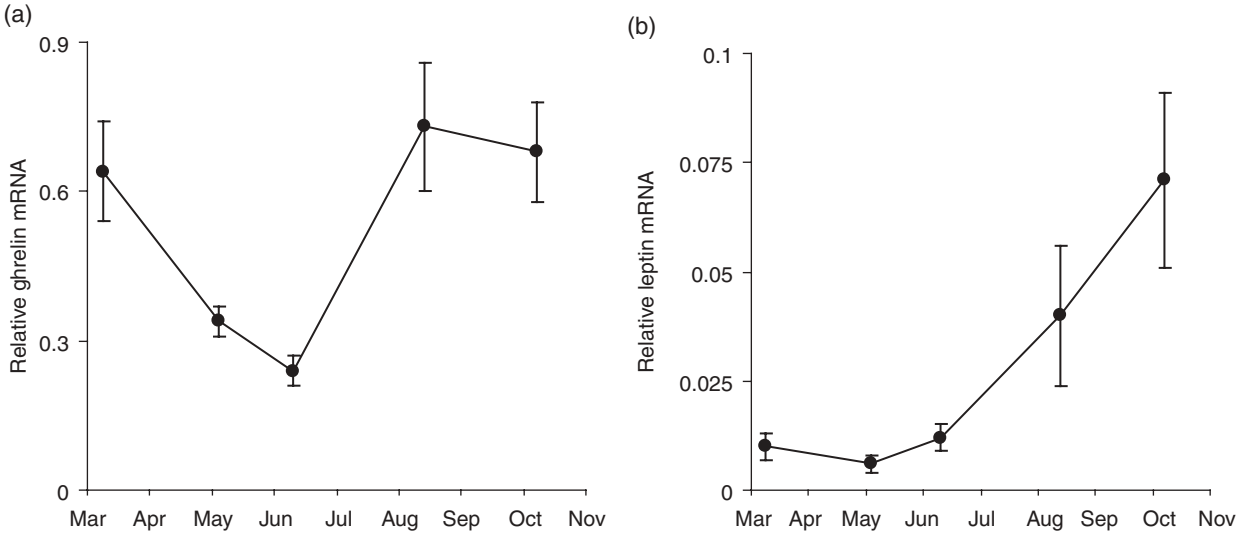


**Figure 7.11.** Seasonal changes in appetite-related gene expression. Relative mRNA expression levels of (a) stomach grehlin and (b) liver leptin in Arctic charr in relation to time of year. Adapted from Froiland *et al.* 2010.

female Atlantic salmon seems to be related to the accumulation of nutrient reserves, with fish apparently continuing to eat until their lean mass and possibly also their reserves of body fat have reached a certain threshold (Kadri *et al.* 1995). Similar mechanisms may also be operative in other salmonids, such as Arctic charr (Tveiten *et al.* 1996).

### 7.2.5 Summary of the mechanisms underlying appetite changes in fish

Food intake in fish is controlled by a series of signals that reflect fluctuating levels of energy reserves, for example, adiposity signals such as leptin and insulin, and the progress of digestion and absorption of individual meals, for example distension of the GI tract and secretion of CCK in response to the arrival of food in the small intestine. This allows fish to adjust their food intake, in terms of both the amount eaten and its nutritional composition, in relation to their needs. There are also a number of mechanisms that modulate appetite in relation to the environment, such as changes in oxygen level or the occurrence of stressful events. This additional level of complexity means that fish can adjust their feeding according to circumstances. These irregular changes are superimposed upon regular feeding rhythms that may be tidal, daily, lunar or annual. In many cases, such feeding rhythms have an endogenous component, but can be entrained to regularly occurring events, including those having an approximately 24 h periodicity. Regular daily changes in light levels are important in this context, but feeding rhythms can also be entrained by the regular appearance of food. Daily rhythms are controlled by cyclic production of melatonin, primarily by the pineal gland, but also from sites dispersed around the body. Links between feeding and the reproductive cycle are influenced by interactions between reproductive hormones, such as sex steroids, and brain mechanisms that activate or suppress feeding. Rhythmicity in relation to geophysical cycles and changes in appetite associated with life history events therefore provide additional mechanisms whereby food intake in fish is related to food availability and to nutritional requirements.

## 7.3 DEVELOPMENT

After their yolk sac has been used up, developing fish start to feed exogenously (Moksness *et al.* 2004; Cyrino *et al.* 2008; Kamler 2008). From this point onward, how much and when fish eat changes with age and size. Knowing about these changes, and especially about the development of appetite during the switch from endogenous to exogenous feeding, might enable effective feed delivery strategies to be developed for cultured fish of all ages. How much an adult fish eats and when it does so is influenced both by its genetic make up and by the feeding environment it experiences during development. Such effects are important determinants of how much fish eat when they

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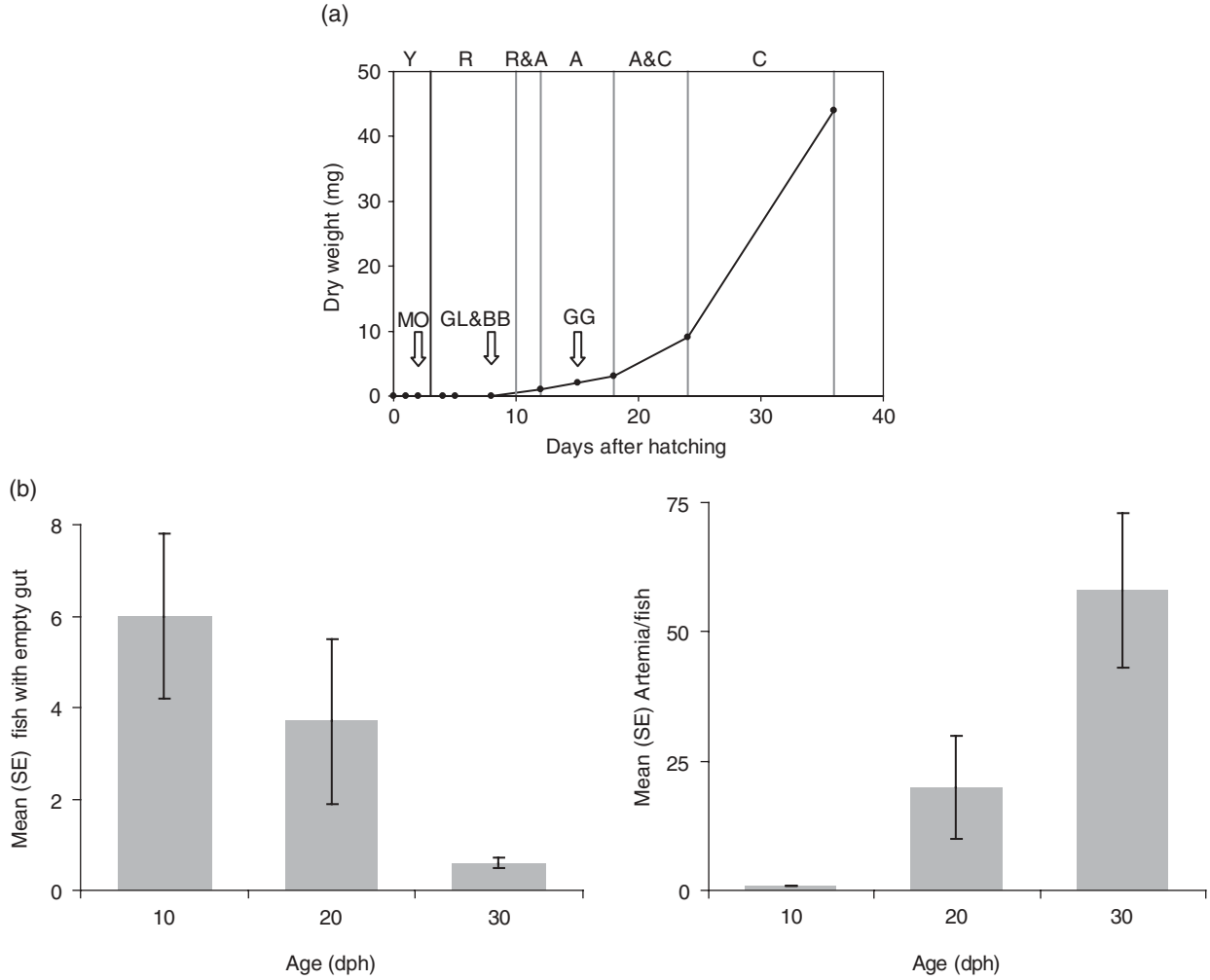


**Figure 7.12.** Development of GI activity and feeding. (a) Dry weight of larval yellow kingfish from 0-36 days after hatching, with major morphological developments indicated. MO = mouth opening. GL = formation of gut loop. BB = formation of brush border. GG = formation of gastric gland. Vertical lines separate periods with different diets. Y = yolk. R = rotifers. R&A = rotifers and Artemia nauplii. A = Artemia nauplii. A&C = Artemia nauplii and compound diet. C = compound diet. Reproduced with permission from Chen *et al.* 2006.
(b) Mean (±SE) number of fish with empty guts (LHS) and number of *Artemia* spp. eaten per fish (RHS) in larval seabass. Adapted from Georgalas *et al.* 2007.

are being cultured and of how effectively they are able to acquire nutrients if they are released into the wild.

### 7.3.1 Ontogeny of appetite patterns

There is an extensive literature on the ontogeny of GI tract structure and function in larval and juvenile fish (Moksness *et al*. 2004; Cyrino *et al*. 2008). Since signals arising from the physical and biochemical process of digestion are a key component of the mechanisms controlling feeding, ontogenetic changes in GI tract function (Figure 7.12a; Chen *et al*. 2006) must have implications for the development of appetite and its control, but there have been few direct studies of the development of appetite patterns in fish. Feeding increases with age and size, as in larval European seabass (Georgalas *et al*. 2007; Figure 7.12b), probably as a result of increasing metabolic demands. During their first week after hatching, larval sculpin (*Myoxocephalus scorpius*) continue to feed in the presence

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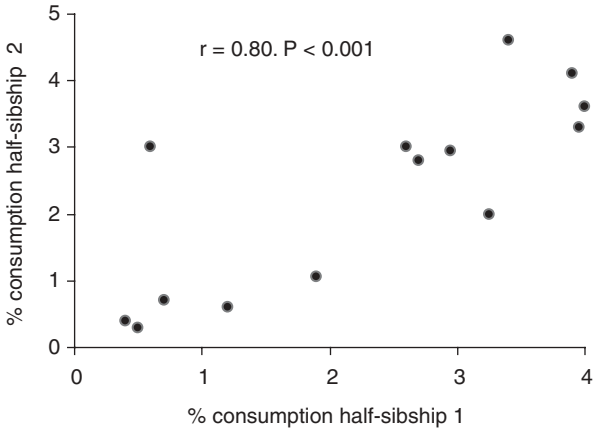


**Figure 7.13.** Heritability of food intake. Relationship between food consumption (% body weight) in half-sib families of channel catfish. Adapted with permission from Silverstein *et al.* 2001.

of a predator, possibly because they have high nutritional requirements to support metabolism and growth. As they increase in size the fish become more cautious and less persistent in feeding when under threat. The first week post-hatching is a time when the mass-specific metabolic rates of fish larvae are particularly high, inducing a strong need to maintain energy supplies (Killen *et al*. 2007). As far as the development of rhythms is concerned, in zebrafish reared on a regime of 14 h light and 10 h dark, circadian oscillators (measured as cyclic production of melatonin) that can be entrained to light cues appear as early as 20–26 h after fertilisation, when pineal photoreceptors, but not retinal photoreceptors, are starting to develop (Kazimi & Cahill 1999).

### 7.3.2 Genetic effects on appetite

Inherited differences in food intake and/or in physiological traits that are closely linked to appetite are known to exist in fishes. For example, in European sea bass the rate at which fish lose weight when food deprived and gain weight when food is made available again, which are related to food intake, both have a significant heritable component (Grima *et al*. 2010). Some strains of channel catfish (*Ictalurus punctatus*) eat less than others when fed *ad libitum* (1–2% compared to 2.5–5% body mass per day) and show stronger inhibitory effects of CCK on feed intake; within a single strain feed intake may have a heritability of 0.4 (Figure 7.13; Silverstein *et al*. 2001). Accurate estimation of heritability of feed intake in fish is complicated by changes in individual appetite over days and also across life history periods, but estimates range from about 0.1 to 0.8 (Kause *et al*. 2006). Food intake by individual fish is higher in brown trout from a line subjected to selection for fast growth for 4 generations than in fish from a control line (Boujard *et al*. 2006). These various studies indicate that genetic differences may account for a significant amount of the variation in appetite seen in fish within a given species. Looking at the effects of specific genes, growth hormone (GH) transgenic coho salmon (*Oncorhynchus kisutch*), which have extra copies of the gene that codes for GH, eat more and grow faster than do non-transgenic conspecifics (Raven *et al*. 2006), do not show decreased appetite during the winter and also have lower CCK levels than non-transgenic conspecifics (Lõhmus *et al*. 2008).

### 7.3.3 Effects of experience on appetite

The various mechanisms that enable fish to adjust their food intake to their life history stage, nutritional status and environmental conditions ensure that appetite changes flexibly in relation to experience. For example, the early diet experienced by a fish can influence GI tract structure and function and can also lead to metabolic programming that can have effects on nutritional requirements and feeding later in life (Chapter 2). Rainbow trout given a short exposure to a high carbohydrate diet at first feeding and then given a carbohydrate challenge some time later show greater up-regulation of genes involved in carbohydrate digestion and metabolism than do control fish. A short exposure to specific nutrients early in life would therefore seem to influence later processing of these nutrients (Geurden *et al*. 2007). Similarly, European seabass exposed to a diet low in highly unsaturated fatty acids (HUFAs) as larvae are better able to adapt to a diet low in HUFAs than are conspecifics fed a high HUFA diet when young (Vagner *et al*. 2007).

Rearing conditions unrelated to food supply can also influence appetite and feeding. For example, when offered prey at low densities, greenback flounder (*Rhombosolea tapirina*) larvae reared in turbid water ('greenwater') eat more than do larvae reared in clear water, possibly because of differences in retinal development in the larvae held in the two environments (Shaw *et al*. 2006). Circadian rhythmicity develops in larval zebrafish during the first 4 days after fertilization, but exposure to entraining signals at around day 3 is needed for the full development of rhythmic behaviour (Hurd & Cahill 2002). In addition to influencing immediate access to food, social experience can have medium- to long-term effects on feeding, development and life history. For example, subordinate juvenile

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Atlantic salmon are more likely to become anorexic during the winter than are their dominant siblings, through an indirect effect of early growth on developmental processes that leads to a divergence in life history between dominant and subordinate individuals (Metcalfe & Thorpe 1992b).

### 7.3.4 Summary of the development of appetite patterns

The changes in feeding that occur as the fish develop from larvae to adulthood are of obvious interest to fish culturists, with particular problems being apparent in the brief period during which the fish change from endogenous to exogenous feeding. Genetic selection of cultured fish stocks for fast growth may also involve selection for feeding behaviour and appetite-related traits, and food intake seems to display a moderate degree of heritability in species such as salmonids and channel catfish. Further, growth manipulation of fish using transgenic biotechnology may have consequences for appetite, feeding behaviour and feed requirements. Throughout life, feeding in fish is flexibly tuned to current needs, but there are also some long term consequences of early experience; these include effects of specific nutrients on the future ability of fish to process food and other programming effects that may have an influence on metabolic and nutritional requirements and on the long-term development of appetite patterns.

## 7.4 FUNCTIONS

Acquiring sufficient food is essential for survival, growth and reproduction. Eating a particular amount of food at a particular time reflects a balance between the benefits gained by taking in food at a certain rate and the costs of doing so.

### 7.4.1 Costs and benefits of feeding at a particular rate

The benefits of consuming food are self-evident, but there are also costs of feeding that often increase in direct relation to the amount of food consumed. In some cases, the costs are direct, as when time spent feeding is time taken from other activities. Ingesting and processing food also consumes non-trivial amounts of energy, depending on the nutrients involved, species and life history stage (Jobling 1981, 1994; McCue 2006; Secor 2009). In general, post-prandial metabolic costs often account for 10–15% of ingested energy in fish (Jobling 1981). In southern bluefin tuna (*Thunnus maccoyii*) they account for about 20% of ingested energy and are higher in fish fed high lipid prey (Fitzgibbon & Seymour 2009). Silverside (*Menidia menidia*) from populations with a high genetic capacity for growth eat larger meals than do those from slow-growing populations and have a higher post-prandial oxygen demand (Arnott *et al*. 2006). The costs of processing food can compromise swimming capacity by competitive effects in relation to metabolic scope (Jobling 1981, 1994); for example, southern catfish (*Silurus meridionalis*) that have been fed have lower critical swimming speed at any given temperature than do fish that have been fasted (Figure 7.14; Pang *et al*. 2010). In addition, fish that are actively feeding as opposed to remaining in shelter are more likely to encounter predators (Munch & Conover 2003; Chapter 8) and where food is in limited supply, gaining access to it may involve fighting, with associated costs (Chapter 9).

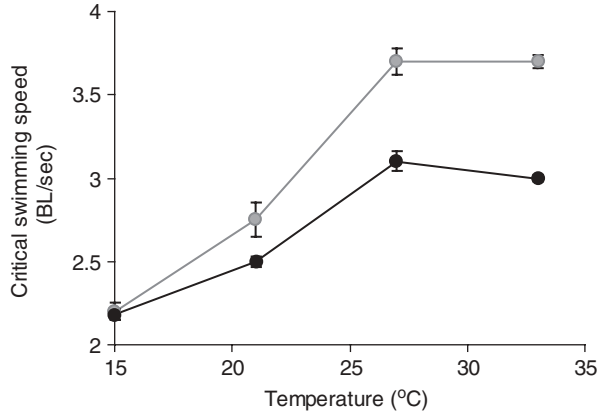


**Figure 7.14.** Effects of feeding on swimming capacity. Critical swimming speed (the maximum current speed in body length (BL)/sec against which the fish can hold station for a fixed period of time) of juvenile southern catfish that had been either fed (black line) or fasted (grey line) in relation to temperature. Adapted from Pang *et al*. 2010.

Other costs of a high feeding rate are indirect, through the costs of fast growth, which is often achieved at the expense of other functions. For example, basal metabolic rate is higher, and metabolic scope lower, in silversides from populations with a high genetic capacity for growth than in fish from slow-growing populations; allocation of nutrients to growth decreases the energy available for other activities through competing metabolic demands (Arnott *et al*. 2006; Jobling 1981, 1994). Fish often display compensatory growth following a period of food deprivation (Jobling 1994, 2010a; Ali *et al*. 2001), but this can come at a cost. For example, green swordtails (*Xiphophorus helleri*) that have experienced a period of compensatory growth early in life have an impaired capacity for sustained swimming and they also

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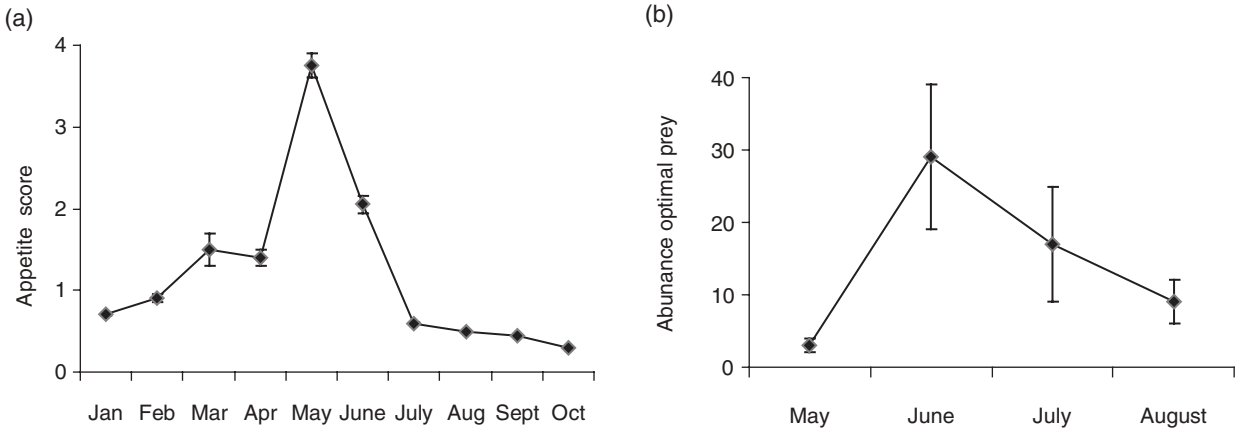


**Figure 7.15.** Adaptive appetite matching. (a) Mean (± SE) appetite score in juvenile Atlantic salmon in successive months from January to October. (b) Mean (±SE) number of drifting food items of the optimal size for growth collected in drift samples in the stream feeding the tanks in which the fish in (a) were held. Adapted from Simpson & Thorpe 1997.

tend to be subordinate to fish that have not experienced such compensatory growth (Royle *et al*. 2005, 2006).

There are many examples of fish adjusting appetite upwards or downwards in relation to the costs and benefits of feeding. Up-regulation of appetite in relation to benefits is illustrated by the fact that many species of fish show compensatory feeding and growth following periods of deprivation or under-nutrition (Jobling 1994, 2010a; Ali *et al*. 2001). Likewise, maturing fish initially show increased appetite in response to the increasing nutrient requirements of developing gonads (Kadri *et al*. 1996). Down-regulation of appetite in relation to costs is illustrated by the many examples of fish feeding less when under predation risk (Chapter 8) and of suppressed appetite in subordinate fishes (Chapter 9).

### 7.4.2 Costs and benefits of feeding at a particular time

As for most physiological and behavioural functions, the temporal organisation of feeding has evolved under the influence of cyclic selective forces (Pittendrigh 1993). Activity rhythms may allow fish to feed at times when prey availability is high and/or when predation pressure is low. At the seasonal level, adaptive changes in appetite are illustrated by juvenile salmonids, which when held under constant conditions in the laboratory show feeding peaks during the early summer (Figure 7.15a), just before a period when suitable food is abundant in nature (Figure 7.15b. Sæther *et al*. 1996; Simpson & Thorpe 1997).

On a shorter time scale, fish of many species show daily fluctuations in feeding, concentrating activity at the times of day when the balance between food availability and predation risk is best (Helfman 1993). For example, the crepuscular activity of stream-living salmonids may reflect a trade-off between food availability and predation risk (Eriksson & Alanärä 1992). According to this view, the timing of activity of juvenile Atlantic salmon corresponds to the dawn and dusk peaks in the drift of mayfly larvae. At the same time, low light intensities impair the ability of visually hunting piscivores; since salmon are also visual predators, a trade-off must exist between predation risk and the efficiency of catching abundant prey (Clark & Levy 1988). The benefits of switching between diurnal feeding at high temperatures and nocturnal feeding at low temperatures are most likely related to seasonal shifts in density of prey and vulnerability to predators. Nocturnal feeding could be a strategy for reducing predator pressure, because fish in cold water have a reduced escape response due to poorer swimming ability. They thereby face an increased risk of predation from day-feeding warm-blooded animals (Fraser *et al*. 1995). In the case of juvenile Atlantic salmon, the fish that feed during the day at colder times of the year have higher growth rates than fish that forage at night, demonstrating a trade-off between growth and survival during foraging (Metcalfe *et al*. 1999).

Control by a biological clock enables fish to anticipate cyclic events in their environment and to respond appropriately. If prey availability, for example, varies predictably

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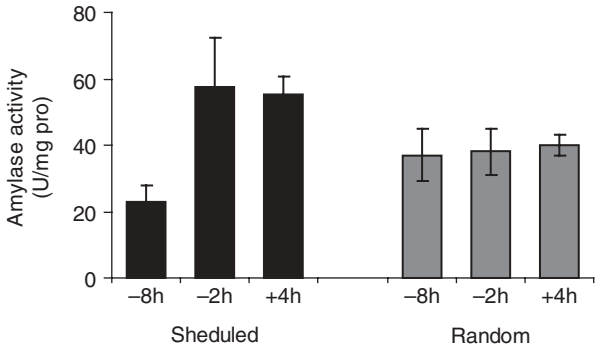


**Figure 7.16.** Beneficial effects of feeding anticipation. Mean (±SE) amylase activity at different time points in relation to delivery of a meal in goldfish fed at the same time each day (dark grey bars) and those fed at random times (light grey bars). Adapted with permission from Vera *et al*. 2007a.

over time, endogenously controlled activity rhythms may allow fish to match feeding effort to food availability without the need to assess food availability directly. The value of such adjustments can be seen in the case of feeding anticipatory activity, because fish capable of anticipating a meal-time can take advantage by being prepared. From a physiological and behavioural point of view, a continuously active state is uneconomical and the ability to anticipate meal-time would seem to be energetically beneficial (Lopez-Olmeda & Sánchez-Vázquez 2010). When animals are able to anticipate meal-times, food acquisition and nutrient utilisation may be improved. For example, production of faeces increases shortly prior to feeding, possibly as a result of an increase in GI tract motility (Madrid *et al*. 1997). Goldfish fed at the same time each day show increased secretion of amylase (a carbohydrate-digesting enzyme) and NPY (an orexigenic neuropeptide) two hours before feeding, whereas fish fed randomly do not show such anticipatory responses (Figure 7.16; Vera *et al*. 2007a). In addition, randomly fed fish need to be continually active and alert to avoid missing an unpredictable meal. As a result, plasma cortisol levels are higher in fish fed at random than in scheduled-fed fish, suggesting that the lack of regular feeding is stressful and may compromise fish welfare (Vera *et al*. 2007a; Sánchez *et al*. 2009).

### 7.4.3 Summary of the costs and benefits of appetite patterns

While eating at a fast rate obviously has the potential to deliver abundant valuable nutrients to fish, there are costs involved. These include direct costs incurred at the time of feeding, in the form of higher energy expenditure during food processing, higher risk of predation and costs associated with competing for limited food. Fish may also incur indirect costs of the high rate of growth that is often associated with high food intake, in the form of a reduced capacity for sustained swimming and reduced competitive ability. How much and how fast a fish eats on any given occasion represents a balance between such costs and benefits, as when fish initially coming into reproductive condition eat more because the benefits of feeding (in the form of gamete production) are high. Regular feeding cycles, whether endogenously or exogenously controlled, allow fish to feed at times when food is abundant and risk of predation, for example, is low. Here too benefits and costs are (unconsciously) balanced against each other, as when fish feed at night when the temperature is low, accepting a reduced rate of food intake for the sake of reduced predation risk. The advantages of endogenously controlled feeding rhythms lie in the fact that when food availability is predictable, they allow fish to prepare, physiologically and behaviourally, for the arrival of food, promoting its efficient harvest and utilisation.

## 7.5 IMPLICATIONS FOR AQUACULTURE

So far in this chapter it has been shown that fish do not always eat when they are offered food, but instead exhibit changes in appetite. Such changes may be irregular, influenced by factors such as the energy reserves of the fish and environmental conditions, but appetite may also change on a regular basis, reflecting the various geophysical cycles to which fish are exposed. Fluctuations in appetite ultimately determine when food is eaten and when it is ignored (Houlihan *et al*. 2001) and this has major implications for the rational cultivation of fish (Le François *et al*. 2010). A failure to provide all fish in a culture system with sufficient food at the right times can compromise production and welfare in a variety of ways. Further, feed is a major cost when fish are farmed, so there is a strong incentive for farmers to ensure that as much as possible of the feed delivered to a production unit is eaten by the fish. In addition, wasted feed can have adverse effects on the environment.

### 7.5.1 Patterns of feed delivery in fish culture

The feed delivery systems used in fish culture vary widely depending on species and life history stage. Table 7.2 provides information on how feed is delivered to the spotlight species of cultured fish described in Chapter 1. How fish are fed also depends on the culture method being used, for example whether it is extensive, semi-intensive or

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**Table 7.2.** Natural appetite patterns and usual feed delivery rates for cultured fish in the 10 spotlight fish species.

| | Natural appetite patterns | Usual feed delivery rates |
|---|---|---|
| Atlantic salmon | Crepescular feeding. Appetite changes with season & reproductive status. | Formulated diets dispensed by automatic feeders for all stages. Fish usually fed to satiation. Hand feeding daily to monitor appetite. Often fed through the day in freshwater & early seawater stages. 1–3 meals per day fed to adults, depending upon fish size, season & water temperature. |
| Rainbow trout | Crepescular feeding. Appetite changes with season & reproductive status. | Formulated diets, increasingly dispensed by demand feeders, though automatic feeders & hand delivery are still sometimes used. Fed several times per day when young, meal frequency decreasing with size. |
| European seabass | Feeding nocturnal in winter & diurnal in spring & summer. | Feeding larvae is critical to avoid starvation, hence feed is always available, in suspension. Adults often fed by feed tables based on body weight & temperature or to satiation, with feed dispensed by automatic feeders, demand feeders or hand feeding. Increased growth during winter months has been demonstrated by feeding at night using demand feeders. |
| Nile tilapia | Diurnal feeding. | Intensive culture: generally fed artificial pellets by automatic feeders or by hand to satiation. Multiple feeds per day based on body weight. Adults often fed around 3% body weight/day delivered over 3– 4 meals. At lower temperature may be fed at lower rates and even every other day. Extensive culture: food available continuously. |
| Pacific salmon | Crepescular feeding. Appetite changes with season & reproductive status. | Hatcheries: Automated or hand feeding twice daily using pellets that float or sink slowly. Net cages: Automatic feeding with supplemental hand feeding to monitor appetite. |
| Seahorses | Opportunistic. Feed whenever prey is nearby. Mainly diurnal. | Food in culture delivered in suspension. 5–10% of wet body weight/day is recommended, spread over 3 meals per day. |
| Koi carp | No natural populations available for comparison | Quantity & frequency of feeding reduced with temperature, with several meals per day at high temperatures to no feeding at temperatures below 10°C. Automatic feeders are used, but a large proportion of feed is hand delivered over the surface. |
| Zebrafish | Mainly diurnal. | Fed manually by suspension or by automatic feeder at a frequency of 2–3 times per day, to satiation |
| Guppy | Mainly diurnal. | Fed manually by suspension or by automatic feeder at a frequency of 1–2 times per day, to satiation |
| Clownfish | Mainly diurnal. | Fed manually by suspension or by automatic feeder at a frequency of 3–4 times per day, to satiation |

intensive, and on the practicality of using a particular feed delivery system. In semi-intensive systems where formulated feeds are used to supplement natural food, as is often the case in farming carps and *Tilapia*, the fish may not be fed every day, as they can forage on natural food (Le François *et al*. 2010; Jobling 2010b). In such cases, the time of day and rate at which food is presented is less important than in intensive culture systems.

In intensive fish culture, a common method of feed delivery is manual feeding, as often used for cultured rainbow trout and pangasius. This may be more labour-intensive than use of commercially available automated

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feeding systems, but the initial capital outlay is less. Manual feeding may be carried out using a hand-held scoop to distribute the food, or it may involve the use of a hand-held feed cannon; this consists of a blower designed to distribute feed over the surface of the pond or cage, with food being cast faster and further than is possible by hand. Feed cannons are often fitted with spreading devices, thereby ensuring a widespread dispersal of the feed. In cases where manual feeding is continued until the feeding activity of the fish is seen to decrease markedly or cease, it offers the opportunity for a reasonable degree of matching of feed delivery to fish appetite. However, manual feeding is constrained by the regularity with which farm workers can gain access to the rearing units, whether these are ponds, tanks or cages, and the time it takes to distribute feed to each rearing unit. For instance, a morning meal may be delivered over 45 minutes at the start of the day for the first unit, but it could take the entire morning to deliver feed to all units on the farm. For this reason, feeding is sometimes carried out using either simple mechanical self-feeding devices that the fish trigger to release feed or automated electric feeders operating on a clock timer, with supplementary manual feeding being carried out to monitor and observe the stock on a regular basis (Houlihan *et al*. 2001; Le François *et al*. 2010).

Rainbow trout, other salmonids and several other cultured species (Table 7.2) are often farmed using highly capitalised, intensive culture systems. These often incorporate automatic feeders that deliver feed at predetermined times and in predetermined amounts, but may also include feeders that have some form of feedback to adjust the frequency of feed delivery and the amount delivered according to appetite and/or feed wastage (Chapter 3). Farmed Atlantic salmon are usually fed by means of automated feeding systems for most of the production cycle. In the freshwater stage and in the period immediately after transfer to sea cages, they tend to be fed several meals each day; this is gradually reduced to three meals per day for larger, on-growing fish in summer and to one meal per day for large fish in winter (Le François *et al*. 2010).

### 7.5.2 Problems for fish culture arising from natural appetite variation in fish

Whatever the purpose for which fish are cultured, they must be fed in a way that allows them to grow to the required size within a reasonable period of time. Fish are adapted to function well in environments where food may be scarce and unpredictable and, as they are poikilothermic ectotherms, they may tolerate relatively prolonged periods without food, so have the option of elective anorexia. Thus, fish can be flexible with respect to how much and when they eat, which is convenient for fish farmers. However, they are only flexible up to a point and failure to deliver food in the correct amounts, at correct times and at the correct rate can cause a number of problems in fish culture (Table 7.3). Some of these are obvious; for example, fish that are given insufficient food will grow poorly and may be injured as they compete for the limited amount of food provided. Others are less obvious; for example, as described in Section 7.4.1, fish often respond to periods of food restriction by hyperphagia and compensatory growth, which may be achieved at the expense of other functions, such as swimming capacity (Arnott *et al*. 2006; Jobling 1981, 1994). The following sections explore such problems, first describing the various adverse consequences of under- and over-feeding and then considering the circumstances in which these might occur in fish culture through a failure to match feed delivery to appetite.

### 7.5.3 The effects of under-feeding

Under-feeding occurs when fish are not offered, or cannot consume, sufficient food to meet their daily energy needs and to grow. Under-feeding can have a number of adverse consequences, including poor survival, poor and possibly inefficient growth, poor flesh quality, poor welfare, stress and increased susceptibility to disease. In the extreme case, prolonged under-feeding can result in the death of fish from starvation. This is unlikely to occur for established culture species on well managed farms, but it can occur when new species are being developed for culture, especially during larval rearing. For example, rock bream (*Oplegnathus fasciatus*) larvae that are given food on the day on which the yolk sac has been used up or one day later survive reasonably well, whereas larvae fed 2 days after yolk exhaustion suffer very high mortality. Survival of larvae that are fed later is almost as poor as in unfed larvae, because the fish rapidly reach a point of no return after which they cannot recover (Shan *et al*. 2008). Under-feeding may increase mortality indirectly through increased incidence of body damage caused by fighting over limited food, with an associated increased risk of infection and disease. It can also increase the prevalence of cannibalism (Baras & Jobling 2002), for example in Nile tilapia fingerlings (Abdel-Tawwab *et al*. 2006) and in juvenile African catfish (*Clarias gariepinus.* Al-Hafedh & Ali 2004). Under-feeding can be detrimental to survival following stressful events; for example, Atlantic salmon that are under-fed prior to the parr–smolt transformation suffer higher mortality after transfer to seawater than do well-fed fish fed (Berrill *et al*. 2006).

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**Table 7.3.** Consequences of natural appetite patterns in cultured fish and some potential problems for aquaculture caused by these.

| Issue | Implications for production | Implications for welfare | Implications for the environment |
|---|---|---|---|
| Failure to match feed delivery to appetite may lead to underfeeding | Low feed intake results in reduced feed conversion efficiency, low growth & less flesh at harvest<br>Competition for food causes high levels of aggression, uneven food intake & uneven growth<br>Competition-induced injury compromises fish health & product quality.<br>Stress caused directly by underfeeding or indirectly through aggression compromises growth & health<br>The integrated result of underfeeding may be higher mortality rates | Inadequate food intake can compromise the welfare of individual fish, both directly & indirectly, through consequent ill health<br>Participation in fights over food can cause injury, stress & poor health | More disease in farmed fish may mean more disease transfer to wild fish<br>Inefficient digestion due to stress may result in nutrient rich faeces |
| Failure to match feed delivery to appetite may lead to overfeeding. | Overfeeding may cause reduced feed conversion efficiency | Overloaded GI tracts and excessive nutrient reserves impair the capacity for effective movement, with adverse effects on welfare. | Release of uneaten food increases nutrient enrichment<br>Inefficient feed conversion results in nutrient rich faeces |



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Under-feeding has negative effects on growth and fish that have been under-fed are generally light for their length at the time of harvest; in other words, they have a low condition factor, which may reduce the amount of flesh that can be harvested from the carcass (Ng *et al*. 2000; Pierce *et al*. 2001; Cho *et al*. 2006). Short periods of under-feeding may not compromise growth in the longer term, since fish have a well developed capacity for compensatory growth, through both increased appetite and improved efficiency of feed processing (Jobling 1994, 2010a; Ali *et al*. 2001). Under some circumstances, periods of compensatory growth may be beneficial for production; for example, compared to continuously fed fish, Atlantic halibut subjected to repeated periods of food restriction (5 weeks feed deprivation followed by 10 weeks of feeding) over 3 years process food more efficiently, show reduced rates of maturation and at harvest have firmer flesh with less gaping (Foss *et al*. 2009). However, as described above, compensatory growth can have hidden costs in the form of impaired swimming ability, low social status and reduced longevity (Royle *et al*. 2005, 2006). Such long-term effects of compensatory growth may be relatively unimportant when fish are reared for food. However, they might be important when fish are being raised for release into the wild, when ability to swim effectively and to gain high status may be critical for survival.

Within a cohort of fish individuals will differ in their ability to compete for food (Chapter 9), so under-feeding may not affect all the fish within a rearing unit equally. As a consequence, feed consumption is not homogeneous within a group of fish that is under-fed and there can be considerable disparity in food intake among individuals (Jobling 1995a, b; Jobling & Koskela 1996). For example, 18% of Atlantic salmon held in a sea cage can monopolise half the distributed feed (Thorpe *et al*. 1990). The net result is that under-feeding can lead to disparities in feed intake, heterogeneous growth and increased size variation of fish within the rearing unit (McCarthy *et al*. 1992; Jobling & Koskela 1996; Hatlen *et al*. 2006). This is undesirable for the farmer, because a wide size range makes fish more difficult to manage and because market forces usually demand fish of uniform size.

Feed deprivation can induce a stress response in fish; for example, in the jundiá (*Rhamdia quelen*), a subtropical South American fish that is cultured in ponds, plasma cortisol concentrations are high in fish that have been deprived of food for 7–14 days, returning to pre-fasting levels within 4 days of refeeding. Cortisol secretion in food-deprived fish is an adaptive response that leads to mobilisation of energy reserves, so whether welfare is compromised during short periods of feed deprivation is not clear (Barcellos *et al*. 2010). It is clear, however, that under-feeding can result in increased competition and aggression (McCarthy *et al*. 1992; Wedemeyer 1997; Øverli *et al*. 1999) and consequently higher rates of injury. For example, underfeeding may increase the incidence of fin damage in salmonids (Damsgård *et al*. 1997) and other species, including juvenile greenback flounder, (*Rhombosolea tapirina*; Shelverton & Carter 1998) and Atlantic cod (Hatlen *et al*. 2006. Chapter 9).

### 7.5.4 The effects of over-feeding

When fish are provided with large quantities of food at times that do not match their natural appetite patterns or when they are fed at such a high rate that they cannot consume the food delivered in the time available, they are being over-fed. Over-feeding can lead to uneaten food passing through the cage or tank into the surrounding water, where it may be eaten by wild fish or may simply be dispersed into the environment. In addition, the food that the fish eat under such circumstances may be processed inefficiently, resulting in the production of large quantities of nutrient-rich faeces (Jobling 1986, 1994). Given that feed costs are high, uneaten and incompletely digested and absorbed food places an extra economic burden on production.

In addition to reducing the efficiency of production, waste feed and excessive faecal wastes due to overfeeding can cause environmental problems (Cho & Bureau 1998; Le François *et al*. 2010). For example, in trout farming, reducing the amount of feed required to produce a given weight gain (feed:gain ratio) from 1.5 to 1.0 reduces phosphorus discharge from 10–13 to 5–7 kg per tonne of fish produced (Håkansson *et al*. 1988; Alanärä *et al*. 1994). Phosphorus discharge can lead to eutrophication and potentially enhances primary production in recipient fresh waters (Cho & Bureau 1997), so reducing the discharge of phosphorus-rich effluents from fish culture might give environmental benefits. Finally, dissolved and particulate wastes within a rearing facility can decrease water quality and be detrimental to fish health (Wedemeyer 1997); this is especially the case in closed, re-circulating aquaculture systems (Le François *et al*. 2010).

### 7.5.5 Failure to match feed delivery to natural appetite patterns

#### *Reasons for discrepancies between delivery and appetite*

Feed deprivation or under-feeding may sometimes be unavoidable in fish husbandry. For example, transport may require that fish are not fed for a period prior to their being moved from one site to another. Even if feeding is not

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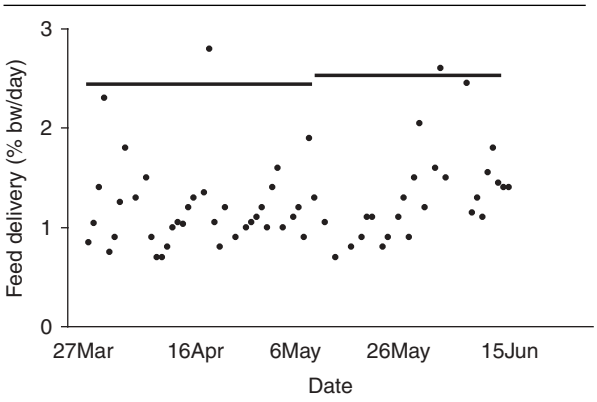


**Figure 7.17.** Daily variation in appetite in cultured fish. Daily feed delivery (% body weight/day) to Atlantic salmon post-smolts fed by an on-demand system (black symbols). Also shown (continuous black line) is the recommended feed amount according to feed tables. Adapted from Noble 2001.

intentionally reduced, unintentional food deprivation can arise from malfunction of feeding systems or from extreme weather conditions preventing access of staff to rearing units to feed the fish manually or to replenish automatic feeders. However, under-feeding can also arise from feeding fish out of synchrony with their appetite or subjecting fish to a feed management strategy that fails to provide them with adequate access to food at appropriate times (Jobling 2010b). Both under- and over-feeding can arise if feed delivery systems are programmed in such a fashion that they fail to take account of changes in the appetite of the fish. Discrepancies may arise in relation to both total amounts of feed provided and the timing of feed delivery. For example, Figure 7.17 shows the amount of food eaten by demand-fed Atlantic salmon post-smolts over a 4 month period after transfer to seawater, together with the amount of feed recommended according to a standard feed table. Most of the time the fish ate less than the recommended feed supply, perhaps because they had been recently transferred to seawater. They would have been over-fed had they been given the amount of feed indicated by the feed table. Reduced feed intake in the period immediately following the transfer of Atlantic salmon smolts from fresh water to seawater has been observed on a number of occasions (Jørgensen & Jobling 1994; Arnesen *et al*. 1998; Toften *et al*. 2003), the severity and duration of the appetite suppression depending upon when the transfer occurs. Although Atlantic salmon post-smolts may have higher plasma cortisol concentrations than do pre-smolts, this does not seem to have any direct and unequivocal relationship to appetite and feed intake.

### *Effects of immediate environmental circumstances*

A number of environmental variables can have a negative impact on feed intake of fish that are otherwise motivated to feed. These include wave action, wind and rainfall, increased concentrations of suspended particulate matter and water turbidity, and sudden changes in salinity, light conditions and temperature (Houlihan *et al*. 2001). Feeding can also be reduced by a number of husbandry practices that farmers impose upon fish. For example, both pre- and post-smolt Atlantic salmon have increased plasma cortisol concentrations (Figure 7.18a), reduced ghrelin (an orexigenic peptide; Figure 7.18b) and reduced appetite (Figure 7.18c) after short confinement stress (Pankhurst *et al*. 2008). Repeated handling leads to reduced feed intake in juvenile perch (*Perca fluviatilis*; Strand *et al*. 2007). Poor or deteriorating water quality such as low dissolved oxygen concentrations (hypoxic water) or increased dissolved ammonia can also result in reduced feed intake. For example, oxygen depletion leads to decreased food consumption in European sea bass (Thetmeyer *et al*. 1999) and increased ammonia concentrations depress feeding by lake trout (*Salvelinus namaycush*; Beamish & Tandler 1990). Disease or increased parasite loads are also potential stressors for fish and may reduce feed intake and appetite (Bloch & Larsen 1993; Roberts & Shepherd 1997).

### *Gut fullness and appetite changes*

Short-term changes in appetite in fish often reflect filling and emptying the GI tract. Failure to offer food at the correct time in relation to such changes can result not only in wastage but also inefficient digestion of the food. For example, Atlantic cod fed to satiation twice a week eat less food and grow less well than do cod fed three or five times per week (Lambert & Dutil 2001). Food intake and food conversion efficiency (FCE) are lower in small juvenile Australian snapper (*Pagrus auratus*) fed a single meal each day than in fish fed more frequently (Booth *et al*. 2008). Nile tilapia that are fed to satiation three times per day eat as much as those fed 5 times daily, but grow better and FCE is higher (Riche *et al*. 2004). This relates to the time required for the stomach to empty, which is longer than the interval between meals on a five meals per day regime. When the interval between meals is shorter than the time taken for the stomach to empty newly eaten food may pass rapidly from stomach to intestine and is digested inefficiently (Figure 7.19; Riche *et al*. 2004). In 200 g gilthead sea bream (*Sparus auratus*) at 25°C, about 60% of the feed is still in the stomach after 6 h, but the stomach is empty after 24 h (Álvarez *et al*. 2010) and juvenile Senegal sole

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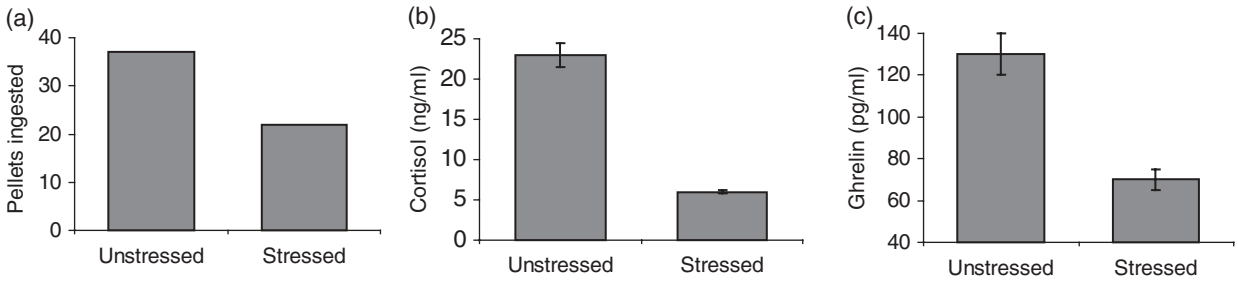


**Figure 7.18.** Effects of husbandry stress on appetite. (a) Number of food pellets ingested per meal; (b) Mean (±SE) plasma cortisol levels (ng/ml) and (c) Mean (±SE) plasma ghrelin levels (pg/ml) in pre-smolt Atlantic salmon after 1 h confinement stress. Adapted from Pankhurst *et al.* 2008.

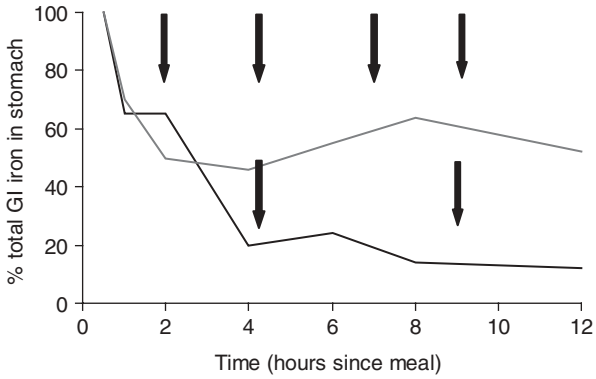


**Figure 7.19.** Meal pattern and stomach emptying. The percentage of total gastrointestinal tract iron in the stomach after feeding to satiation with a diet containing ferric oxide in *O. niloticus* fed the same daily ration either as three meals (black line) or as five meals (grey line).Vertical arrows represent subsequent feeding to satiation on 5 meals (top) and 3 meals (bottom). Adapted from Riche *et al.* 2004.

(*Solea senegalensis*) empty their stomach in 14 h at 26°C (Vinagre *et al*. 2007).

### *Regular feeding rhythms*

Superimposed upon irregular changes in appetite, fish may express more regular cycles of feed intake with tidal, daily, lunar or annual periodicity. If fish farmers fail to take account of such regular feeding cycles, fish may be over- or under-fed, with adverse consequences for fish welfare, the economics of the farming venture and the environment. One consequence of not matching feed delivery to feeding rhythms can be reduced growth of the fish, and this has been demonstrated in many species, including goldfish (Noeske & Spieler 1984), Indian catfish (*Heteropneustes fossilis;* Sundararaj *et al*. 1982), channel catfish (*Ictalurus punctatus;* Noeske-Hallin *et al*. 1985), African catfish (*Heterobranchus longifilis;* Kerdchuen & Legendre 1991), rainbow trout (Boujard *et al*. 1995; Gélineau *et al*. 1996) and European sea bass (Azzaydi *et al*. 1999). Further, failure to feed fish according to their natural appetite rhythms can lead to metabolic disturbances, such as lower body lipid concentrations and poorer protein retention (Boujard *et al*. 1995; Gélineau *et al*. 1996). Feeding regimes that fail to match the regular appetite rhythms of cultured fish may also result in low feed conversion efficiency (defined as fish weight gain in relation to the amount of food delivered), as observed in Atlantic salmon (Noble *et al*. 2007a, b) and European seabass (Azzaydi *et al*. 1999).

## 7.5.6 Solutions to problems for fish culture arising from natural appetite variation in fish

### *Feed management*

For well-established culture species, effective feed management is possible because feeding systems exist that enable feed to be delivered to the fish in amounts and at times and rates that match natural patterns of appetite. To achieve effective feed management, farmers use strategies that involve regulation of the rate, frequency and duration of feed delivery, and thereby the total amount of feed supplied to the fish within a rearing unit (Talbot 1993; Talbot *et al*. 1999). Feeding intensity, or the rate at which food is supplied within a meal, is an important aspect of feed management and should be adjusted to life history stage, to species and to environmental conditions. For example, in fish as in other poikilothermic ectotherms, low temperatures lead to reduced metabolic rates, low levels of activity, reduced feed demand and reduced rates of feed

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consumption (Fraser *et al*. 1995; Jobling 1994; Graham *et al*. 1996). If food is presented at too fast a rate, it may be wasted because the fish are unable to capture and swallow it before it passes out of the rearing unit (Ang & Petrell 1998). This is especially important in cage farming systems, where pellets may quickly pass out of reach of the fish. For example, when pellets are presented to rainbow trout held at at 5 °C at rates of between 0.2 and 4.3 pellets per fish per delivery, the faster rate of delivery results in poor growth and increased feed waste (Bailey & Alanärä 2006c). When the temperature is increased to 10 °C and then 15 °C, the fish become more active and eat larger proportions of the pellets delivered at the faster rates. The rate of feed delivery can also influence competition, with high feed delivery rates improving access to feed, and reducing competition (Grant 1993; Ryer & Olla 1995).

As far as meal frequency is concerned, studies on salmonids have shown that between one and four meals per day usually result in good growth (Elliott 1975; Landless 1976; Grayton & Beamish 1977; Juell *et al*. 1994; Thomassen & Fjæra 1996; Ruohonen *et al*. 1998), but the frequency required for best growth varies with life history stage, fish size and water temperature. For example, Cho (1990) suggests that rainbow trout larger than 200 g might be fed one to two meals per day, whereas fish smaller than 50 g should be provided with three to four meals per day. Large Atlantic salmon reared in sea cages grow well when fed one meal per day if this lasts approximately 2 h, with feed delivered in 34 portions and a pause of between 2 and 4 min between each portion (Bailey *et al*. 2003). However, meal duration has little effect on growth, body composition and feed conversion efficiency of adult Atlantic salmon (Sveier & Lied 1998). In short, it is difficult to predict in advance how much feed will be required by any given group of fish, because the amount of food needed for fish to reach satiation varies between meals (Jobling 1994) and days (Blyth *et al*. 1993). In addition, recent feeding history will also influence hunger levels and feeding activity (Houlihan *et al*. 2001; Le François *et al*. 2010).

### *Adjusting feed delivery to the natural feeding rhythms of fish*

As discussed above, fish do not feed with equal intensity at all times of the day, nor do they feed equally avidly every day; rather there are peaks in food intake both within and across days (Jobling 1994; Houlihan *et al*. 2001). Nevertheless, there are ways in which such variation can be accommodated in fish farming. When fish are fed manually, signs that the fish are becoming sated, such as reduced response to feed, can be used to decide when to stop feed delivery, but this may be inaccurate as subsurface feeding may be taking place even though surface feeding has ceased (Juell 1995; Ang & Petrell 1997; Talbot *et al*. 1999). Some automated feed delivery systems can be programmed to match what is known about natural variation in feeding activity, over a range of time scales. Thus farmers might adapt feeding regimes to coincide with patterns of activity of the fish, perhaps feeding Atlantic salmon in the morning and evening (Alanärä *et al*. 2001b). Night feeding should generally be avoided, because salmon are inefficient at detecting and capturing pellets when light intensity is low, thereby increasing the risk of feed wastage (Alanärä 1992b; Smith *et al*. 1993). Even under the most favourable night-time conditions, with a full moon and clear sky, the efficiency with which juvenile Atlantic salmon capture feed is low (35% of diurnal efficiency) and the fish may feed at less than 10% of the daytime rate when the moon is not full and the sky is overcast (Fraser & Metcalfe 1997). On a longer time-scale, European seabass undergo a seasonal change, feeding at night in winter and during the day in summer, but in spring they may be fed at different times (day, night or crepuscular) with little effect on growth (Boujard *et al*. 1996). On the other hand, seabass that are fed during the night in winter, receiving one-third of the food just before dawn and two-thirds after dusk, grow significantly better than those fed during daytime by three equally-sized meals in the morning, at mid-day and in the afternoon (Azzaydi *et al*. 2000).

### *Appetite-based demand feeding systems*

Several automatic feeding systems have been developed that allow feed delivery to be matched to changes in appetite of farmed fish. The feeding regime is adjusted to the appetite of the fish and is neither imposed nor predetermined by the farmer. Such feed delivery systems take fluctuations in fish appetite into account, something that is not done by preprogrammed, timed-release automatic feeders that deliver predetermined amounts of feed each day. Appetite-based demand feeders are of two kinds (Chapter 3), self-feeders, in which fish obtain food by pulling, pushing or biting a trigger (Alanärä 1992b), and interactive feedback systems; these detect either fish feeding activity or waste feed using infra-red sensors (Blyth *et al*. 1993), underwater video-cameras (Ang & Petrell 1997) or hydro-acoustic instruments (Juell 1991; Summerfelt *et al*. 1995) and then adjust feed delivery accordingly (Houlihan *et al*. 2001; Le François *et al*. 2010). Feeding by means of operant self-feeders has been used successfully for a number of species, including rainbow

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trout (Landless 1976; Alanärä 1994, 1996), European seabass (Sánchez-Vázquez *et al*. 1994), Atlantic salmon (Paspatis & Boujard 1996) and yellowtail (Kohbara *et al*. 2003). Interactive feedback systems are often deployed in Atlantic salmon sea cage culture (Blyth *et al*. 1993; Noble *et al*. 2008) and can also be used effectively for feeding yellowtail (Kadri *et al*. 1998), European seabass and gilthead sea bream (Andrew *et al*. 2002).

Beneficial effects of feeding to demand have been demonstrated for several species. For example, rainbow trout provided with food at 5-min intervals throughout the day grew less well than those fed using self-feeders (Alanärä 1992a); repeated feeding at short intervals seemed to induce stress. Use of demand-feeders might result in reduced aggression, as observed in African catfish (*Clarias gariepinus*; Almazán-Rueda *et al*. 2004), reduced levels of scramble competition, as seen in European seabass, gilthead sea bream and Atlantic salmon (Andrew *et al*. 2002; Noble *et al*. 2007b) and reduced fin damage (in Atlantic salmon; Noble *et al.* 2007a, c, 2008) and stress (in Nile tilapia; Endo *et al*. 2002).

### 7.5.7 Domestication and captive rearing

***Effects on feed intake***

When fish are reared for release, whether for supplementation or to re-establish populations of endangered species, it is important that they are able to display natural feeding patterns. Being motivated and able to eat the correct amounts and at the correct time can make the difference between surviving or dying, especially in the critical period just after release. For these reasons, although much remains unknown about natural appetite patterns in wild fish, it is worthwhile considering the effects of domestication and captive rearing on appetite and feeding patterns of fish.

A number of studies report differences in growth between wild and domesticated fish of the same species. For example, in Japanese flounder (*Paralichthys olivaceus*) the offspring of cross-bred brood-stock grow faster than offspring of wild-caught brood stock (Shimada *et al*. 2007). Growth and feed efficiency are higher in strains of Atlantic salmon (Thodesen *et al*. 1999) and rainbow trout (Cho 1992; Bailey & Alanärä 2006b) selected for fast growth over several generations than in the offspring of the founder populations; selected stocks have 20–25% higher growth efficiency. Differences in growth between stocks or strains of fish might result from differences in feed intake, the efficiency of nutrient digestion and uptake, or differences in metabolic rates (Billerbeck *et al*. 2000).

Differences in growth efficiency between individuals or strains might be related to the energetic costs of competitive feeding in the rearing environment or to differences in stress responsiveness (Doyle & Talbot 1986; Chapter 8). Such variation is probably reduced by selection simply due to general domestication processes; in other words, fish that thrive and grow well in captive-rearing environments may be the most efficient foragers and have the lowest energy expenditure in such environments. In a few cases appetite-related differences between wild and domesticated stocks of fish have been documented directly. For example, compared to hatchery-reared fish from unselected lines, coho salmon (*Oncorhynchus kisutch*) selected for rapid growth over many generations ingest more food, grow faster and grow more efficiently; fish of the selected line seem to be particularly efficient at using lipids for energy, sparing protein for growth (Figure 7.20; Neely *et al*. 2008).

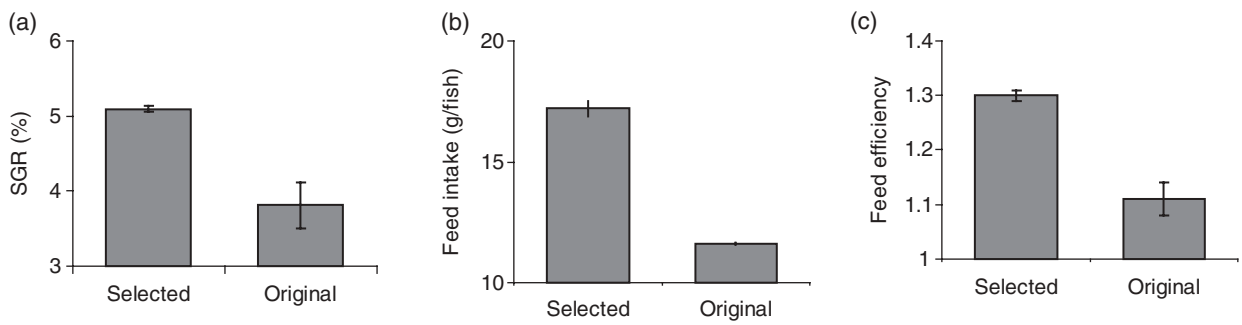


**Figure 7.20.** Effects of selection for fast growth on feed intake and processing efficiency. Mean (±SE) (a) specific growth rate (SGR), (b) feed intake (g/fish) and (c) feed efficiency (weight gain / dry food fed) in coho salmon from a strain selected for fast growth (selected) and wild fish from the original source population reared under identical conditions in the laboratory. Adapted from Neely *et al.* 2008.

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Considering the post-release effects of domestication and captive rearing, wild juvenile Atlantic salmon have fuller stomachs than do hatchery-reared fish soon after release, though this difference is short-lived (Orlov *et al*. 2006) and no differences are reported between domesticated and wild brown trout (Johnsson *et al*. 1996). Finally, captive-bred butterfly splitfins (*Ameca splendens*) are less likely to feed and more likely to fight than are wild fish (Kelley *et al*. 2006). It is not always possible from such studies to distinguish the effects of domestication and captive rearing, but whatever their origin differences in appetite and feeding patterns between wild and cultured fish could compromise survival after release.

### *Mitigating the effects of domestication and captive rearing*

When captive stocks of fish are selected for fast growth this may also lead to selection for increased food intake. Fish of highly selected domesticated stocks may therefore be at a disadvantage should they be released into the wild. They may also suffer increased rates of predation whilst foraging to meet their high food requirement and their welfare may be compromised as they compete with wild fish for food resources. Where fast growth is not at a premium, as when fish are cultured for the ornamental trade or for release for stock enhancement or re-introductions, captive rearing and breeding programmes should be designed such that they do not inadvertently select for fish with rapid growth and high food requirements.

The structure and function of the GI tract are influenced by the types and amounts of food given to fish. These, in turn, have effects on meal sizes and frequency, on short-term regulatory mechanisms and on the efficiency with which the nutrients within a given meal are digested absorbed and utilised. As such, the exposure of young fish to a range of feed types and feeding regimes prior to release may be beneficial. In addition, changes in feeding environment experienced early in life have been shown to improve learning ability and cognitive function (Kotrschal & Taborsky 2010), something that could serve to improve the chances of survival of fish reared for release into the wild.

## 7.6 SYNOPSIS

How much fish eat at any given time varies in relation to the filling and emptying of the GI tract and in relation to unpredictable environmental events such as changing water quality and the occurrence of a wide variety of stressful events. Appetite also varies in relation to regular geophysical cycles with periods ranging from tidal to annual. Rates of feed intake depend on physiological mechanisms that enable fish to monitor both their nutrient reserves and the contents of their GI tract. The signals produced serve to modulate the neuronal activity of centres within the brain that, in concert, control feeding behaviour and feed intake, as well as generating feeding rhythms. Patterns of food intake vary with fish size, age and life history stage and how much a given fish eats and when it feeds depends on both genetic and environmental influences acting on a variety of time scales, fine-tuning appetite to current and future needs. There are a number of costs to maintaining a high rate of food intake, including energy expenditure and predation risk, and to the fast growth that often results. How fast and when a fish eats represents a balance between such costs and the obvious benefits of the acquisition of a good supply of nutrients.

Fish bring these adaptive mechanisms with them into captivity. Although fish may display a degree of flexibility in when and how much they will eat, a failure to take account of the natural attributes of fish feeding biology can have many detrimental consequences for production of farmed fish. Since feed provision represents a major cost for the culture of established species and first feeding is a major bottleneck in the development of new culture species, identifying and solving such problems is important for sustainable aquaculture. A number of problems arise when cultured fish are underfed, including slow, uneven growth, high stress levels, high levels of aggression and high mortality rates. A different suite of problems can arise when fish are overfed; these include costly, inefficient production and increased environmental impact. Overfeeding and under-feeding of cultured fish arise when there is a discrepancy between delivered food and current appetite. Such a discrepancy can be the result of unpredictable changes in appetite due to immediate environmental circumstances or from failure to take account of the filling and emptying of the GI tract or of natural appetite rhythms related to geophysical cycles.

Some of the problems arising from variable feed intake in cultured fish can be addressed by adopting feeding strategies and feed management routines that comply to as great an extent as possible with the natural feeding biology of the species and life history stage being cultured. However, even the best solutions practised represent a compromise between the desirable and the practicable. Manual feeding has the advantage of being relatively cheap and of allowing some opportunity for direct monitoring of the feeding behaviour of the fish concerned. However, it is labour-intensive and time-consuming and in

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general feed is still provided at times, and sometimes also in quantities, decided upon by the farmer and not the fish. Automated feeding systems have been developed that overcome some of the problems associated with manual feeding and the use of preprogrammed, timed-release automatic feeders is common in fish culture. Timed-release automatic feeders are often programmed to dispense predetermined amounts of feed at preset time intervals, so feed delivery may not coincide with the natural feeding rhythms of the fish and so may result in either under-feeding or over-feeding, with negative consequences for both production and the environment.

On-demand feeders enable the fish to control their feeding by adjusting feed delivery to current appetite, either directly (self-feeders) or indirectly (interactive feedback systems); such systems have a number of advantages, but there are also disadvantages. For example, the simplest types of mechanical self-feeder may release feed when subjected to wind and wave action, leading to feed wastage. In addition, such feeders often deliver feed at a point source rather than dispersing it widely over the water surface; a small number of fish may gather round the feeder and exclude others from gaining access to feed. Electronically controlled self-feeders are more sophisticated in design and usually overcome these problems, but care is required to ensure that the portion of feed delivered at each trigger activation is of the correct size. The amount of feed delivered needs to be neither too small, which could induce high levels of competition, not too large, which may lead to excessive feed wastage. The feeders may also need to be programmed to prevent excessive feed delivery in the event of very high frequencies of trigger activations taking place over short time intervals. Interactive feedback systems usually rely upon the detection of waste feed to curtail delivery and so would seem to be best suited for use in the feeding of fish species that consume large meals at infrequent intervals. This is especially the case for species that display distinct rhythmic patterns with a high degree of co-ordination of feeding within the rearing unit, because of the relative ease of discrimination between feeding and non-feeding periods. Thus on-demand systems offer a number of advantages, but they are far from being a universal solution for all problems that arise from natural variation in appetite in cultured fish.

A few studies have documented higher appetite in farmed fish than in wild fish, although it is usually not possible to ascribe such differences unambiguously to genetic effects of domestication and environmental effects of captive rearing. Where differences in appetite and patterns of feeding occur as a result of domestication and/or captive rearing, this could compromise survival in released fish, but there are various ways of mitigating such effects.

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# 8
# Avoiding Predators

*Felicity Huntingford, Susan Coyle and William Hunter*

**Abstract:** This chapter describes the behaviour that protects wild fish from predators, the external stimuli that elicit such behaviour, how it is affected by nutrient status and its link with stress physiology. The way antipredator behaviour develops is considered, including how inherited differences and experience influence this process, as are costs of showing effective antipredator behaviour and how these are traded off against its obvious benefits. Although cultured fish are protected against predation, they may still experience encounters with predators and much husbandry practice may be perceived by farmed fish as a potential threat. The problems for production, welfare and the environment caused by antipredator responses in cultured fish are discussed, as are problems arising from the fact that the behaviour of released fish may deviate from that shown by fish reared in nature. Potential solutions to such problems are reviewed, based on selecting appropriate fish for culture and on using husbandry practices that reduce the incidence of antipredator responses and, where fish are cultured for release, that mitigate the effects of domestication and captive rearing. Finally, some ways in which fish farmers can make use of the natural antipredator responses of their fish to improve the effectiveness of farming operations are discussed.

**Keywords:** domestication; foraging/predation trade off; life skills training; Mauthner system; refuges; predator inspection; schooling; selective breeding; stress coping strategies; vigilance.

## 8.1 INTRODUCTION

In nature, fish are eaten by a wide variety of predators and most species and life history stages are rarely free from the threat of predation, including in some cases cannibalistic attacks. With this diversity of animals that eat fish, it is not surprising that predation is a strong selective force that generates adaptations in morphology, physiology and behaviour. This chapter describes the behaviours that protect wild fish from predation and the mechanisms that generate such protective responses, including the stimuli fish use to recognise predators. It also gives information on how genes and environment interact to determine the way antipredator behaviour develops and how the benefits of antipredator behaviour are balanced against its costs. Farmed fish are largely protected from direct predatory attack, but they have retained a set of natural defences against predators that can influence their performance in culture conditions. The final section discusses some problems in fish culture that arise through the natural protective responses of fish and how these problems can be solved using what is known about the antipredator behaviour of the species concerned.

### 8.1.1 How fish avoid being eaten by predators

The animals that eat fish, both specialised piscivores and some generalist carnivores, attack in very different ways. Consequently a variety of antipredator responses have evolved, acting at different points in the predatory

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sequence. These include adaptations that prevent fish from coming into contact with potential predators, from being detected or recognised if they do come into such contact, from being attacked once detected, from being captured if attacked and from being eaten if captured.

### *Avoiding contact with predators*

Like other prey animals, fish can avoid predation by choosing to occupy areas and habitats that are not suitable for their predators; such choices may be permanent or may be a temporary refuge sought in the presence of predators. For example, juvenile (0+ year class) perch (*Perca fluviatilis*) hide in areas of vegetation when predators are present, especially when water is clear and they can be easily detected (Snickars *et al*. 2004). Less obviously, areas of hypoxic water can potentially act as a refuge for prey species, since smaller fish tend to be more tolerant of hypoxia than larger ones (Robb & Abrahams 2003).

Prey fish can also protect themselves by being active at times when predators are inactive or when they cannot hunt efficiently (see Chapters 2 and 5–7). Young salmonids disperse from nests, or redds, at night, when risk of attack by visually hunting predators is relatively low (Mazur & Beauchamp 2003) and emergence is delayed when predatory fish are nearby (Jones *et al*. 2003). Overwintering juvenile Atlantic salmon (*Salmo salar*) change from diurnal to nocturnal activity at low temperatures, avoiding visually hunting predators such as birds and mammals that are endothermic and so can hunt efficiently at temperatures at which escape responses of fish are impaired (Valdimarssen & Metcalfe 1998, Greenwood & Metcalfe 1998; Chapter 7). In larger water bodies, many species of fish show regular daily movements through the water column (diel vertical migration – see Chapter 4). For example, in Lake Superior the cisco (*Coregonus albula*), also called lake herring, is eaten by the siscowet (*Salvelinus namaycush*), the native lake trout. Ciscos move vertically through more than 150 m each day, ascending at dusk and descending at dawn, tracking low light levels that offer protection against siscowet predation, while allowing the ciscos themselves to feed (Hrabik *et al*. 2006).

### *Avoiding detection and recognition by predators*

Prey fish that coexist with potential predators have a number of adaptations that allow them to avoid being detected or recognised as potential prey. A striking example is provided by juveniles of the Caribbean reef fish *Lobotes surinamensis*, which are the same shape and colour as dead mangrove leaves. When a leaf falls onto the surface of the water, the fish swim close to it and take up a characteristic posture with their body flush with the water surface and their small thin head bent so that it looks like the stalk of the leaf (Breder 1946). In other cases, detection is avoided by moving to and hiding in cover, as young Atlantic cod (*Gadus morhua*) do in the presence of cannibalistic conspecifics (Gotceitas *et al.* 1995). The effectiveness of such protective behaviour depends on early detection of the predator and small fish tend to be highly vigilant for signs of danger. For example, salmonid fish can detect very low concentrations of the amino acid serine (found in the skin of mammals), to which they respond by moving away (Idler *et al*. 1956). In some species, particularly cyprinids and including several that are cultured, fish whose skin has been damaged by a predator secrete a chemical alarm substance that alerts their companions to danger (Pfeiffer 1977). Among other effects, alarm substance induces fish to move away from the place in which it is detected, combining with other chemical cues in allowing prey fish to identify and avoid areas where predators are hunting and feeding.

### *Avoiding attack if detected*

A prey fish that has been detected and recognised by a predator can avoid being attacked by pre-emptive counterattack, by aggressive mimicry or by what is called 'pursuit deterrence'. In spite of being smaller than their predators, some prey fish can mount a potentially injurious counterattack, which can effectively deter predators, as when small torpedo rays (*Torpedo marmorata*) repel attacking predators by electric discharges (Belbenoit 1986) and when poison-fang blennies (*Meiacanthus atrodorsalis*) bite would-be predators with their sharp, poisonous teeth (Losey 1972). Groups of bluegill sunfish (*Lepomis macrochirus*) sometimes approach predatory turtles, effectively mobbing them into moving away (Dominey 1983). Harmless prey fish can deter attack by mimicking dangerous species, a dramatic example being the roundhead (*Calloplesiops altivelis)*, which has dark spotted skin and an eyespot behind its dorsal fin; this looks very much like the head of a Moray eel. When threatened by a predator, *C. altivelis* makes for cover, but leaves its tail exposed, presumably mimicking a disturbed and therefore dangerous eel (McCosker 1977). In some cases, prey fish make direct use of other species to avoid attack; for example, young jack mackerel (*Scomberomorus niphonius*) may associate with jellyfish as a refuge against predatory attack by other species (Masuda 2006). Predators may refrain from attacking if it is clear that a potential prey fish has detected them and so is unlikely to be captured and prey fish sometimes give pursuit-deterrence signals indicating that the predator has been detected (Hasson 1991). For example,

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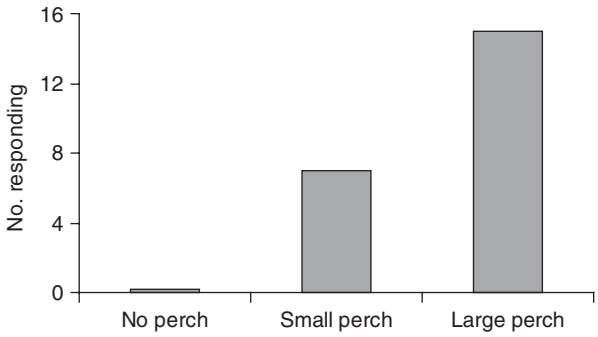


**Figure 8.1.** Escape responses adapted to predation risk. The number of pike larvae fleeing or freezing in the presence of perch, of different sizes. Adapted with permission from Engström-Öst & Lehtiniemi 2004.

characin fish (*Hemigrammus erythrozonus*) often approach a potential predator alone or in small groups and perform lateral displays in front of them. Such displays not only alert conspecifics to danger, but also discourage predators from attacking (Brown *et al*. 1999).

### *Avoiding capture if attacked*

Despite having adaptations for avoiding detection and capture, fish are often attacked by predators, but this is not the end of the story, since many species have well-developed escape responses. If an approaching predator is detected early, the prey fish often move gradually away from the predator, heading for shelter, but if a predator is close when detected, a rapid escape response is initiated. Typically, this starts with contraction of the muscles along one side of the trunk, throwing the fish into a C or S shape; the fish then flicks the tail in the opposite direction, producing rapid acceleration away from the approaching predator (Domenici & Blake 1997). Fast start responses are often followed by rapid flight from danger, details of which depend on the nature of the predator and the circumstances under which the encounter occurs. For example, pike (*Esox lucius*) larvae are more likely to show escape responses to larger predators (Figure 8.1; Engström-Öst & Lehtiniemi 2004) and escape is mostly in the horizontal plane when the predator is another fish and mostly vertically away from the water surface when the predator is a bird.

### *Avoiding being eaten once cornered by a predator*

Many kinds of fish have physical defences that protect them if captured and are often named after these defences; examples include pufferfish and porcupinefish, sticklebacks, thornbacks, surgeonfish (so-named because of their scalpel-like spines) and stingrays. Besides directly protecting fish from being eaten, painful consequences resulting from attacking fish with spines or spikes may teach predators to avoid such prey in future. Such defences have their costs; for example, for hydrodynamic reasons escape responses are slower in sticklebacks (*Gasterosteus aculeatus*) with more elaborate spines (Bergstrom 2002). Fish, therefore, sometimes have inducible defences that only develop when needed. For example, crucian carp (*Carassius carassius*) become deeper-bodied when they are exposed either to the scent of damaged conspecifics or to the scent of pike that have been feeding on carp; the deeper-bodied fish are difficult for the pike to swallow (Petterson & Brönmark 1999; Pettersen *et al*. 2000).

### *Collecting information about predators*

In order to adjust their antipredator responses to the risk posed by potential predators (Chivers *et al*. 2001), fish need to gather information about them. On encountering something that may be dangerous such as a large, unfamiliar object, larger fish or genuine predator, small fish often swim slowly towards it with frequent pauses and may spend several minutes inspecting it before retreating. During inspection visits, fish collect information about, amongst other things, species, size and motivational state of the potential predator. Inspecting paradise fish (*Macropodus opercularis*) can distinguish between predatory and non-predatory species and between real predators and models (Csanyi 1985), guppies (*Poecilia reticulata*) can distinguish between hungry and satiated predators (Licht 1989) and fathead minnows (*Pimephales promelas*) can distinguish between potential predators with different levels of hypoxic stress and therefore presenting different threats (Figure 8.2; Robb & Abrahams 2002). Prey fish such as fathead minnows (Mathis & Smith 1993) and juvenile yellow perch (*Perca flavescens*; Mirza & Chivers 2001) can also detect whether a predator has recently been feeding on prey of their species, in which case they may represent a special risk, through chemical cues emitted by the predators.

Predator inspection is risky and prey fish have various adaptations for reducing risk. For example, inspecting fish approach potential predators from the back and side, avoiding the area in front of the mouth (Magurran & Seghers 1990) and inspection is often carried out in groups. Group inspection reduces the risk for each individual, but requires complex rules about how the risks of inspection are divided. For example, given a choice, sticklebacks (*G. aculeatus*) prefer to carry out inspection with

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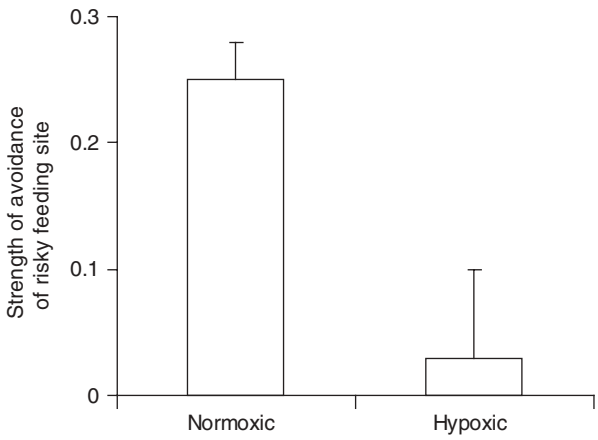


**Figure 8.2.** Using information gained during predator inspection. Mean (± SE) strength of avoidance response (relative use of a feeder in the presence and absence of the predator) in fathead minnows when exposed to yellow perch held in either normoxic or hypoxic conditions. Adapted with permission from Robb & Abrahams 2002.

companions that on previous occasions cooperated by moving towards the predator, rather than defected by hanging back (Milinski *et al*. 1990; Walling *et al*. 2004).

***Schooling as an antipredator adaptation***

One of the most striking antipredator adaptations in fish, and one with implications for aquaculture, is the formation of shoals or schools (Krause *et al*. 2002). Briefly, fish are described as being in a shoal when they form groups, but do necessarily all take up the same orientation within the group; they are said to be in a school when members of the group swim in a polarised and coordinated manner (Pitcher & Parrish 1993). Herring (*Clupea harengus*) provide a particularly dramatic example of schooling, swimming in a highly coordinated way in huge, dense schools composed of millions of fish (Nøttestad *et al*. 1996). Although shoals or schools are often large and conspicuous, swimming in a group protects fish from predators in several ways. Many vigilant individuals are better at detecting predators than one fish alone and information transfer within schools is rapid, so schooling fish are able to detect and respond to predators quickly. In addition, if a predator does attack, being in a group reduces an individual fish's chance of being captured, through a simple dilution effect (Morgan & Godin 1985). Moreover, the complex behaviour shown by schooling fish following an attack, including splitting and rejoining and forming vacuoles and fountains, serves to confuse the predator (Magurran & Pitcher 1987; Nøttestad *et al*. 2002).

Not all potential shoaling or schooling companions are equally attractive. Pelagic marine species select schooling companions on the basis of species and body size, forming groups composed of unrelated and probably unfamiliar individuals of the same species and frequently leaving one group and joining another. In contrast, some coral reef fish form stable schools composed of familiar conspecific fish of the same size. Many freshwater fish, including juveniles of several salmonid species, prefer to shoal with fish to which they are related (Krause *et al*. 2002; Parrish *et al.* 2002). Larval bluegill sunfish form more cohesive shoals in response to cues from a predator when they are in groups of related fish than when shoaling with unrelated fish. However, this effect of kinship is only seen in the offspring of males that gain fertilisations by sneaking and not in the offspring of nest-guarding, parental males (Chapter 10). Offspring of sneakers may have a greater need and ability to discriminate kin from non-kin because, unlike the offspring of parental males, they are often raised in broods of mixed parenthood (Hain & Neff 2009).

### 8.1.2 Individual variation in risk taking

Individual fish, belonging to a particular species, are not necessarily equivalent in how they respond to an actual or perceived threat of predation. Striking and consistent individual differences have been described for many species, including a number that are cultured (Huntingford & Adams 2004; Huntingford *et al.* 2011). The context in which such differences are shown include exploration of a novel, potentially-dangerous environment, predator inspection and rate of recovery from attack. This is not to say that individual performance cannot be modified by environmental influences, but that underlying differences in response are consistent when the same groups of fish are observed on different occasions. In some cases, risk-taking when confronted with a potential predator is correlated with levels of aggression or the ability to out-compete rivals, for example, brown trout (*Salmo trutta*; Sundström *et al*. 2004), rainbow trout (*Onchorhynchus nerka*; Schjolden *et al*. 2005) and grayling (*Thymallus thymallus*; Salonen & Peuhkuri 2006), so there is often a link between antipredator behaviour and aggression (Chapter 9). This pattern of individual variation, sometimes referred to as 'personality' or 'temperament', influences how fish respond to a variety of challenges, encounters with predators being just one, and so has important implications for aquaculture.

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## 8.2 MECHANISMS

This section describes some of the mechanisms that enable fish to show the behavioural responses that protect them from predation and to adapt their responses to the circumstances in which predatory encounters occur. These are relevant to fish in culture systems, since they determine how fish will respond to real or apparent danger.

### 8.2.1 External stimuli

Fish are capable of detecting and localising low frequency sounds through the lateral-line and inner ear (see Chapter 2). The neurons that control fast start responses (see below) are connected to and activated by hair cells in the lateral line system that respond to pressure waves. Inactivating these hair cells significantly impairs the reactivity of Atlantic menhaden (*Brevoortia tyrannus*) to the mechanical cues emitted by a potential predator, reducing escape distance (Higgs & Fuiman 1996). At a closer range, the visual cues presented by potential predators are important in eliciting escape responses. Relative size and movement are two important features and may act together through what is called 'looming threshold', whereby escape is initiated if the rate of change in the angle subtended on the prey's retina by the image of an approaching predator exceeds a certain threshold. This would mean that larger, faster-moving predators elicit earlier escape, as seen in both zebra danio (*Danio rerio*; Dill 1974) and in pike (Engström-Öst& Lehtiniemi 2004). Blacknose dace (*Rhinichthys atratulus*) use speed of movement to distinguish between harmless and predatory species of the same size (Fraser & Mottolese 1984), while wide-spaced eyes and a large mouth are interpreted as representing a predator by several species of small fish, for example cichlids (*Chromis caeruleus*; Karplus *et al.* 1982). In paradise fish, eye form and position are not initially used to distinguish predatory from non-predatory species, but are key in eliciting predator inspection, from which recognition follows (Csányi, 1985). Chemical cues provide a wealth of information about the presence and activity of potential predators (Kats & Dill 1998). Alarm substances not only elicit antipredator responses in fish such as minnows, but can also promote learning about other chemical cues. For example, predator-naïve minnows (*Phoxinus phoxinus*) exposed to the scent of a pike initially show no response, but after exposure to pike odour and alarm substance together, they show antipredator behavior, switching from foraging to schooling and hiding, in response to pike odour alone (Magurran 1989).

### 8.2.2 The internal dynamics of fish schools

In the wild, one important context in which visual, mechanical and olfactory cues modulate antipredator behaviour in fish is during schooling. Since many farmed fish belong to schooling or shoaling species and since they are often held at very high densities, exactly how fish respond to other fish in a group could be very important in dictating how they behave in culture systems. Attraction and subsequent response to schooling or shoaling companions depends on visual cues. For example, wild-type zebrafish prefer striped fish over those with other colour patterns (Engeszer *et al*. 2004) and three-spined sticklebacks shoal more strongly when they can detect ultraviolet signals emanating from potential shoal mates (Modaresie *et al*. 2006). Chemical cues are important in governing choice of shoal- or school-mates; for example, white cloud mountain minnows (*Tanichthys albonubes*) spend more time shoaling with fish that have eaten the same diet as themselves (Webster *et al* 2008). Hydroacoustic cues are also important; for example firehead tetras (*Hemigrammus bleheri*) without intact neuromasts in their lateral lines are unable shoal effectively (Faucher *et al*. 2010).

Knowledge of the cues that fish use to detect school mates and to coordinate their behaviour within schools have been used to explore how complex effects at the group level can emerge from a series of simple behavioural rules at the individual level. Typical 'traffic rules', as these are called, are that fish will move away from a neighbour if these fish are closer than a defined threshold distance, will move towards them if they are beyond a certain distance and will swim parallel to schoolmates if they are between these two distances. Such models include no built-in concept of a school, but examine the group-level behaviour that emerges when simulated individual fish obey such simple rules (Parish *et al.* 2002) and in some cases, the real fish in schools behave as predicted (Viscido *et al*. 2007). The important point here is that complex responses observed in a group can arise from simple decisions made by individual fish; although in nature using such traffic rules can be beneficial to the fish concerned, this may not be the case when fish are in culture systems.

### 8.2.3 Some internal factors that control and mediate antipredator behaviour

#### *The neurobiology of escape responses in fish*

The neurobiology of fast escape responses to a rapidly approaching predator has been extremely well characterised and is based on what is called Mauthner system. This system arises in the brain stem and consists of one large myelinated fibre on either side of the brain, each extending the whole length of the spinal cord on the opposite side of the trunk. These large fibres activate motor neurons innervating the trunk muscles on that side and inhibit those

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on the opposite side. Because the axons are large, action potentials are transmitted rapidly down the spinal cord. The Mauhner neurons are connected to and activated by hair cells that are sensitive to pressure waves (Chapter 2); activation is extremely rapid, taking 3–4 ms. As the Mauthner neurons cross over, pressure waves on one side of the body stimulate muscles on the opposite side and once one Mauthner neuron is activated, it inhibits activity in its opposite number. The overall response is extremely rapid, as it needs to be (Zottoli & Faber 2000).

***Nutritional status and antipredator behaviour***

Exactly what a fish does when confronted by a predator is adjusted according to its needs and a variety of internal factors mediate the response of fish to the cues emitted by potential predators. One important internal variable is energetic status, antipredator responses often being suppressed by food deprivation; for example, hungry juvenile Atlantic salmon spend less time in a refuge when there are predators about than do well fed fish (Vehanen 2003). Response to predators is also suppressed by increased metabolic needs; for example, growth hormone (GH) stimulates both growth and metabolic demand (Chapter 2). The effects of GH on behaviour has attracted interest because GH transgenic fish of several species have been generated. In rainbow trout raised levels of GH suppress responses to simulated attack by an overhead predator, probably through the increase in appetite that the hormone induces (Johnsson *et al*. 1996). Sham injected wild brown trout tend to avoid a feeding area when it contains a predator, whereas trout injected with GH fail to do so (Johnsson *et al*. 1996b).

***Stress physiology and antipredator behaviour***

Physiological stress responses provide strong links between internal state and antipredator responses. Acute activation of a physiological stress on encountering a predator facilitates effective antipredator responses in prey fish, although longer tem activation of the same system can compromise the ability of fish to respond effectively to predators. For example, antipredator responses are impaired in recently-handled coho salmon (*Oncorhynchus kisutch*; Olla & Davis 1989), in juvenile walleye pollock after exhaustive exercise (Ryer 2002) and in juvenile Atlantic salmon held at low pH (Olivier *et al*. 2006). Individual variability in responsiveness to predators is associated with differences in neuroendocrinological stress responses. It is well documented in mammals and birds that some, so-called proactive, individuals tend to take risks in various contexts, typically responding to challenge by activation of the sympathetic nervous system and strong release of adrenaline. In contrast, reactive individuals avoid risk and their stress response is typically based on activation of the parasympathetic nervous system and release of cortisol. Additionally, proactive and reactive individuals also show differences in post-stress serotonin metabolism. Together, such differences in stress responsiveness, or coping strategy, may underpin variable responses to predation risk in fish. The best evidence for this comes from comparison of behaviour and brain biochemistry in rainbow trout selectively bred for differences in cortisol responsiveness to confinement stress (Schjolden *et al*. 2006; Figure 8.3a). High responsive fish that show a strong cortisol response to stress not only take longer to resume feeding after transfer to a novel tank than do low responsive fish (Figure 8.3b), but also tend to lose pairwise dominance encounters with size-matched low responsive opponents.

### 8.2.4 Summary of the mechanisms that control predator avoidance in fish

Fish use a range of cues, including visual, mechanical and chemical, to detect and assess predators. On detection of a fast approaching predator, a rapid escape response initiated by the Mauthner system facilitates predator avoidance, while during schooling, visual and possibly mechanical cues from nearby companions can generate and modulate complex responses at the group level. How a fish responds to the cues presented by a predator is flexible and mediated by internal factors such as nutrient status and stress physiology. Although acute activation of the neuroendocrine stress system may promote effective antipredator behavior, fish that have been stressed by handling or forced swimming are more prone to predation. Both the neuroendocrine and behavioural responses to risk of predation depend on an individual's stress coping strategy. Proactive fish, that have stress responses based on activation of the sympathetic nervous system and adrenaline release, take greater risks than do reactive fish that have stress responses based on activation of the para-sympathetic nervous system and cortisol release.

## 8.3 DEVELOPMENT

The predators that threaten fish of a particular species change as the fish increase in size and age and this is often reflected in shifts in antipredator behaviour as they develop from larvae to adults. Such changes, and hence the responses of adult fish to predators, depend partly on the genes that the young fish have inherited from their parents and partly on the environment in which they develop.

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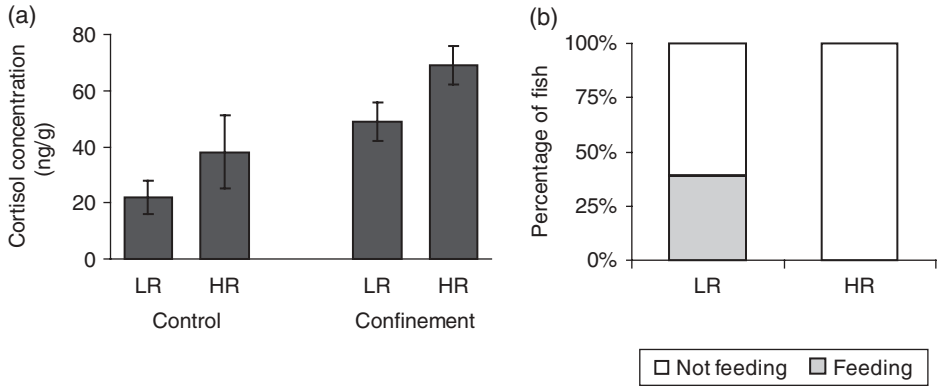


**Figure 8.3.** Stress-coping strategies in rainbow trout. (a) Mean (±SE) plasma cortisol concentrations in rainbow trout subjected to selection for low (LR. Open bars) and high (HR. Grey bars) cortisol production in response to confinement, in both base line conditions and after 1h of confinement. Adapted with permission from Øverli *et al*. 2002. (b) The percentage of fish from the LR and HR lines feeding and not feeding after 7 days in isolation in a novel tank. Adapted with permission from Øverli *et al*. 2005.

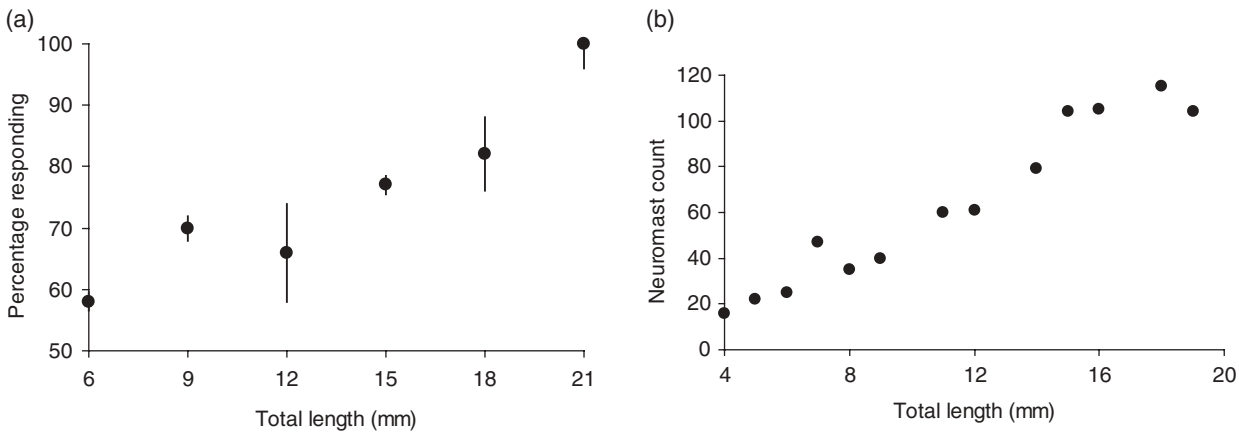


**Figure 8.4.** Ontogeny of escape responses in menhaden. (a) Percentage of larvae, of different lengths, tested in the light responding to an approaching object. Adapted with permission from Higgs & Fuiman 1996. (b) Mean number of superficial neuromasts on one side of the body in relation to total body length. Adapted with permission from Higgs & Fuiman 1996.

### 8.3.1 The ontogeny of predator avoidance

Incipient protective responses appear very early in development; for example, both rainbow trout and zebrafish embryos respond to touch from an early age and complete startle responses are shown just before hatching (Eaton *et al*. 1977), by which time the neural and musculoskeletal systems needed for an escape response have developed. Although coordinated escape responses appear early in development, they improve in effectiveness with age, in terms of both the readiness with which escape responses are elicited (Figure 8.4a; Higgs & Fuiman 1996) and their speed (Fuiman *et al.* 1999).

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***Development of sensory systems***

Ontogenetic changes in sensory morphology have important consequences for larval antipredator behaviour. For example, inflation of the auditory bulla in larval herring coincides with a dramatic increase in responsiveness to predatory attacks (Blaxter & Batty 1985). In menhaden (*Brevoortia tyrannus*), responsiveness to mechanical stimuli increases gradually with size, reflecting ontogenetic development of neuromasts (Figure 8.4b) and formation of lateral line canals on the head (Higgs & Fuiman 1996). Comparison of rates of development of sensory responsiveness in three species of clupeid fish (bay anchovy, *Anchoa mitchilli*, scaled sardine, *Harengula jaguana*, and menhaden) suggest that these may be adaptations to local predation regimes. For example, the relatively early development of visual and acoustic sensitivity in anchovies may relate to earlier exposure to predators in their estuarine habitat (Higgs & Fuiman 1998). In terms of more complex sensory processing, paradise fish develop the ability to recognise the eyes of predators between 15 and 20 days of age (Miklosi *et al*. 1995).

***Development of motor systems***

The development of the Mauthner system has been studied in detail in zebrafish; the Mauthner axons continue to grow throughout the life of the fish, but the extracellular matrix stops growing after 6 months (Arata & Nakayasu 2003). Once the basic components of the Mauthner system are in place, gradual changes occur in the nature of the fast start response as fish get older. In rainbow trout, the distance travelled during the fast start response increases with body length, regardless of developmental stage, whereas maximum speed, which also increases with age, depends more strongly on developmental stage (in particular, strengthening of the skeletal system and growth of muscles) than simply on body length (Webb 1978). Age-related increases have been reported in the size and number of muscle fibres in several species of fish. The ability of larval red sea bream (*Pagrus major*) to escape from predatory jelly fish increases as bones and other tissues needed for effective swimming become better developed (Nakayama *et al*. 2003).

***Ontogeny of schooling***

In many marine species, young fish start to school at the time of metamorphosis from the larval to the juvenile stage. In young striped jacks (*Pseudocaranx dentex*), the ability to hold station with reference to moving objects, based the optomotor response (Chapter 4), appears at a size of 4–6 mm, mutual attraction between conspecifics is not observed until a size of about 12 mm and full schooling behaviour does not occur until the fish are at least 16 mm in length. By this time, the receptor cells in the eyes and the lateral line organs have developed (Masuda & Tsukamoto 1998). In Spanish mackerel (*Scomberomorus niphonius*) schooling starts from about day 17–19 posthatch, with nearest neighbour distances getting smaller and swimming within groups becoming polarized. This coincides with completion of metamorphosis and a change in the risk of sibling cannibalism, which is intense in this species (Masuda *et al*. 2003).

### 8.3.2 Genetic influences on antipredator behaviour in fish

***Effective escape responses in predator-naïve fish***

The gradual appearance of escape responses as young fish develop is often the result of hard-wired maturational processes, effective evasive responses in fish with no previous experience of predatory attacks being seen in pike (Engström-Öst & Lehtiniemi 2004), Altantic salmon (Hawkins *et al.* 2004), Chinook salmon (*Oncorhynchus tshawytscha*; Berejikian *et al*. 2003) and Arctic charr (*Salvelinus alpinus*; Vilhunen & Hirvonen 2003). More complex aspects of antipredator behaviour can also develop without direct experience of predators. For example, young paradise fish readily explore larger heterospecific fish at first encounter (Gerlai & Hogan 1992) and fish with no experience of natural predators still respond strongly to model predators with eyespots (Gerlai 1993; Miklosi *et al*. 1997). Predator-naive bluegill sunfish larvae shoal more cohesively when exposed to the scent of a predatory fish than they do in the absence of such a chemical stimulus (Hain & Neff 2009).

***Inheritance of antipredator responses***

As described above, individual fish can differ strikingly in how they respond to potential predators and one possible cause is genetic differences between the fish concerned. Evidence that this might be the case is provided by observed differences in antipredator behaviour in fish from different populations, especially when these persist when fish are reared under standard conditions. For example, zebrafish with different genetic background differ in response to a novel object (Wright *et al*. 2003) and in the extent to which foraging is suppressed by the presence of a predator (Oswald & Robison 2008). Captive-reared guppies (*Poecilia reticulata*) originating from populations that are naturally exposed to a high risk of predation show stronger behavioural responses when confronted with a potential predator than do laboratory-reared progeny of fish collected from low-risk sites; these behavioural

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differences are associated with larger swimming muscle mass (Odell *et al*. 2003). Such results suggest that the original differences between populations are the result of genetic differences, though maternal effects (Chapter 2) are often not ruled out by such studies.

A number of studies using classic genetic research tools have identified inherited differences in antipredator behaviour in fish. Thus, family studies and comparison between inbred strains in several species of fish have identified a significant heritability for components of antipredator responses. Examples include rate of exploration of a potentially dangerous environment and response to a novel object in paradise fish (Gervai & Csanyi 1985), predator inspection in three-spined sticklebacks (Bell 2005) and avoidance of predator models in paradise fish (Miklosi *et al*. 1997). In a slightly different context, vulnerability to recreational angling is a heritable trait in largemouth bass (*Micropterus salmoides*), high vulnerability being associated with higher resting heart rate and lower scope for cardiac output (Cooke *et al*. 2007). Rapid selection-induced divergence in physiological stress responsiveness in rainbow trout, with an estimated 41% of the initial variation in stress responsiveness being be explained by genetic differences (Pottinger & Carrick 1999), is associated differences in risk taking between strains (Øverli *et al*. 2002). Rainbow trout with inherited differences at the major histocompatibility locus show significant differences in brain structure and these are reflected in behavioural differences. Fish that are homozygous for one particular allele are quick to explore a novel environment, those homozygous for the alternative allele are slow and heterozygotes are intermediate (Azuma *et al*. 2005). Analysis of F2 hybrids between two strains of zebrafish that differ in response to a novel object identified three loci with a large effect on this behaviour (Wright *et al*. 2006). As a final example, antipredator responses are suppressed in GH-transgenic Atlantic salmon (Abrahams & Sutterlin 1999) and channel catfish (*Ictalurus punctatus*; Dunham *et al*. 1999).

### 8.3.3 Environmental effects

Even though young fish often respond appropriately on their first encounter with a predator and inherited differences in antipredator behaviour exist in many species, how an individual fish responds when threatened or attacked is influenced by experiences at various points during its life.

#### *General environmental effects*

In some cases, environmental effects on the development of antipredator behaviour are of a general nature. Fish size is a critical determinant of predation risk; for example, young of the year perch in the size range 30–70 mm are particularly vulnerable to cannibalistic attacks (Magnhagen 2006) and any factor that alters growth rate will influence vulnerability to predation, as young fish come into and pass out of such 'predation windows'. Zebrafish embryos develop more rapidly when exposed to alarm substance from adult fish (Mourabit *et al*. 2010), perhaps improving their survival chances. Somewhat more specifically, particular nutrients may speed up the development of effective avoidance responses. For example, larval red sea bream fed diets rich in highly unsaturated fatty acids are more effective at escaping from jelly fish than are those given diets without these essential fatty acids (EFAs). The EFAs are needed for ossification of the vertebral column, for development of the nervous and sensory systems and for maintenance of intra- and intercellular signalling (Nakayama *et al*. 2003). Newly emerged brown trout that have been exposed to low oxygen levels (hypoxia) during development are less effective at escaping from piscivorous fish than are those reared under normoxic conditions, possibly because of detrimental effects of oxygen deficiency on neuro-endocrine development (Roussel 2007).

Effects of environmental conditions on the development of antipredator responses can also be indirect, via maternal effects (Chapter 2). Larval croakers (*Micropogonias undulates*) whose mothers were exposed to methyl mercury show slower escape responses to both vibratory and visual stimuli than do larvae whose mothers were not exposed to this toxicant (Alvarez *et al*. 2006). Sockeye (*Onchorhynchus nerka*) salmon parr hatched from eggs of moribund females fertilised by healthy males show diminished startle responses and weaker shoaling than do parr from eggs laid by females in better condition (Tierney *et al*. 2009). Damselfish (*Pomacentrus amboinensis*) that develop from eggs treated with cortisol hatch at a smaller size than control fish and they have smaller eyes and yolk sacs (McCormick 1998). Since size, visual acuity and nutrient status all influence antipredator responses, the indications are that maternal stress will influences this behaviour in their young. Given the stressful nature of many culture systems and husbandry practices, such effects may well be relevant in aquaculture.

#### *Learning and the development of antipredator responses*

Environmental effects on the development of antipredator behaviour can be based on learning, but not necessarily through direct encounters with a predator (Kelley & Magurran 2003). For example, as described in Chapter 1, three-spined stickleback removed from their father before

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hatching and reared as orphans show less effective escape responses than do those reared by their father. Parental sticklebacks chase straying young, catch them in their mouth and spit them back into the nest and it seems that fry learn effective escape manoeuvres when avoiding their assiduous father (Tulley & Huntingford 1987). Paradise fish that have been reared by their father show stronger avoidance of models with eyespots than do orphaned fish, perhaps because they have learned about the significance of eyes during interactions with their father (Miklosi *et al*. 1997).

Paternal chases are usually benign, whereas predatory attacks are dramatic and aversive events, so are likely to represent a much stronger conditioning stimulus. Encounters with predators have profound and long-term effects on subsequent antipredator behaviour in fish through various forms of learning. Fish can learn to associate specific areas with an aversive experience, including attack by a predator. For example, in paradise fish electric shock promotes avoidance of a previously favoured area, an effect that is amplified by the presence of a model with eyespots (Csányi & Gervai 1986). Fish can also learn which potential predators are dangerous through a process of habituation. For example, minnows (Magurran & Girling 1986) and paradise fish (Csányi 1986) cease to respond to dummy predators when these are presented repeatedly with no adverse effects. Fish can also learn the reverse lesson, namely that a possible predator is in fact dangerous, through conditioned association of its presence with an aversive experience. For example, after a few simulated chases by a novel predator, predator-naïve Nile tilapia (*Oreochromis niloticus*) develop effective protective responses, including freezing, scattering and avoidance, and these effects persist for many weeks (Mesquita & Young 2007). The conditioned stimulus need not be a direct attack, but can take the form of aversive odorants (Kelley & Magurran 2003). Thus, predator-naïve glowlight tetras (*Hemigrammus erythrozonus*) can be conditioned to avoid the odours of non-predatory species such as goldfish (*Carassius auratus*) by exposure to odours from such a species mixed with that of a predator, the largemouth bass (Darwish *et al*. 2005).

The ability of young green swordtails (*Xiphophorus helleri*) to avoid cannibalistic attacks by adults improves during the first few hours *post-partum*, possibly due to learning from experience of avoiding earlier attacks (Jones *et al*. 2008). Early social experience can also influence shoaling decisions; for example, when zebrafish are given a choice of shoals consisting of fish with different colour patterns, they prefer to shoal with fish of the colour pattern with which they have been reared (Spence & Smith 2007). In addition, information about predators and effective responses to them can be transferred between shoal mates; for example, naive zebrafish can learn an escape route by watching other fish using it (Lindeyer & Reader 2010).

### 8.3.4 Summary of the development of predator avoidance

Young fish often show effective escape responses to appropriate stimuli on first encountering a predator. Subsequently, strongly size- and age-dependent improvements in the effectiveness of antipredator responses are often seen, due to the development of the sensory and musculoskeletal systems that underpin such responses. In several species, breeding studies have shown that differences in antipredator responses are heritable and in a few cases the specific genetic loci responsible for changed responses have been identified. Inherited antipredator behaviour may be modified throughout a fish's life by experience and learning, so environmental and genetic effects combine to determine just how juvenile and adult fish respond to potential predators.

## 8.4 FUNCTIONS

In a general sense, the benefits of the various responses of prey fish to the risk of predation are obvious and, in some cases, behavioural biologists have been able to measure the effectiveness of antipredator responses. It is worth noting that when prey fish encounter predators they are often in groups, so to be sure of surviving, the important thing for an individual is not necessarily to have perfect protection, but simply to be better protected than at least some of its companions.

### 8.4.1 Benefits of antipredator behaviour

#### *Benefits of avoiding contact with predators*

By way of illustration of the importance of appropriate timing for avoiding predators, Atlantic salmon that disperse from the nest in which they were laid late in the season enjoy higher survival rates than those that disperse earlier. Survival rates being approximately 54% and 8%, respectively (Brännäs 1995). The importance of appropriate use of space is demonstrated by the fact that juvenile pink salmon (*Oncorhynchus gorbuscha*) that remain in shallow, near-shore habitats experience lower predation rates than those that disperse into deeper water, predation risk increasing by a factor of 5 in deep water (Willette 2001). When cannibalistic adult perch are present, juvenile perch survive much better when shelters are available

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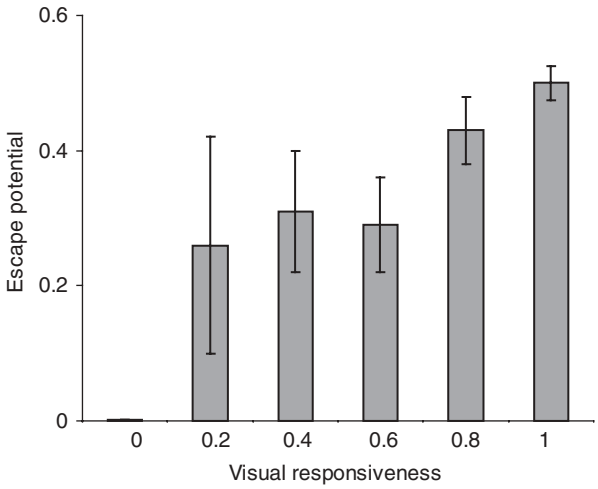


**Figure 8.5.** Benefits of vigilance. Mean (± SE) escape potential (proportion of escapes in relation to the number of predatory attacks received) in relation to visual responsiveness (proportion of visual stimuli eliciting a response) in red drum larvae. Adapted with permission from Fuiman *et al.* 2006.

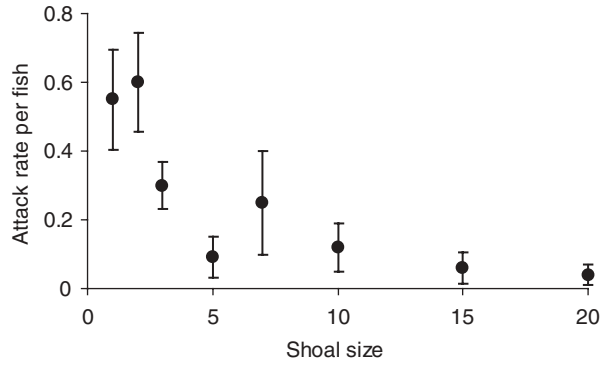


**Figure 8.6.** Effectiveness of shoaling as an anti-predator defence. Mean (± SD) attacks per fish per min in killifish exposed to a perch in shoals of different sizes. Adapted from Morgan & Godin 1985.

(Eklov & Persson 1995). The benefits of using a refuge can be indirect; juvenile Atlantic salmon in shelters have a lower metabolic rate than do those without shelter, thereby gaining an energetic as well as a safety benefit from hiding (Millidine *et al*. 2006).

***Benefits of vigilance and escape trajectories***

When red drum (*Sciaenops ocellatus*) larvae are attacked by killifish (*Fundulus similis*), individual differences in responsiveness to visual stimuli prior to attack account for 11% of the variation in survival (Figure 8.5; Fuiman *et al*. 2006). Exactly how a fish responds to an attack also influences the effectiveness of escape attempts. For example, angelfish (*Pterophyllum eimekei*) fleeing from a sound stimulus concentrate their responses between 130 and 180° of the direction of the stimulus. This maximizes the potential for escape because, although a predator will be larger and able to move faster, the prey, being smaller, can turn at a sharper angle (Dominici & Blake 1993; Dominici 2002).

***Benefits of mimicry and counterattack***

Mimicry can be an effective antipredator measure as shown by the fact that potential predators approach fish models less as they increasingly resemble a toxic species of pufferfish (*Canthigaster valantini*; Caley & Schluter 2003). The effectiveness of counterattack is illustrated by poison-fang blennies, which have sharp, poisonous teeth that they use to bite predators that capture them. In such cases, the predators make vigorous shaking movements, as though in pain, and often spit the blennies out; removing the teeth of the blennies removes their protection (Losey 1972). The effectiveness of predator deterrence signals is illustrated by the fact that cichlid predators are much less likely to attack glowlight tetras that are showing fin flicking than those that are not (Brown *et al*. 1999).

***Benefits of group living***

On detecting a predator, prey species often form shoals, switch from shoaling to schooling and jostle for central positions within the group. Such responses help to protect fish from predation, via a dilution effect (Figure 8.6) and through exchange of information. Thus, fathead minnows in a shoal with companions that have been prevented from producing an alarm substance gain less protection from predatory attacks by pike than do those whose shoal mates produce an alarm substance (Mathis & Smith 1993). The benefits of being in a group may depend on an appropriate choice of companions; for example, fathead minnows perform more effective antipredator behaviour when in the company of familiar, as opposed to unfamiliar shoal mates (Chivers *et al*. 1995).

### 8.4.2 Costs of antipredator behaviour

Clearly, the responses of fish to the threat of predation confer protection, but this may come at a cost. Developing and maintaining the physical attributes needed for effective

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antipredator responses can involve substantial metabolic costs, as can performance of the responses themselves. For example, cardiac output increases in prey fish (largemouth bass) following simulated non-lethal predatory attack by piscivorous birds to an extent dependent on species of predator and size of prey (Cooke *et al*. 2003). In addition, some components of the antipredator responses of fish may lead temporarily to increased predation risk. In particular, predator inspection provides useful information about the risk posed by a potential predator, but this information is obtained at the expense of increased risk of attack and injury. Thus, the probability of a three-spined stickleback being attacked while inspecting a pike increases markedly as it approaches the predator, though risk is substantially reduced by inspecting in pairs (Milinski *et al*. 1997).

Another major cost of antipredator interactions comes through interference with other important activities, foraging being the one that has received most attention. For example, the deeper body that crucian carp develop in response to risk of predation by piscivorous fish makes them harder to eat and so provides protection, but it increases the metabolic costs of swimming (Pettersson & Brönmark 1999) and impairs effective competition for food (Pettersson & Brönmark 1997). Likewise, habitat shifts that take prey out of contact with potential predators may put them in situations that are less suitable for feeding. Japanese minnows (*Pseudorasbora parva*) move into shallow water in the presence of predators; they experience fewer attacks, but the price they pay is reduced food intake and slower growth (Sunardi *et al*. 2007). Atlantic salmon fry that emerge from the nest late in the season suffer low predation during dispersal, but they have poorer survival than early-emerging fish after dispersal (approximately 25% and 57% survival respectively), probably because by the time they settle, the best feeding sites are already occupied (Brännäs 1995).

Maintaining vigilance also imposes a foraging cost. Juvenile Atlantic salmon foraging under predation threat feed indiscriminately rather than selecting optimally-sized prey (Metcalfe *et al*. 1987). Capture success by perch feeding on smaller conspecifics is decreased by the presence of predators in a rather complex way that depends on the size difference between the fish concerned (Lundvall *et al*. 1999) and scanning for predators impairs spatial learning in minnows (Johnsson & Sundstrom 2007). Such short-term responses have cumulative effects on growth and young walleye over-wintering in the presence of predators lose significantly more weight and deplete their energy reserves more quickly than do those over-wintering in the absence of predators (Pratt & Fox 2002). On the other hand, bluehead wrasse (*Thalassoma bifasciatum*) in groups grow slower than do solitary fish, even though they spend more time foraging, paying a cost for this antipredator behaviour in terms of increased competition (Wilson-White & Warner 2007).

### 8.4.3 Integrating costs and benefits

Fish balance the costs and benefits of their antipredator responses, optimizing fitness in a variety of ways, one being by adjusting antipredator responses to hunger level. For example, well-fed Brazilian catfish (*Pseudoplatystoma coruscans*) show a full alarm response (rapid escape followed by freezing) to conspecific skin extract, but when food-deprived they show only a partial response, moving away but not freezing (Giaquinto & Volpato 2001). Hungry juvenile Atlantic salmon spend less time hiding in the presence of a predator (Vehanen 2003) and less time immobile after a simulated attack (Gotcietas & Godin 1991) than do well-fed fish. For overwintering juvenile Atlantic salmon, daytime feeding is profitable in terms of rapid growth, but suboptimal in terms of risk of predation and hiding in shelters during the day and emerging by night to feed poses less of a predation risk per unit of food gained (Metcalfe *et al*. 1999). In the context of schooling, there is competition for food among group members and hungry fish sometimes leave schools and forage alone. For example, walleye pollock (*Theragra chalcogramma*) that have been deprived of food form less cohesive shoals than do well fed fish, even when attacked by a predator (Sogard & Olla 1997). Fish at the periphery of schools and shoals are more vulnerable to predators than those in the centre of the group, but fish at the front of a school will often gain more feeding opportunities (Figure 8.7a). Hungry fish tend to position themselves near the front of a group, whereas satiated fish move back towards the rear (Krause *et al*. 1992; Figure 8.7b).

### 8.4.4 Summary of the functions of antipredator behaviour

There are obvious benefits in avoiding predation and the various antipredator responses of fish promote survival in different ways. However, showing such responses incurs costs in terms of energy expenditure and of time taken from other important activities such as feeding. How fish behave in any specific encounter with a predator represents a balance between such costs and benefits. Of particular relevance to fish culture is the fact that fish trade off the need (real or perceived) to avoid predation against the need to acquire food, taking greater risks when hungry and

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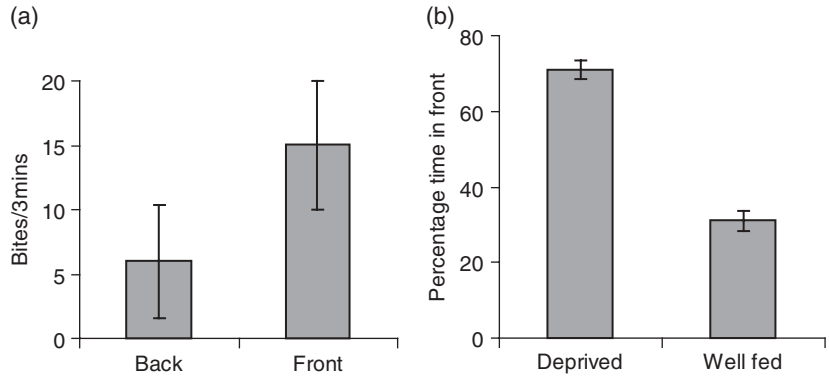


**Figure 8.7.** Trading off hunger and shoaling. (a) Mean (± SE) feeding rates (bites per 3 minutes) of juvenile roach at the front and back of a small shoal. Adapted from Krause *et al.* 1992. (b) Mean (± SE) percentage of time spent in the front of a shoal of 2 by roach that had been deprived of food for 4 days or well fed. Adapted from Krause *et al.* 1992.

avoiding danger when well fed, with clear consequences for growth rates.

## 8.5 IMPLICATIONS FOR AQUACULTURE

Even though cultured fish are to a large extent protected from predators, such protection is not perfect and a variety of predators make attacks on cultured fish. In addition, many husbandry practices may be perceived as threatening by cultured fish and so may elicit antipredator responses The following sections explore the circumstances in which real or apparent predatory attacks occur in culture systems and highlight the potential problems arising from the way fish respond to them. Potential solutions to these problems are also considered.

### 8.5.1 The incidence of antipredator behaviour in culture systems

Within farm environments, fish are usually protected from direct predatory attack, but natural antipredator adaptations are still relevant to fish culture for a number of reasons. In spite of the efforts of farmers, piscivores sometimes attack farmed fish, causing stress, injury and mortality. In the case of farmed salmonids in sea cages, predators include grey and harbour seals (*Halichoerus grypus* and *Phoca vitulina*), otters (*Lutra lutra*), mink (*Mustela vison*), grey herons (*Ardea cinerea*) and cormorants (*Phalacrocora carbo*). Seals are reported as predators at many salmon farms in Scotland (Quick *et al*. 2004) and seals are also known to attack farmed sea bass and sea bream (Güçlüsoy & Savas 2003). Bluefish (*Pomatomus saltatrix*) congregate around seabass and sea bream farms, breaking into the cages and attacking the fish confined in them (Sanchez-Jerez *et al*. 2008). First feeding larvae of the pacu (*Piaractus mesopotamicus*) and tambaqui (*Colossoma macropomum*) are reared in nursery ponds that are fertilised to build up the zooplankton populations upon which the larvae feed. Adults of predaceous zooplanktonic copepods present in the ponds attack and damage the larval fish (Fregadolli 2003) and the fish larvae may have limited escape opportunities within the nursery ponds. In addition, where farmed fish are carnivorous there is a threat of cannibalistic attacks on smaller individuals, at least during early life history stages (see Chapters 4 and 5). Cannibalism is estimated to be responsible for between 15 and 90% of mortality experienced in larviculture (Hecht & Appelbaum 1988).

In addition to direct attacks, farmed fish may be exposed to cues that in nature would be indicative of predation risk, often without the fish having the opportunity to take evasive action. Examples might include exposure to visual, olfactory or mechanical cues from predators outside farm cages. In addition, farm workers may inadvertently send out signals that are interpreted by the fish as indicating the presence of a predator; these might include scents, as when salmonids avoid serine from mammalian skin (Idler *et al*. 1956), visual cues, as when people and objects loom over the water surface, and mechanosensory cues, as when farmed fish are exposed to noise from boats, pumps and other farm equipment. Finally, common farming practices such as netting, handling and slaughter may simulate a predatory attack on the fish. All these effects are likely to elicit stress responses in fish held in culture conditions (see Chapter 2).

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**Table 8.1.** Predatory interactions and antipredator responses in cultured fish and some potential problems caused by these.

| Event | Implications for production | Implications for welfare | Implications for the environment |
|---|---|---|---|
| Direct attacks by predators & cannibals | Mortality rates increase<br>Production lost through injury & related diseases | Injury & disease compromise the welfare of individual fish | More disease in farmed fish may mean more disease transfer to wild fish |
| Exposure to unsuccessful attacks by predators & cannibals. | Growth lost through stress-induced reduction in feeding & in feed conversion efficiency | Chronic or repeated stress responses compromise the welfare of individual fish | Less efficient use of food due to stress means that more feed is needed & wasted |
| Injury arising from anti-predator responses executed in a confined space | Production lost through injury & stress-related related diseases | Injury & disease compromise the welfare of individual fish | More disease in farmed fish may mean more disease transfer to wild fish |
| Stress responses to husbandry events interpreted as predation risk | Growth lost through stress-induced reduction in feeding & in feed conversion efficiency | Chronic or repeated stress responses compromise the welfare of individual fish | Less efficient use of food due to stress means that more feed is needed & wasted |

### 8.5.2 Adverse effects of antipredator behaviour in culture systems

Thus in spite of living in a protected environment, cultured fish experience real and perceived predatory attacks and the responses that these elicit can have adverse consequences for production, welfare and the environment (Table 8.1). In the first place, attacks by predators can directly compromise production and welfare through mortality and injury. For example, having entered sea bream cages through holes in the net walls, bluefish feed on the cultured fish, often taking some body parts and leaving numerous severely injured fish (Sanchez-Jerez *et al*. 2008). Predaceous copepods can cause severe fin damage to larval *Piaractus mesopotamicus* and larvae held in enclosures that prevent the entry of such copepods experience much lower mortality (Figure 8.8a) and fin damage (Figure 8.8b) than do those reared without this protection (Fregadolli 2003). In addition, the adverse effects of cannibalism among cultured fish are well documented (Chapters 5) and mortality resulting from predatory attack by conspecifics can be very high. For example, green swordtails cultured for the ornamental trade may suffer high levels of cannibalism just after birth, with more than half of the neonates being eaten by adults (Jones *et al*. 2008). Larval swordtails can evade would-be cannibals by moving downwards towards the substratum (Jones *et al*. 2008), but the fleeing fish may injure themselves or their companions.

Experiencing and responding to real or perceived attack elicits stress responses, which bring with them a number of adverse consequences (Chapter 2). Cortisol levels are higher in zebrafish exposed to a predatory species (*Parachromis managuensis*) than in fish reared in the absence of a predator (Barcellos *et al*. 2007). When fish are disturbed and stressed, they eat less; for example, an object moving over the water surface suppresses feeding in zebrafish (Oswald & Robison 2009) and any food that is eaten may be processed inefficiently (Chapters 5 and 7). An additional effect of cortisol secretion is to mobilise nutrient reserves that might otherwise be used for growth, so there are several effects of stressors that can impair growth (Chapter 2). Such direct and indirect consequences of the responses of farmed fish to danger may have different outcomes for fish with different coping strategies. To speculate, proactive individuals may be particularly liable to injury through active escape attempts, whereas reactive individuals may be more vulnerable to the effect of chronic stress on cortisol levels.

Overall, the stress and injury caused by experiencing and responding to real or perceived risk of predation will have adverse effects upon feeding, growth and, at the

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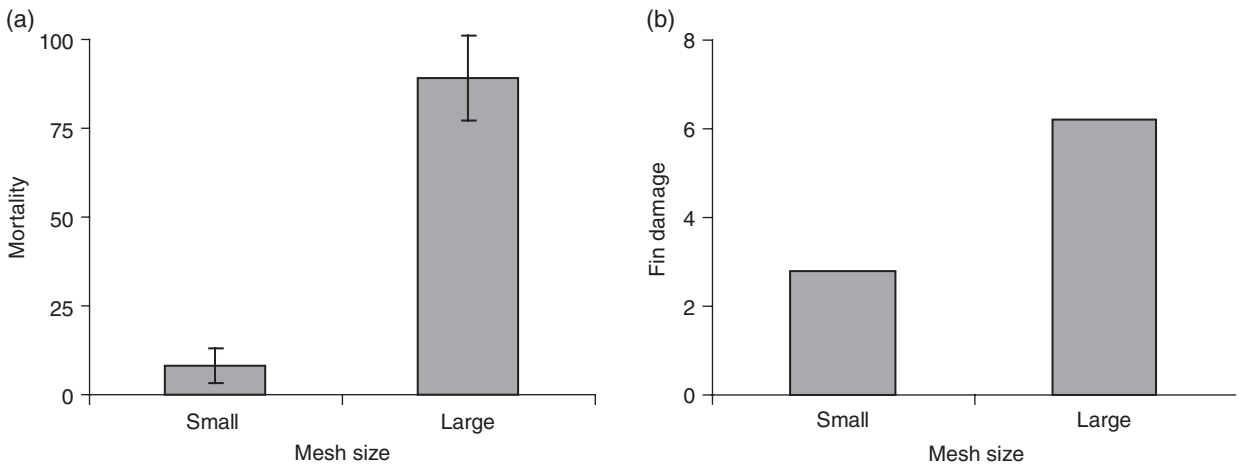


**Figure 8.8.** Effects of predator exclusion. (a) Mean (± SE) percentage mortality and (b) Mean index of fin damage in cultured larval *Piaractus mesopotamicus* larvae held in small mesh enclosures that exclude predacious copepods and large mesh cages that do not. Adapted from Fregadolli 2003.

level of individual fish, may increase susceptibility to parasite infestation and disease, compromising welfare. Antipredator responses probably have few implications for direct environmental effects of fish farms, although increased incidence of disease in farmed fish due to injury and stress might perhaps increase the risk of disease transmission to wild fish and the behavioural and physiological effects of perceived predation risk may increase feed waste due to disturbances to feeding.

### 8.5.3 Effects of domestication and captive rearing

#### *Antipredator responses in cultured fish*

Once fish that are farmed for food reach marketable size, the possession of effective antipredator responses has little relevance, except for possible effects of stress at slaughter on flesh quality. For ornamental fish arguably having poorly developed antipredator responses may be advantageous to the fish owner, since fish that are not easily frightened will be more visible. This may or may not be the case for fish reared for scientific study, depending on the purpose for which they are cultured. For example, captive-reared red drum larvae differ from wild caught fish of the same age in several aspects of their fast start response, suggesting that caution is needed when extrapolating from the laboratory-reared fish to their wild conspecifics (Smith & Fuiman 2004).

Possession of a full spectrum of effective antipredator responses is critical for fish that are cultured for release, whether for supplementation programmes and for conservation-based reintroduction. Survival of released fish is often very poor and in some cases predation is largely responsible. For example, fingerling Florida largemouth bass stocked into reservoirs may be attacked by several predatory species and endure large losses within a few hours of release (Buckmeier *et al*. 2005). Survival rates of hatchery-reared juvenile tiger pufferfish (*Takifugu rubripes*.) released into ponds that contain predatory sea bass are low, whereas pufferfish released into predator free ponds survive well; the implication is that predation immediately after release of the pufferfish is an important mortality factor (Shimizu *et al*. 2008). Almost half of the Atlantic salmon fry stocked into streams may be consumed by piscivorous fish within the first 2 days of stocking (Henderson & Letcher 2003) and survival of coho salmon from juvenile to adulthood ranges from about 8% for wild fish, to 2–5% for fish released from hatcheries (McNeil, 1991).

While it is important not to lose sight of the fact that the larval period is a time of very high natural mortality in wild fish populations, the success of supplementation and reintroduction programmes could potentially be compromised by deficits in antipredator behaviour in released fish. The culture environment is usually very different from that experienced by wild fish in ways that are likely to influence antipredator responses (Chapter 1). In particular, cultured fish are often exposed to structurally simple environments from which predators are excluded and in which abundant food is provided in a safe context; high densities also alter living conditions. In any given generation, captive

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rearing in this highly unnatural environment is likely to compromise the development of normal antipredator responses. Over generations of relaxed selection for effective antipredator behaviour, domestication could generate inherited deficiencies in this respect. Therefore, the effects of captive rearing and domestication may have serious implications for the antipredator behaviour of fish reared for release into the wild.

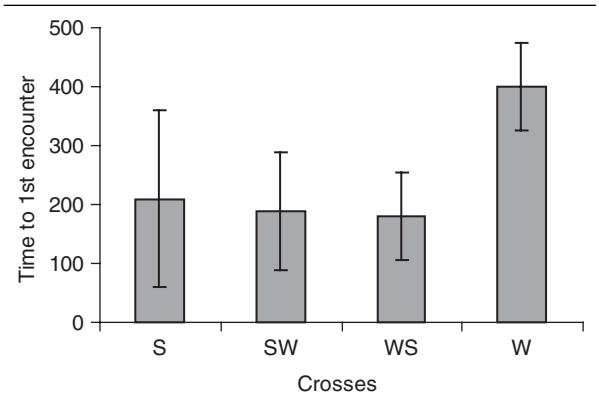


**Figure 8.9.** Effects of domestication on antipredator behaviour. Mean (±SD) time to emerge from shelter and receive a simulated predatory attack from a model heron in brown trout from four crosses. S = pure sea ranched cross. SW = sea ranched female × wild male. WS = wild female × sea ranched male. W = pure wild cross. Adapted from Petersson & Järvi 2006.

### *Effects of domestication on antipredator behaviour*

Many studies have demonstrated reduced behavioural and physiological responses to predators in fish from domesticated stock compared to wild fish of the same species, and sometimes from the same site of origin, reared under hatchery conditions. By way of example, laboratory strains of zebrafish that have been reared without exposure to predators for upwards of 100 generations show reduced shoaling, reduced startle responses and less inspection of a novel object (perhaps predator inspection) compared to laboratory-reared undomesticated fish (Wright *et al*. 2006). Domesticated zebrafish also show a weaker suppression of feeding response under predation risk (Oswald & Robison 2009). As an example from a species often farmed for supplementation, hatchery-reared juvenile brown trout of wild origin are slower to enter an experimental arena than are hatchery reared fish from a sea-ranched strain. They also react more rapidly to a simulated attack by a heron and remain immobile for longer after the attack. As a matter of concern with regard to potential for survival in the wild, reciprocal crosses between wild and sea-ranched strains are closer in their behaviour to their sea-ranched than their wild parent (Figure 8.9; Petersson & Jarvi 2006). When stocked into lakes, domestic rainbow trout selected for fast growth take greater risks than do hatchery-reared fish of wild origin. In the absence of predators, fish of the domesticated strain survive better than do wild-origin trout and grow at similar rates (Figure 8.10); however, as predation risk increases, while domesticated fish start to grow faster than wild-origin fish, their relative survival falls sharply (Biro *et al*. 2004). Differences in antipredator responses between farmed and wild fish have also been described for Masu salmon (*Onchorhynchus masou*: Yamamoto & Reinhardt 2003), steelhead trout (Johnsson & Abrahams 1991) and brown trout (Ferno & Jarvi 1998).

Such differences in antipredator behaviour between wild and domesticated fish reared under common conditions are often interpreted as being illustrative of genetic differences produced inadvertently by the effects of domestication. It is rarely possible to rule out the possibility of non-genetic maternal effects, because female fish transfer a number of factors to their offspring via the egg, including hormones, growth factors as well as essential nutrients (Chapter 2; McCormick 1998) and these could potentially generate differences in the next generation. Whatever their origin, domestication effects have a strong influence on the way antipredator behaviour develops in young fish, with a number of implications for aquaculture.

### *Effects of captive rearing on antipredator behaviour*

Deficits in antipredator responses have been reported in fish reared in captivity compared to fish of the same species and age and sometimes of the same stock captured in the wild, perhaps due to the impoverished nature of the hatchery environment. For example, wild-caught juvenile brown trout make greater use of shelters in the presence of predators than do hatchery-reared fish of the same age and population of origin, suggesting an adverse effect of captive rearing on the development of this aspect of predator avoidance (Álvarez & Nicieza 2003). Such effects can be important for survival; for example, hatchery-reared Chinook salmon of wild origin have a small but significant survival disadvantage compared to wild fish of the same stock (Fritts *et al*. 2007). Newly-released hatchery reared white seabream (*Diplodus sargus*) tend to ignore areas of refuge, suggesting a lower chance of avoiding predation (D'Anna *et al*. 2004) and wild-caught juvenile sea bream remain immobile for longer after a simulated predatory

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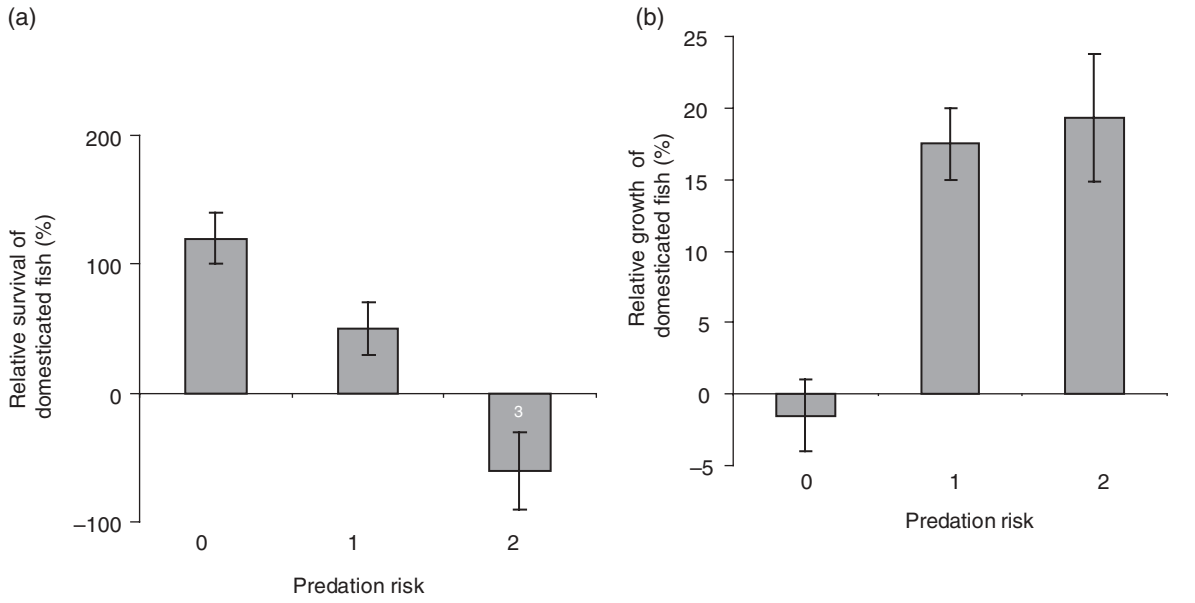


**Figure 8.10.** Implications of domestication for performance in the wild. (a) Mean (± SE) relative survival advantage (%) and (b) Mean (± SE) relative growth advantage (%) in domesticated compared to wild rainbow trout released into experimental lakes with different levels of predation risk, assessed by the abundance of piscivorous birds. Adapted from Biro *et al.* 2004.

attack than do hatchery-reared fish (Malavasi *et al.* 2008). Not all studies have shown impoverished antipredator responses in hatchery-reared fish; for example, hatchery-reared pike adjust their escape responses sensitively to predator size and risk in the same way that wild pike do (Engström-Öst & Lehtiniemi 2004).

***Implications for wild stock***

As well as compromising the effectiveness of supplementation and reintroduction programmes, ineffective predator avoidance in cultured fish released into the wild will have adverse effects on the welfare of individual fish. In addition, how cultured fish respond to predation risk has implications for interactions between cultured fish and wild stocks. If released fish or farm escapees show more robust feeding responses in the presence of predators than do their wild counterparts, this may make them formidable competitors. On the other hand, such competition may be short-lived if released fish and farm escapees, being less responsive, are likely to be attacked, killed and eaten by predators. Where impaired antipredator responses in farmed fish are the result of lack of appropriate experience during captive-rearing, any adverse effects will be restricted to a single generation. If, however, impaired responses are partly due to inherited differences resulting from domestication and released fish and escapees survive and breed, there is the possibility that offspring produced by the interbreeding of these fish with wild stocks will inherit impaired antipredator responses, as well as other behavioural deficiencies that could influence survival (Chapter 10).

### 8.5.4 Solutions to the problems arising from antipredator behaviour in fish culture

***Strategies***

The examples described in the previous sections show how the responses of fish to the risk of predatory attack can cause problems in culture. Hence there is a need for strategies to minimise their occurrence. A range of measures have been developed to reduce access of predators to cultured fish, some of these, such as the use of acoustic deterrents, being based on knowledge of the behaviour of the predators. Nets placed underwater around farm cages can deter seals and nets placed over ponds, outdoor tanks and cages can deter birds, but seals are skilled at finding ways around protective nets. Even if the nets keep predators at bay, fish may be stressed by their attempts to enter the rearing units. Overall, in many culture systems fish will

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experience a real or perceived risk of predation. Possible strategies for mitigating such effects include choosing appropriate fish for culture, devising husbandry routines that reduce the risk that fish will express their behavioural and physiological antipredator responses and allowing these to be expressed harmlessly.

***Using appropriate fish for aquaculture***

When candidate species for culture are being considered, just how sensitive they are to predation risk could be used a selection criterion. For example, amongst the flatfish species that may be candidates for culture, the English sole (*Parophrys vetulus*) is risk-prone, in the sense that frequent exposure to a predator does not lead to cessation of feeding, whereas in the Pacific halibut (*Hippoglossus stenolepsis*) and Northern rock sole (*Lepidopsetta polyxystra)* feeding is suppressed by the risk of predation (Boersema *et al*. 2008). Arguably, on this basis, English sole would be the best candidate of the three for intensive culture as a food-fish.

Within a particular species, where there are domesticated strains, these are perhaps the ones that should be farmed, in the interests of both production and welfare, provided the fish are not being cultured for release. For example, domesticated strains of zebrafish, which have relatively weak antipredator responses, show less suppression of feeding than do wild-type zebrafish when disturbed. They also grow faster under laboratory conditions than do fish from strains that have been recently derived from wild fish (Oswald & Robison 2009). Fish might be selectively bred for low stress responsiveness, as has been done for rainbow trout (Pottinger & Carrick 1999) and common carp (*Cyprinus carpio*; Tanck *et al*. 2002). If domesticated or selected strains are not available, problems arising from antipredator responses could potentially be reduced by screening to identify fish that are behaviourally suitable for culture. For example, in both halibut (*Hippoglossus hippoglossus* Kristiansen & Fernö 2007) and puffer fish (Hosoya *et al*. 2008) patterns of swimming in very young fish could potentially be used to identify fish that will be relatively unstressed in intensive aquaculture. However, another problem then arises, because such proactive fish often show above average levels of aggression (Sih *et al*. 2004; Korte *et al*. 2005) it would be necessary to find ways of uncoupling boldness and aggression, without compromising growth (Chapter 9).

***Developing appropriate husbandry systems***

As well as choosing the correct types of fish to farm, an additional strategy for mitigating the effects of antipredator responses is to develop systems and routines that either reduce the chance that antipredator responses will be elicited or enable the fish to show appropriate responses without causing harm to themselves and their companions.

As discussed in Chapter 1, fish are capable of various kinds of learning that allow them to form expectations about the occurrence of both positive and negative events. By adopting certain husbandry routines a farmer could make the culture environment more predictable and, thus, less stressful for the fish. For example, juvenile chinook salmon conditioned to associate brief dewatering with the delivery of food subsequently show reduced physiological stress responses to transport and better survival during disease challenge and hypoxic exposure than do unconditioned fish (Schreck *et al*. 1995). The fright response initially shown by Atlantic salmon to a flashing light attenuates through habituation and if the light is paired with feed delivery changes to a positive, anticipatory response (Bratland *et al*. 2010). Development of husbandry systems that make use of the natural orientation responses of fish might also aid in mitigation of stress in cultured fish (Chapter 4).

Providing farmed fish with environmental features that are needed for them to express their natural behaviours, such as cover and/or the opportunity to move to areas of reduced light, might also function as a mitigation measure. For example, the presence of sediment reduces physiological stress responses in crucian carp (Höglund *et al*. 2005) and several species of flatfish perform better in tanks with a sandy substrate in which they can bury than in bare tanks (Moksness *et al*. 2004; Le Francois *et al*. 2010). Cannibalism in young green sword tail (Jones *et al*. 1998) and sharptooth catfish (*Clarias gariepinus*; Hecht & Appelbaum 1988) can be reduced by providing shelters, allowing more harvestable fish to be reared. In sharptooth catfish, competition for refuges can be reduced and growth rates increased by reducing light intensity (Britz and Pienaar 1992). Lowered light levels also reduce the incidence of cannibalism in Japanese flounder (*Paralichthys olivaceus*; Dou *et al*. 2000). In fingerling jundia (*Rhamdia quelen*), a fast-growing cultured South American fish, provision of shelters reduces the magnitude and duration of the physiological stress response to the acute challenge of being chased with a net (Figure 8.11. Barcellos *et al*. 2009).

### 8.5.5 Using predators and antipredator behaviour in fish culture

***Using predators to maintain quality***

It is worth noting that, as well as causing problems, predatory attacks and the responses of cultured fish to them can be put to good use in fish culture. For example, rearing

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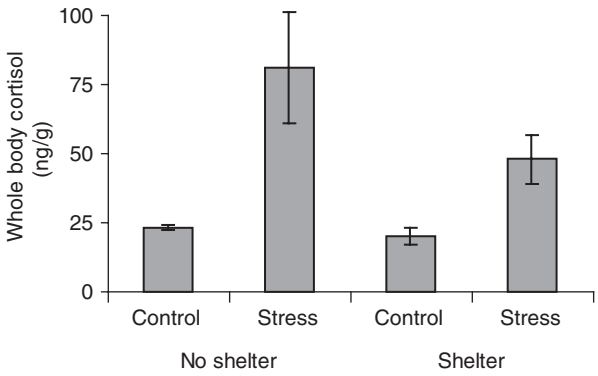


**Figure 8.11.** Effects of provision of shelter up on stress responses in cultured fish. Mean (± SE) whole body cortisol concentrations in response to chasing in fingerling jundia held in white tanks, either without shelter or with shelter. Adapted from Barcellos *et al.* 2009.

*Tilapia aurea* in ponds together with the predatory cichlid *Cichlasoma managuense* can improve the production of marketable fish of both species (Dunseth & Bayne 1978). This arises because the predatory cichlids consume small tilapia, thereby promoting their own growth. At the same time overcrowding and stunting within the tilapia population is prevented. Similarly, populations of *Oreochromis mossambica* in seawater ponds can be managed by allowing small predatory elops (*Elops hawaiensis*) to enter the ponds and consume excess tilapia fry. The elops population itself is regulated by intraspecific competition (Popper & Lichatowich 1975). In traditional pond culture of common carp, piscivorous fish are used to remove unwanted fry from ponds containing broodstock.

***Operational welfare indicators***

The presence of piscivorous birds foraging at traditional carp farms may provide an early warning of poor water quality, because under such conditions the carp move closer to the surface and attract the attention of predatory birds. Thus, acting as an indirect indicator of environmental conditions that might impair welfare. In general there is considerable interest in developing sensitive, easily measured indicators of fish welfare that could be applied on fish farms. The natural behavioural and physiological responses of fish to predators and predation risk offer possibilities in this context. Cortisol and melanotropins (MSH) induce colour changes that are part of the suite of stress and protective responses in many fish species and observation of colour change could potentially provide a method for assessing stress and welfare in cultured fish (Chapter 1). For example, the fluorescent system in the epidermis of Cardinal tetras (*Paracheirodon axelrodi*) differs between stressed and non-stressed fish and the spectral pattern reflects whole-body cortisol levels (Brinn *et al*. 2009). Similarly, melanophore density in the skin of salmonid fish also changes in response to changes in potential stressors (Kittilsen *et al* 2009), suggesting that this could be used for non-destructive stress assessment.

### 8.5.6 Mitigating the effects of domestication and captive rearing

As discussed above, poor antipredator responses in cultured fish could be the result of domestication selection acting over a number of generations, differential mortality of behavioural phenotypes during the period from hatching to release or differential experience during ontogeny. Knowing about all these processes offers potential for mitigation. In addition, knowledge of the natural antipredator behaviour of cultured fish can also be used to improve release procedures.

***Choosing and rearing suitable fish***

Where poor antipredator responses in released fish comes about because domesticated fish have been used, the solution lies in using undomesticated strains or to institute breeding programmes and culture systems that minimise domestication (Chapter 1 and 10). This is especially important where fish are part of a captive breeding programme for conservation, since marked changes in antipredator behaviour within populations of fish can occur rapidly through differential mortality by behavioural phenotype. For example, a single generation of hatchery-rearing makes brown trout relatively insensitive to predation risk compared with wild fish (Álvarez and Nicieza 2003). If fish that die in culture are reactive fish with strong stress responses, the released populations may lack exactly those fish that are likely to survive predation. Ideally, since fish with different coping strategies perform well under different environmental conditions (Chapter 9), the distribution of behavioural phenotypes in a released population should match that of the wild population that the cultured fish are intended to supplement. This could potentially be achieved by creating culture conditions that enable all behavioural phenotypes to survive, for example by providing cover close to food delivery sites or by offering a mixture of poor but safe and rich but exposed feeding stations. It might also be possible to identify within a cohort of young fish those that are likely to survive well in the face of natural predation.

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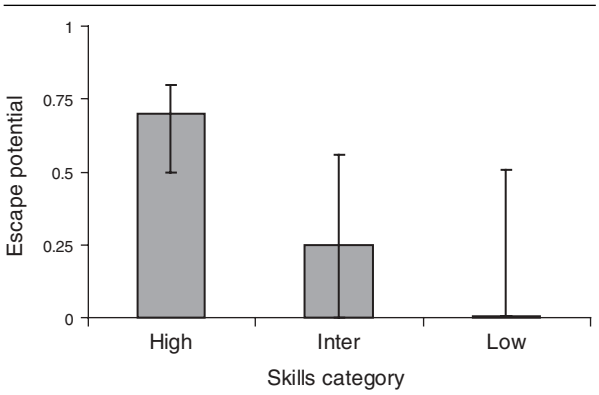


**Figure 8.12.** Predicting potential to avoid predation from the results of simple behavioural screening. Median (and interquartile range) escape potential (proportion of attacks from which an individual escapes) in red drum larvae classified into three categories on the basis of a series of simple tests. Categories = skilled fish (High), unskilled fish (low) and intermediates (Inter). Adapted from Fuiman *et al.* 2006.

For example, newly hatched red drum larvae show repeatable individual differences in behavioural responses (including routine swimming ability and responsiveness to visual and auditory cues) that can be assessed relatively easily using non-lethal assays. Such assessment allows separation of fish into clusters according to their overall performance in tests. These clusters predict the ability to escape from direct predatory attack (Figure 8.12) and so may predict the performance of cohorts of larvae under natural conditions (Fuiman *et al*. 2006).

### *Improving captive rearing procedures and life skills training*

Impaired antipredator responses in released fish might arise because the generally impoverished nature of most hatcheries and the absence of natural predators deprive the fish of the experience needed for the development of effective antipredator responses. The strategy here might be to devise more complex and variable hatchery systems. For example, at hatching Atlantic salmon reared in incubation units with a seminatural gravel substratum and water flow mimicking that found in natural redds are larger and heavier than those reared in standard hatchery trays. They also show similar patterns of emergence to wild fry, emerging synchronously in the dark, which is likely to reduce predation during emergence (Bamberger 2009).

Another strategy for mitigating the effects of captive rearing is to expose cultured fish to experiences that improve their antipredator behaviour, or to give them 'life skills training' (Brown & Laland 2001). For example, hatchery-reared juvenile Coho salmon that have been exposed briefly to a predator have a better chance of survival than predator-naïve fish. This could, in part, be due to the fact that fish in better condition were more likely to survive both the initial attack and the subsequent exposure. However, learning may well be involved as well, because Coho salmon that have been exposed to a predator behind a transparent screen, together with a mixture of vibrational and chemical cues, also show improved antipredator responses (Olla & Davis 1989). Learning is clearly involved in governing the subsequent responses of Chinook salmon given a single pairing of northern pike odour with conspecific skin extract. Exposed fish show enhanced predator recognition, though this is context-specific and may habituate (Berejikian *et al*. 2003). Arctic charr exposed to the odour of pike-perch (*Sander lucioperca*) followed by an encounter with a predator become more responsive to the odour (Vilhunen *et al*. 2005). Perhaps surprisingly, charr become increasingly sensitive to pike-perch odour when exposed to it repeatedly without associated predator attack. Far from habituating the charr appear to become sensitised and this translates into better survival in the presence of a predator (Vilhunen 2005). In the same species, allowing predator-naïve fish to observe a trained conspecific respond to predator odour is also effective in inducing a response (Vilhunen *et al*. 2005). Such social learning offers good potential for improving antipredator responses without having to sacrifice too many fish.

Life skills training programmes may need to take account of inherited differences in learning ability. Arctic charr show individual variation in how strongly they respond to pike-perch odour on first exposure; the high responders, both naïve and after antipredator training, show stronger responses when subsequently exposed to a pike perch and survive longer. In this case, learning from experience complements, but does not override, inherited differences in response to predators (Vilhunen & Hirvonen 2003). Domesticated steelhead rainbow trout show weaker antipredator responses in laboratory tests and survive less well when exposed to predators than do hatchery-reared wild fry. Training by allowing fish to see other fry being eaten by a sculpin improves antipredator responses in both domesticated and hatchery-reared wild trout, but trained domesticated fish still survive less well than untrained wild-derived fish. This suggests that

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training may not have a major influence on survivorship if the fish designated for release are from a domesticated stock (Berejikian 1995).

The abiotic environment in which training takes place also has important consequences for subsequent actions and performance. For example, Atlantic salmon given a single pairing of a novel odour (lemon essence) with the scent of a damaged conspecific in the laboratory spend more time hiding and less time moving than do unconditioned fish when subsequently released into the wild and presented with lemon scent. However, this response is only seen in streams with neutral pH and not when the water is acidic (Leduc *et al*. 2007). Olfactory conditioning is most effective when the pH experienced during conditioning and subsequent testing is the same, but exposure to odorants at low pH may not be effective because of impaired olfactory sensitivity under such conditions (Smith *et al*. 2008).

### *Improving release procedures*

When it comes to releasing cultured fish into the wild, knowledge of the natural antipredator behaviour of the species concerned can be used both in selecting release sites and in devising release procedures. Clearly, release sites should have features that enable released fish to avoid predators; for example, survival of hatchery-reared Atlantic salmon fry exposed to predation by brook trout (*Salvenilus fontinalis*) and brown trout is positively correlated with the percentage of riffle available within artificial stream environments (Henderson & Letcher 2003) and juvenile cod that settle on a complex rocky substrate survive better than those that settle on soft substrate or in sea grass beds (Tupper & Boutilier 1995). Other aspects of the release site are important; for example, the response of juvenile Atlantic salmon to chemicals released by injured conspecifics is impaired in acidic streams (Olivier *et al*. 2006; Tierney *et al*. 2010).

Poor antipredator responses in released fish might be a short term effect of the stress of transport, which suggests that minimising stress during transport and allowing the fish to acclimatise before release might improve survival. For example, juvenile coral trout (*Plectropomus leopardus*) given 7 days acclimatisation to a reef release site in net cages are more likely to take cover in coral rubble and less vulnerable to predation than are non-acclimatised fish (Hamasaki *et al*. 2004). Common Snook (*Centropomus undecimalis*) held in acclimation cages before release survive better than do fish released directly from the nursery (Brennan *et al*. 2006). However, holding fish in acclimation cages could attract potential predators to release sites. For example, predators such as cyprinids, smallmouth bass (*Micropterus dolomieui*), sunfish (*Lepomis* spp.) and walleye (*Stizostedion vitreum*) aggregate at sites where cultured shad (*Alosa sapidissima*) larvae are released (Johnson & Ringler 1998). The winter flounder (*Pseudopleuronectes americanus*) is reared for supplementation programmes, but cultured fish experience poor survival on release. Survivorship can be improved by holding the fish in cages on the sea bed for a few days prior to release, allowing the fish to recover from transport stress, practise burying in the substrate and develop appropriate pigmentation. However, the fish do not necessarily survive better on release because predatory green crabs congregate around the cages in large numbers. Moving the cages may alleviate the problems of crab aggregations, but could stress the fish, thereby counteracting the beneficial effects of acclimation (Fairchild *et al.* 2010). This example illustrates just how much we need to know about the behaviour of prey fish and their predators to devise effective release strategies for supplementation and conservation programmes.

## 8.6 SYNOPSIS

In nature, fish fall victim to many different kinds of predators hunting in a variety of ways and as a group they have evolved a rich repertoire of antipredator defences. Many of these are behavioural, including avoiding contact with predators by appropriate habitat choice, high levels of vigilance, effective escape responses and schooling, and their expression is fine-tuned to predation risk. Antipredator responses are elicited and controlled by a range of different stimuli indicative of risk, with chemical cues being particularly important. Encountering and being attacked by a predator represents a strong challenge to a fish and the behavioural responses shown to predation risk are closely linked to stress responses. Individual fish within a population often differ in how strongly they respond, behaviourally and physiologically, to the risk of predation; the term ‘coping strategies’ is often used to describe interindividual variations in such responses. Selecting fish of a particular coping strategy could potentially be exploited within aquaculture.

Effective antipredator responses develop gradually in young fish as their sensory and motor systems become functional and may change in response to ontogenetic shifts such as those occurring around during metamorphosis and larval settlement. Variations in the antipredator responses of fish may be the result of genetic differences, of differences in the environment in which development takes place, and of interactions between genetic and environmental factors. Because predatory attack is aversive, both direct and indirect experience of predators

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facilitates learning of effective protective responses. Although effective antipredator behaviour obviously promotes survival, performing such behaviour involves costs. Thus, how fish behave when exposed to the risk of predation has been moulded by natural selection to balance such costs and benefits.

Antipredator responses are relevant for aquaculture in several ways. Where fish are farmed for food, they are usually protected from predators, but antipredator responses are still relevant, not least because farmed fish may be exposed to stimuli that, in nature, would indicate the presence of a predator. Behavioural and physiological responses to such stimuli may have adverse effects, such as suppression of feeding and growth. Husbandry routines and culture systems that protect fish from potentially threatening stimuli can lead to improvements in both production and welfare. In addition, the natural protective responses of fish can be used to improve the efficiency of farming practices, for example by using stress-induced feeding suppression as an early warning of husbandry problems. Where fish are farmed for release, with a view to supplementing or reinstating wild populations, this can be made more effective by having knowledge and understanding of their antipredator responses and how these develop. For example, such knowledge might be used in choice of release sites and in devising rearing environments and programmes for 'life skill training' that promote effective protective responses. How fish respond to predation risk when released into the wild, either accidentally or for restocking, will determine how well they survive and how vigorously they will compete with wild fish for food and other resources. This in turn will play a part in determining the effects of farmed fish on wild stocks, a critical point for sustainable aquaculture.

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# 9
# Fighting and Aggression

*Børge Damsgård and Felicity Huntingford*

**Abstract:** Aggression (behaviour that actually or potentially causes harm to another animal) is widespread among fishes, often taking the form of territoriality or dominance. The mechanisms that control aggression in fish are described, including the effects of stimuli from opponents, the importance of the context in which an aggressive encounter occurs and the effects of nutritional condition, endocrine status and brain biochemistry. The way aggression changes during development is then considered, evidence given for inherited differences in aggressiveness and an account presented of the environmental factors that influence the way aggression develops. The benefits that fish gain from winning fights, the costs that they incur from fighting and how they balance costs against benefits to promote their individual fitness are described. Data are then given on the incidence of aggression among cultured fish, on some resulting problems for production, welfare and environmental protection and on the effects of domestication and captive rearing of aggressiveness. Possible solutions to such problems are discussed, based on selecting appropriate fish for culture and the design of husbandry systems that minimise aggression. Finally, some systems for mitigating the effects of domestication and captive rearing on the aggressive behaviour of cultured fish are described.

**Keywords:** behavioural syndromes; dominance; economic defensibility; feed distribution; hierarchy; fighting; injury; stress response; territoriality; water current.

## 9.1 INTRODUCTION

Aggression is a behavioural mechanism for gaining assesses to key resources that are in short supply. It is so important to the animals concerned that it is often maintained even in conditions when resources (for example food) are abundant, as is usually the case in fish culture. A number of problems in aquaculture arise from the fact that fish fight each other and to solve these it is necessary to understand the biology of aggressive behaviour in fishes, its causes, development and functions. This chapter addresses all these issues and explores their implications for aquaculture.

### 9.1.1 What aggression is

An important point to make is that aggression is a natural behaviour and part of the way in which animals in nature acquire resources. Animals may compete simply through the efficiency with which they exploit resources, taking part in so-called scramble competition. Considering food as the disputed resource, under scramble competition all animals have access to a food supply and each individual animal eats as much as possible without spending time interfering with its rivals. This is in contrast to interference competition, in which rivals are actively excluded from

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access to resources; in other words, animals fight or show aggressive behaviour in order to control a resource. A simple but useful definition of aggression is: *behaviour that actually or potentially causes harm to another animal*. Killing other animals as food and attacking a potential predator are excluded from this term; such behaviour patterns are considered to concern feeding or anti-predator responses and are discussed in other chapters of this book (Chapters 5, 6 and 8). Cases of fighting between different species are included only when the animals concerned are competing for resources, as in the case of the dusky damselfish (*Eupomacentrus dorsopunicans*), an algal-grazing reef fish that defends a food source against other species in direct proportionality to how much those species compete with them for food (Mahoney 1981).

### 9.1.2 Aggression in the lives of fish

Aggression is a widespread and natural response to competition in many different kinds of animal and fish are no exception, fighting over resources such as food, feeding sites, shelter, mates and spawning sites. There is large variation among species in how readily and fiercely fish fight, which has implications for aquaculture. This variability has probably arisen because over evolutionary time different species have been adapted to different habitats, many features of which influence whether or not fighting is profitable. In general, mobile, pelagic fish species such as herring (*Clupea harengus*) tend to be relatively unaggressive, whereas fish that are spatially restricted (many reef species, for example) are often aggressive. Species that change between site-attached and pelagic phases, such as many salmonids, tend to switch between aggressive and non-aggressive modes in parallel with this habitat change.

Fights between fishes include not just direct attacks, when fish nip and bite each other, but also a variety of displays and postures. Figure 9.1 shows the stages of a fight over mating opportunities between two adult male cichlid fish (*Nannacara anomala*). The interaction starts when one fish approaches the other, with gill covers flared and brightly coloured fins expanded. Such behaviours are called threat displays, since they often signal an intention to attack. If the other fish responds in kind, after a time, the rivals may switch to more energetic behaviour, turning sideways to each other and beating their tails. Again after a time spent in this more vigorous activity, the fish may start to circle rapidly around each other, slipping in quick bites at the flank of their opponent. At some point in this sequence, one fish will give up, often quite suddenly, folding its fins and darkening its colour and taking up what is called a submissive posture, after which the fight ends (Jakobsson *et al*. 1979). Species

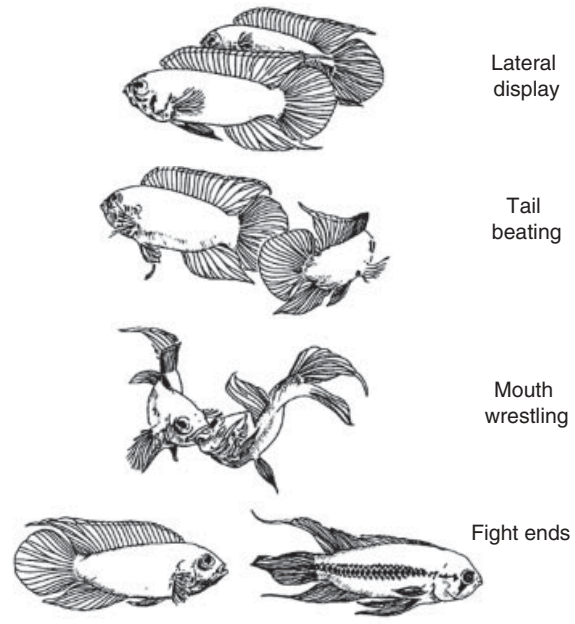


**Figure 9.1.** Fighting and escalation. Behaviour patterns shown at different stages of a fight between male cichlid fish (*Nannacara anomala*). Fights start when fish approach each other and orient laterally, displaying erect fins. After this, the fish exchange tail beats, still from a distance, before escalating to mouth wrestling and then to circling and biting. At some point in this sequence, one fish gives up, often changing colour, and flees. Reproduced with permission from S. Jakobsson.

of fish differ in the details of their aggressive displays, but the broad pattern of escalation through displays of increasing intensity and eventually to biting attack is typical, with the energy used and the risk of injury increasing through this sequence and with fights ending at various points in this process. Most fish do not have formidable weapons such as the fangs, talons and horns of some mammals, but they do have teeth, which can be sharp. Fierce fighting does happen and can cause injury in the form of fin damage and scale loss (Maan *et al*. 2001), which will clearly be a problem if this happens in fish culture.

### 9.1.3 Territoriality and dominance

While fights often take place directly over a disputed resource, equally often animals fight over a 'proxy' that will give them access to resources in the future. The proxy may be space, in which case winners gain control of a defined area or territory; alternatively it may be individual status, with winners gaining social control over losers. Both these patterns of aggression are common in fish.

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The term territoriality refers to defence of the space around an animal or a group of animals against intruders, usually of the same species. Territoriality is an important determinant of both spacing and resource distribution in fish. Mudskippers (*Boleophthalmus boddarti)* emerge from their burrows at low tide and build hexagons of temporary mud walls around the area surrounding their burrows. These are defended against intruding neighbours and the resident fish browse on the algae on the sand in these exclusive territories, returning to their burrows as the tide rises (Clayton 1987). In these mudskippers, territory holders gain exclusive access to shelter and food. In the cichlid fish described in the previous section, fights are over spawning sites and consequently over the opportunity to breed.

Territoriality is common in fish, but not ubiquitous and its distribution can be explained in part by habitat. Defence of a feeding territory is relatively rare in freshwater and in most marine species, occurring in 9% and 6% of species respectively (Grant 1997), but is common in reef fishes, occurring in 68% of species. In contrast, males of most fish species from these three habitats (78% of species overall) defend a reproductive territory. As discussed in more detail below, these striking differences can be explained in terms of the distribution and predictability of resources. Food is predictable on coral reefs and so worth defending, but this is not the case in the wider marine and freshwater environment. In contrast, breeding opportunities are often in short supply and so are usually worth fighting over. Defence of feeding territories is part of the natural behavioural repertoire of several commonly cultured species food, as least at some point in their life cycle, and this has implications for the control of unwanted aggression in aquaculture.

In the case of territoriality, the outcome of aggressive encounters is predicted by location, since in general territory owners defeat and drive off intruders. In the case of dominance–subordinance relationships, the identity of the fish concerned is critical. Where the same two individuals meet and fight on a number of occasions, one (the dominant) often wins repeatedly; after a few defeats the loser (the subordinate) starts to give way at the approach of the dominant. When pairs of Arctic charr (*Salvelinus alpinus*) are housed together, initially fights are common. However, over time a clear distinction emerges between the dominant fish, which retains the usual bright colour of these fish, and a subordinate fish, which becomes darkly coloured in its body and around its eye. The subordinate fish tends to remain motionless and does not attempt to feed and such behavioural suppression can persist for long periods, even after the dominant fish had been removed (Øverli *et al*. 1998). Although dominant status is initially gained by winning fights and subordinate status by losing, once such a relationship is established, there is no simple link between dominance and aggression. Strictly speaking, the terms dominance and subordinance refer to a relationship between two animals, rather than to a trait of a single animal. However, there are some individuals that tend to dominate over many other fish, in which case these may simply be described as dominant; likewise, animals that tend to be subordinate to many other individuals may be simply called subordinates.

In larger groups of fish relationships become more complex and hierarchies of dominance may form. Such hierarchies can be linear, with individuals ranked in descending order of how many other fish defer to them. Alternatively, they may be at least partially despotic, with one or a few fish consistently dominating all others in a group, a number of fish that are consistently subordinate and a group of fish with intermediate status. More or less stable dominance hierarchies, often involving priority of access to food, are found in a number of salmonid fish, including Atlantic salmon (*Salmo salar*, for example, Metcalfe *et al*. 1989; Kadri *et al*. 1996), Arctic charr (for example, Damsgård *et al*. 1997) and rainbow trout (*Oncorhynchus mykiss*, for example, McCarthy *et al*. 1992; Jobling & Koskela 1996; Moutou *et al*. 1998). Dominance hierarchies are also described for other groups of fish that are farmed for food, for example, gilthead seabream (*Sparus aurata*; Goldan *et al*. 2003; Montero *et al.* 2009) and Nile tilapia (*Oreochromis niloticus*; Correa *et al*. 2003; Vera Cruz & Brown 2007), as well as several species that are cultured for the ornamental trade (for example, green swordtails, *Xiphophorus helleri*; Earley & Dugatkin 2006) and for scientific purposes (for example, medaka, *Oryzias latipes*; Magnuson 1962).

### 9.1.4 Individual variation in aggressiveness

Dominance–subordinance relationships are one manifestation of the fact that not all members of the same species are equally good at fighting. At its simplest, some fish are larger and stronger than others and above a certain threshold this dictates the outcome of fights. In such circumstances poor competitors may use tactics other than fighting to gain resources. Commonly, this involves sneaking inconspicuously up to the resource and taking it while better competitors are otherwise engaged. For example, when juvenile Atlantic salmon coexist with brown trout (*Salmo trutta*), the salmon, which are smaller, tend to be subordinate, but are able to gain food by sneaking (Harwood *et al*. 2002). During the breeding seasons it is not uncommon to find small male Atlantic salmon with fully functional

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gonads (mature parr) hiding near large adult females that are ready to spawn. Even though large fierce adult males usually surround the females, the small mature parr achieve fertilisations by sneaking quickly into the nest after the female has spawned. DNA fingerprinting shows that a significant proportion of eggs are fertilised by small, sneaking males. Such alternative male mating strategies, which are common among fish (Oliveira 2006) and represent an important source of individual variability in aggressiveness, are discussed in more detail in Chapter 10.

Setting aside dominance–subordinance relationships, levels of aggression can be highly variable among fish of the same species, age and size. In some cases, this reflects population differences, with fish from different populations being more or less aggressive as a result of local conditions. For example, brown trout from populations in Finland differ strikingly in the levels of aggression shown within small groups, with sea run populations being more aggressive than lake-run or resident populations (Lahti *et al*. 2001). In other cases, variable aggression reflects gender differences, male fish often being more aggressive than females. However, even among fish of the same population, sex and age, it is quite common to find striking and consistent differences between individual fish in how fiercely they fight or compete for resources (Huntingford & Adams 2005; Huntingford *et al*. 2010). As discussed in Chapter 8, such variation in aggressiveness is often associated with more general differences in risk taking, reflecting different coping styles (Korte *et al*. 2005). The existence of such variation in aggressiveness is likely to have an impact on how individual fish perform in culture and on their welfare.

## 9.2 MECHANISMS

Competition for resources is ubiquitous and in many species of fish it is mediated through aggressive interactions; as a consequence, aggression or the threat of it is a very important aspect of the lives of fishes. Since aggression is potentially dangerous to both participants, whether, how and how much fish fight is finely tuned to needs and circumstances and the underlying mechanisms that control this behaviour reflect this complexity. As far as external stimuli are concerned, a potential opponent sends out various cues about its status as a competitor and about its probable effectiveness as a fighter. Some of these cues are intrinsic to the opponent and some depend on its properties relative to those of the fish that is sizing it up. In both cases, signals may have different effects depending on the context in which the encounter takes place and on the internal state of the animals concerned. Internal state often differs between opponents at the start of a fight and changes dramatically as the encounter progresses and is resolved. The interplay between external stimuli, internal state and aggressive behaviour is complex, but understanding it offers potential for managing this behaviour in fish held in production systems.

### 9.2.1 Stimuli from potential opponents

#### *Cues that are intrinsic to the opponent*

The displays exchanged during a fight between two male cichlids (Figure 9.1) clearly involve visual cues such as the sight of brightly coloured fins and flared gill covers. They also involve mechanical cues, such as water currents generated during tail beating, and auditory cues, such as sounds produced by grinding pharyngeal teeth (Schwarz 1974a, b). Some fish species emit olfactory cues during fights; for example, breeding male goldfish release large quantities of the reproductive hormone androstenedione in their urine and this elicits aggression in other males (Sorensen *et al*. 2005). In weakly electric fish such as *Brachyhypopomus pinnicaudatus*, fights between breeding males involve an exchange of complex electrical signals, the detailed form and timing of which differentiates dominant from subordinate individuals (Perrone *et al*. 2009). Some of the signals exchanged during fights make the receiver more aggressive, while others have the opposite effect. For example, when male cichlid fish (*Cichlasoma centrarchus)* fight, short sounds with long gaps stimulate attack, whereas long, rapidly repeated pulses inhibit aggression. (Schwarz 1974a, b).

Both the signals used and the response to them may change during a fight, as one fish gradually emerges as the winner. For example, in yellow bullhead (*Ictalurus natalis*) losing a fight changes the chemical cues released by a previously dominant fish, such that aggression is no longer suppressed in its subordinate companions (Todd *et al*. 1967). Such experience-mediated shifts in signalling are particularly well documented in the case of colour changes. Male swordtail fish (*Xiphophorus cortezi*) have vertical bars on their flanks that change in intensity at key points in a fight, for example becoming darker just before a bite is delivered. Removing the bars (by freeze branding) makes the receiving fish significantly more aggressive, so the bars inhibit attack, perhaps serving as a signal of intention to bite (Morris *et al*. 1995; Moretz & Morris 2003). In Arctic charr and in other salmonid species, the colour of the ring surrounding the eye (the sclera) is important, with the sclera darkening in subordinates, making them less likely to be attacked (O'Connor *et al*. 1999). Similarly in Nile tilapia, eye colour of the loser darkens as that of the winner

pales (Volpato *et al*. 2003). Such colour changes could be important in aquaculture, since they potentially allow farmers a quick and non-invasive way of determining the behavioural status of their stock.

***Cues about the relative condition of potential opponents***

In addition to factors intrinsic to the signaller, other external stimuli that influence what happen during fights depend in various ways on the relationship between the two fish. For example, the size of a potential opponent relative to a focal fish is a critical determinant of what happens when rivals meet. Oscars (cichlid fish, *Astronotus ocellatus*) chase and bite fish that are smaller than them, but avoid larger opponents (Beeching 1992). As a consequence of this kind of effect, fights between evenly matched fish are commonly longer and fiercer than those where there is a clear size difference between potential opponents (Huntingford & Turner 1987).

Other relational cues that influence of what happens during fights include relatedness to and familiarity with potential opponents. Levels of aggression are higher in groups of unrelated Atlantic salmon and brown trout than in groups of related fish (Brown & Brown 1996). Less fighting is seen in groups of juvenile brown trout housed with familiar fish than those in groups whose members are frequently changed (Ward & Hart 2003). Trout that initiate fights are more likely to win against familiar fish than against strangers, so some effects of familiarity may be due to memories the outcome of previous interactions with specific individuals (Höjesjö *et al*. 1998). Certainly, when rainbow trout encounter a similar-sized opponent with which they have previously fought, the second encounter is less aggressive than it would be with a stranger (Johnsson 1997). In contests between juvenile Atlantic salmon, submissive darkening of the eye occurs sooner when the opponents have fought before than when they are unfamiliar to each other (O'Connor *et al*. 2000).

### 9.2.2 Effects of environmental factors

The examples given in the previous section show that what happens when fish come into conflict over resources depends on a complex exchange of information about the identity and likely fighting ability of potential opponents. It also depends on the context in which an encounter occurs, one important factor here being how long each fish has been in its current location. A prior residence advantage has been demonstrated for many fish species and is part of the mechanism that underpins the widespread occurrence of territorial behaviour. For example, a two-day prior residence is sufficient to ensure victory in 85% of contests between size-matched juvenile brown trout (Johnsson *et al*. 1999). The strength of a prior residence effect is dependent on the quality of the area concerned; brown trout resident on a preferred gravel substratum win more encounters with an intruder than do those on a less preferred plain substratum, though a prior residence advantage is seen in both cases. Owners of gravel patches attack sooner and are more aggressive, suggesting that the effect might come about through knowledge of the value of the disputed territory (Johnsson *et al*. 2000). There are many examples of fish adjusting their aggressive behaviour in response to cues relating to the value of the resource for which they are competing. For example, male Siamese fighting fish (*Betta splendens*) defend the breeding territories more vigorously when gravid females are around (Doutrelant *et al*. 2001).

At least one reason why brown trout defend territories with a gravel substratum more vigorously than those with a plain substratum (Johnsson *et al*. 2000) lies in the fact that, in order to show effective territorial behaviour, fish need spatial cues around which to organise their activities (Chapter 4). In the absence of such cues, Arctic charr, for example, switch from territorial behaviour to schooling (Mikheev *et al*. 1996). Other influences of the substratum on aggression are indirect, through an effect on body colour. Salmonid fish get darker when living on a black background and this can suppress attack, as in the case of Arctic charr, which are less aggressive when interacting on a dark background than on a light one (Höglund *et al*. 2002). The fact that fish make such adjustments to background colour offers the possibility of manipulating their behaviour in culture by simple changes in the design of holding systems.

### 9.2.3 Internal factors

***Reversible changes in aggressiveness***

When the same fish is exposed to an identical stimulus presented in an identical environment, it does not always attack and, if it does, does not always attack equally fiercely. Clearly, events taking place inside the animal (or motivational changes) must be responsible for such differences in behaviour. There is an extensive literature on the nature of the motivational processes that determine whether and how animals fight (Huntingford & Turner 1986), reflecting at least two broadly distinct processes. According to one view, most famously formalised by the Nobel Laureate Konrad Lorenz (1966), animals have an aggressive drive that inevitably accumulates as time passes since they last had a fight and is dissipated by the act of fighting. As a result weaker and weaker stimuli will trigger attacks.

Clearly, if this is right, simply keeping animals away from rivals will not prevent their fighting; instead, to keep aggression under control, animals need to be given the opportunity to fight moderately from time to time. According to a very different view, aggression occurs when the situation in which an animal finds itself (for example, in its territory, with plenty of food, but in the presence of an intruder) is different from the ideal stimulus situation (in its territory, with plenty of food and no intruder). A successful attack that repels an intruder corrects this discrepancy and so brings the fight to an end. Clearly, if this is right, keeping animals apart is sufficient to prevent fighting, so these two frameworks come up with very different recommendations about the best way to reduce aggression. Which come closest to reality will have important implications for the management of aggression in farmed fish, or indeed in any animals.

Some evidence supports the idea of an accumulating aggressive drive in fish. Juvenile yellowtail damselfish (*Microspathodon chrysurus*) will learn a task for the reward of threatening a rival behind a glass wall. The longer the fish have been kept in isolation without the opportunity for fighting, the more time they spend in aggressive display when a rival is presented. This is compatible with the concept of an inevitably accumulating aggressive drive (Rasa 1971). However, there are other possible explanations. For example, during a period in isolation, green swordtails fish (*Xiphophorus helleri*) forget about defeats and so become more aggressive (Röhrs 1977) and brown trout learn the value of a site in which they are being held on their own and so defend it more fiercely (Johnsson & Forser 2001). In addition, in some cases, far from aggressiveness decreasing as a consequence of fighting, the reverse can be the case, for example in Siamese fighting fish (Clotfelter & Paolino 2003).

Whatever the nature of the processes that generate temporal fluctuations in aggressiveness, it is clear that fighting is not just a reflex-like response to the relevant stimulus and that whether or not an animal has recently taken part in a fight has feedback effects on aggressive motivation. Much research effort is now directed at understanding the physiological processes involved. These will depend to some extent on the resources over which fish are fighting; at its simplest, when fish are fighting over food, nutritional status is likely to influence aggressiveness, but when they are fighting over mates, gonadal status is likely to be more important. In any event, fish come to a possible fight with a certain internal state that determines how likely they are to fight and this state changes in both the eventual winner and the eventual loser as fights escalate and are resolved. The following sections describe some of the physiological processes that might be responsible for such changes in responsiveness.

### *The role of metabolic physiology and nutritional status*

Fighting can be extremely vigorous, using up energy reserves and producing metabolic biproducts that must be excreted. Therfore even in fights that are not about food, nutritional status and metabolic physiology form part of the mechanism that determines how fiercely fish fight. Individual fish vary in resting metabolic rate and in some cases this variability is consistent over time; in general, fish with a high resting metabolic rate have a good capacity for performing energetic activity such as fighting. In fights between pairs of size-matched, first-feeding Atlantic salmon (Metcalfe *et al*. 1995) and rainbow trout (McCarthy 2001), the individual with the higher resting metabolic rate is most likely to win. In juvenile masu salmon (*Oncorchynchus masou*) there is a significant positive relationship between resting metabolic rate and the ability of fish to monopolise large profitable territories (Yamamoto *et al*. 1998). Compared to subordinates, dominant juvenile Arctic charr, which have high resting metabolic rates, also have higher activity of enzymes involved in respiratory metabolism in their muscles (Le Francois *et al*. 2005). The rate of accumulation and removal of metabolic biproducts can influence the outcome of fights, as demonstrated by the fact that lactate accumulates faster in adult male cichlid fish (*Tilapia zilii*) that lose fights over breeding territories than in their victorious opponents (Neat *et al*. 1998). Fish with a high resting metabolic rate need more food to fuel their expensive lifestyle than do fish that use less energy and this may be why they are particularly aggressive over food. Certainly, fish often fight more fiercely after a period of food deprivation, the coho salmon (*Onchorhynchus kisutch*) providing an example (Damsgård & Dill 1998). The effect of food deprivation on aggression depends on its duration; after long periods without food, fish become less aggressive as conserving depleted energy stores rather than fighting for what little food there is becomes the imperative. Since cultured fish may receive variable rations, such effects may well be important in determining the levels of aggression occurring in production systems.

### *Hormones, brain biochemistry and aggression*

The effects of hunger on aggression described above may be partly mediated through the behavioural effects of growth hormone, at least when fish are fighting over food. In rainbow trout, high levels of growth hormone increase

aggressiveness, though not probability of winning, most likely through an effect on hunger (Johnsson & Björnsson 1994). In vertebrates generally, reproductive hormones, and particularly androgens, often stimulate aggression when adult males are competing for access to females, although the effects are not universal and may be complex. In many species of fish, the testosterone metabolite 11-keto-testosterone (11-KT) is strongly implicated in determining levels of aggression where fish fight over mates. For example, elevated levels of 11-KT (among other hormones) increase the incidence of aggression in male Arctic charr (Elofsson *et al*. 2000). Such effects may arise through a direct effect of hormones on the brain mechanisms that control aggressive behaviour, but they may also come about indirectly by altering structures used in fights, for example the hooked snout or kype of breeding male salmon (Chapter 10). In addition to modifying the signals exchanged during fights, androgens may themselves act as a source of signals; for example, the breakdown products of androgens function as chemical signals modulating levels of aggression in male Mossambique tilapia (*Oreochromis mossambicus*) fighting over females (Barata *et al*. 2008).

Particularly striking demonstrations of the role of androgens in the control of aggression are seen when male fish show alternative reproductive tactics (Chapter 10). For example, in the peacock blenny (*Salaria pavo*) large, brightly coloured, scented males fight to establish breeding territories on which they court to attract females. Smaller, dull-coloured males avoid fights and sneak fertilisation. These morphological and behavioural differences are associated with higher levels of 11-KT in territorial males compared to sneakers. Similar results have been described in cultured species, including the Mosambique tilapia and the Atlantic salmon (Oliveira 2006). Androgens are also implicated in the control of aggression in fish that undergo sex change (Chapter 10). For example, if the dominant male is removed from a group of bluebanded gobies (*Lythrypnus dalli*), in a few hours the dominant female changes sex, undergoing dramatic behavioural changes that include becoming increasingly aggressive. This is associated with, and probably caused by, falling levels in the brain of the enzyme aromatase, which converts testosterone to oestrogen, generating more testosterone available for conversion to 11-KT (Black *et al*. 2005).

Other hormones can influence aggressiveness in fish. For example, thyroid hormone controls the changes that accompany the parr–smolt transformation in salmonids, including the switch from aggression to shoaling seen at this transition; experimentally-induced increases in thyroxine cause a drop in aggressiveness (Hutchinson & Iwata 1998). However, the relationship between falling levels of aggression and stage of smoltification is not simple and may be due to the habitat shift rather than to the hormonal changes themselves (Damsgård & Arnesen 1998). Melanocyte-stimulating hormone (MSH), as its name implies, promotes body darkening in fish. In Arctic charr plasma MSH levels are higher in subordinate fish, contributing to their darker colour (Höglund *et al*. 2000) and intracranial MSH injections reduce aggressiveness in a cichlid fish (Munro *et al*. 1986). In addition, hormones involved in the stress response, for example cortisol, can have an effect of aggression. Short-lived increases in cortisol levels make fish more aggressive; for example, in the brown ghost knifefish, injection of cortisol facilitates the production of aggressive signals (Dunlap *et al*. 2002). In contrast, chronic increases in circulating cortisol levels suppress aggression and rainbow trout and brown trout that have high cortisol levels before an aggressive encounter are less likely to win fights than are those with lower levels (Pottinger & Carrick 2001; Sloman *et al*. 2001). In juvenile rainbow trout, experimental elevation of cortisol reduces aggression towards other fish (Figure 9.2; Øverli *et al*. 2002). Differences in cortisol production are often involved in the individual differences in aggressiveness shown by fish with different coping strategies (Chapter 8). For example, rainbow trout from a line selectively bred for high cortisol responsiveness (Pottinger & Carrick 1999) tend to lose pairwise fights against fish from a line selected for low responsiveness (Pottinger & Carrick 2001).

The serotonin system in the brain is closely involved in mediating the effects of stress, including cortisol-induced suppression of aggression. This system is highly conserved and serotonin has an inhibitory effect of aggression in many vertebrate groups, including fish. Experimentally elevated brain serotonin levels inhibit aggression in cichlid fish (*Aequidens pulcher*, Munro 1986; *Cichlasoma meeki*, Adams *et al*. 1996), in brown ghost knife fish (Maler & Ellis 1987) and in bluehead wrasse (*Thalassoma bifasciatum*; Perreault *et al*. 2003). Differences in brain bioamine activity also contribute to the individual differences in aggressiveness shown by fish with different coping strategies; rainbow trout from the high stress responsiveness line (Pottinger & Carrick 1999) show striking stress-induced increases in brain concentrations of various bioamines, including serotonin (Øverli *et al*. 2001).

### 9.2.4 Effects of aggression on the neuroendocrine system

The previous sections have shown how various hormones and brain biochemicals can alter the way fish behave during a fight. There is also an extensive literature showing the

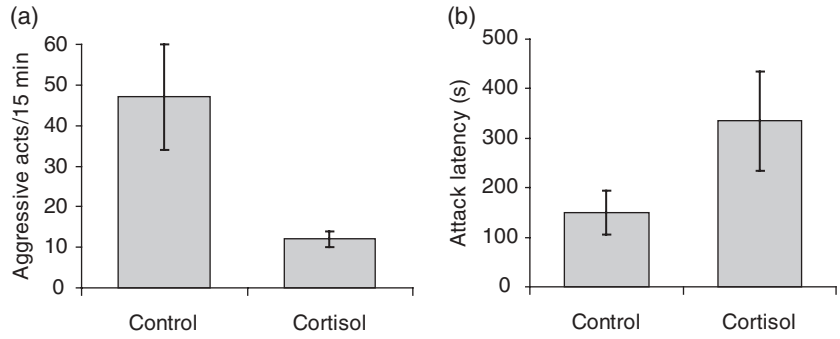


**Figure 9.2.** Effect of hormones on aggression. (a) Mean (±SE) number of aggressive acts per 15 min and (b) mean (±SE) time elapsing between the start of an encounter and the first attack (attack latency) in juvenile rainbow trout 48 h after either a control implant or an implant with cortisol (110 mg/kg). Adapted from Øverli *et al.* 2002.

converse, because what happens during aggressive interactions has profound effects on neuroendocrine status. Such effects can be seen on a second-by-second basis, as fights escalate and are resolved, on a day-by-day basis, as dominance–subordinance relationships are established, and in a longer time scale, as life history patterns are influenced by success or failure in competition for resources. To illustrate the kind of short-term effects that can occur during fights, male Mozambique tilapia that experience territorial intrusions (as well as encounters with females) show a rapid increase in circulating androgen levels (Figure 9.3a; Hirschenhauser *et al.* 2004; Oliveira *et al.* 2002; Oliveira 2009). Simply watching other males fight can be sufficient to produce a similar effect (Oliveira *et al.* 2001). Such effects are probably responsible for the higher circulating androgen levels in territorial male cichlid (*Haplochromis burtoni*; Francis *et al.* 1993) and they mean that fish that have recently fought or witnessed a fight are ready to meet a challenge, primed to fight by their hormonal status (Oliveira 2009).

Once a fight gets under way, both participants experience rapid changes in circulating hormones. For example, in male green swordtail fish, sharp increases in levels of circulating testosterone and cortisol occur in both the eventual winner and the eventual loser. The testosterone surge is greater and longer-lived and the cortisol surge smaller and shorter-lived in the eventual winner, which ends up with higher testosterone and lower cortisol levels than the loser (Figure 9.3b; Hannes *et al.* 1984). Nile tilapia show a four-fold increase in plasma cortisol levels following one-hour exposure to a larger conspecific (Baretto & Vopato 2006). Because aggression is promoted by androgens and suppressed by sustained elevation of cortisol levels, such experience-mediated changes in hormonal state represent part of the mechanism by which fights escalate and are resolved.

A number of neuroendocrine changes are set in train by the establishment of dominance–subordinance relationships. These are complex and variable, depending on species and circumstances and there are questions over the extent to which similar effects are seen in the wild as in the laboratory (Sloman & Armstrong 2002). In general, higher concentrations of circulating androgens, particularly 11-KT, are found in dominant Mozambique tilapia (Oliveira *et al.* 1996), rainbow trout (Cardwell *et al.*1996) and Arctic charr (Elofsson *et al.* 2000). Conversely, cortisol levels are higher in subordinate Nile tilapia (Barretto & Volpato 2006), rainbow trout (Winberg & Lepage 1998) and Arctic charr (Elofsson *et al.* 2000). Finally, there are well-documented effects of subordinate status on brain bioamine metabolism in several species of fish. For example, serotonin activity is higher in subordinate Arctic charr than in dominant fish (Winberg & Nilsson 1993), as it is in rainbow trout (Øverli *et al.* 1999) and in territorial male cichlids (*Haplochromis burtoni*) compared to non-territorial males (Winberg *et al.* 1997). Given the fact that low levels of androgen, chronically elevated cortisol and high serotonin activity are all associated with reduced aggression, this spectrum of physiological changes explains in mechanistic terms why subordinate fish avoid fights with dominant companions. Night-time production of melatonin (involved in the control of circadian rhythms) is higher in subordinate rainbow trout (Larson *et al.* 2004), which may help to explain why subordinate fish sometimes feed at night when dominant fish are not active (Alanärä *et al.* 2001).

### 9.2.5 Summary of the mechanisms of aggression in fish

Aggression is a complex and flexible behaviour and the mechanisms that control it are also complex. Potential

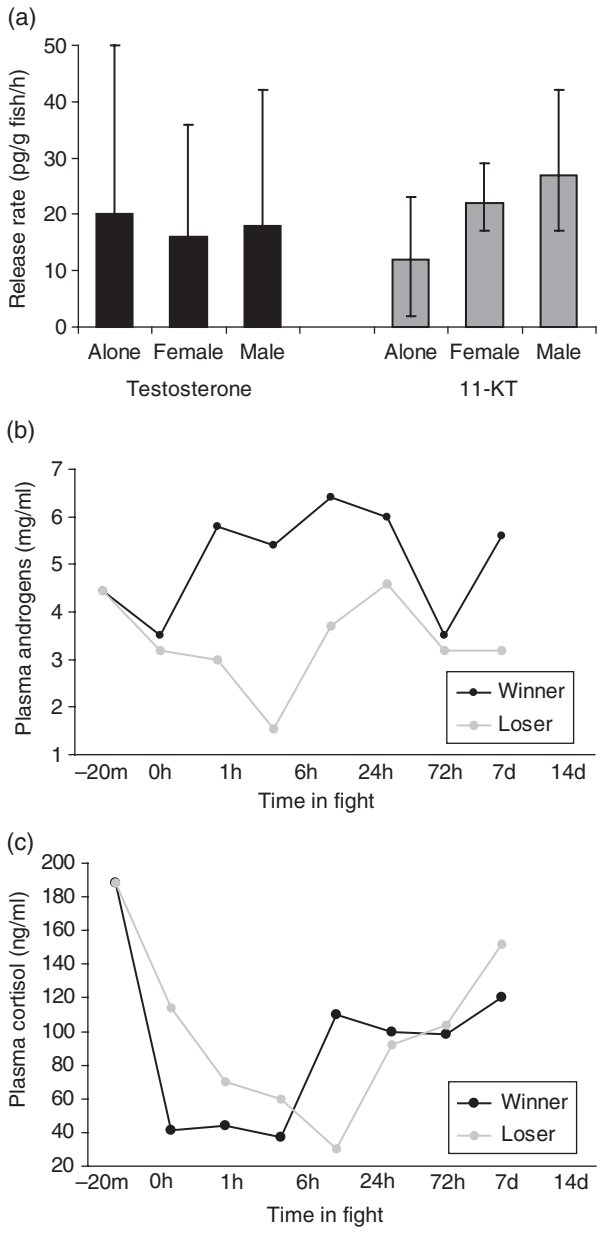


**Figure 9.3.** Effects of experience on endocrine status. (a) Mean (±SE) rate of excretion of testosterone and 11 ketotestosterone (11-KT) in male Mossambique tilapia in social isolation and after interacting with a receptive female and a male intruder. Adapted from Hirschenhauser *et al.* 2004. (b) Levels of androgens and (c) levels of cortisol in male swordtails at various points with respect to the onset and decision of a pairwise aggressive encounter, with winners and losers differentiated. –20m = –20mins after the first threat. –0h, –1h, –6h, –24h and –74h = hours after decision of fight. –7d and 14d = days after decision of fight. Adapted from Hannes *et al.* 1984.

rivals provide cues or signals in various modalities that influence the behaviour of the receiving fish, either increasing or decreasing the probability of attack. Some of these cues are conditional, in the sense that they depend on the relationship between the fish involved, relative size being a case in point. How a fish responds to aggression-eliciting or aggression-inhibiting cues also depends on the context in which an encounter occurs, with prior residence and valuable resources facilitating attack. It also depends on the fish' internal state, nutritional status being particularly important when fish fight over food and levels of circulating androgens when fish fight over mates. Endocrine status changes during fights, with short-term increases in cortisol and, in adult fish, androgens occurring in both winners and losers. As fights are resolved, fish that lose, and in particular subordinates that have lost a series of fights, show longer-lasting changes in neuroendocrine status, including decreased androgens, increased cortisol and increased serotonin turnover, all of which reduce the probability of their engaging in further fights.

## 9.3 DEVELOPMENT

As earlier sections in this chapter make clear, there are many examples of striking differences in how frequently and fiercely fish fight, at the level of species, population and individual. In developmental terms, the origins of such differences in aggressiveness lie in the interacting effects of the genetic constitution of individual fish and the environment in which they develop. This section starts by describing the ontogeny of aggressive behaviour as a newly hatched egg develops into an adult fish, before considering the extent to which differences in aggressive behaviour can be explained by genetic differences between fish and by differences in environment in which fish develop. Understanding the genetic and environmental factors that influence the development of aggression in cultured fish can potentially help farmers to control this behaviour in their stock.

### 9.3.1 Ontogeny of aggression

Young fish often experience competition for food, so it is not surprising to find that aggression appears early in the behavioural repertoire or that it changes in form and frequency as the fish get older and their needs and circumstances change. For example, in young groupers (for example *Epinephelus septemfasciatus*, one of a number of grouper species that are a target for culture both for supplementation programmes and for food) aggression is first observed at 52 days post-hatching, when dorsal pigment appears and larvae start to settle out of the oceanic

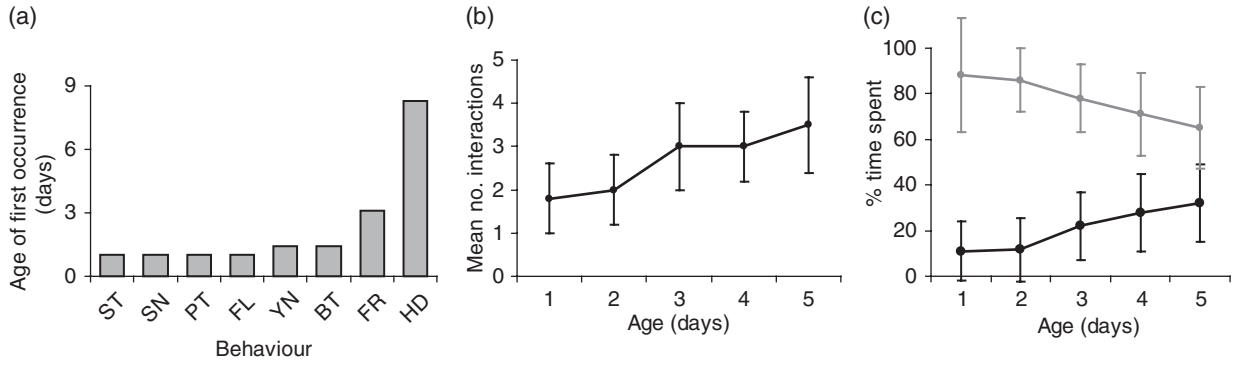


**Figure 9.4.** The ontogeny of aggressive behaviour. (a) Age of first appearance of components of aggressive behaviour in rainbow trout. ST=stationary. SN=snap. PT=pursuit. FL=flight. YN=yawn. BT=bite. FR=dorsal fin raised. HD=head down. (b) Mean (±SD) frequency of aggressive interactions and (c) mean (±SD) frequency of overt aggression (grey) and threats (black) in relation to time since 50% of larvae were free swimming. 1=days 1–6, 2=days 7–12, 3=days 13–18, 4=days 19–24, 5=days 25–30. Adapted from Cole & Noakes 1980.

column to shallow rocky shores (Sabate *et al*. 2009). Young salmonids disperse from the under-gravel nests in which they hatch at about the time that their yolk sacs are depleted and they start to feed independently. They move to a suitable first feeding habitat, where they may defend territories or establish dominance hierarchies, depending on local conditions. In rainbow trout, simple aggressive acts such as nips and chases and fleeing from such attacks appear once the yolk sac is absorbed and the fish are feeding independently. Threats take a little longer to develop, with fin erection appearing first. Head down threat is seen a few days later and becomes more common compared to overt attack as the fish get older. The frequency and duration of aggressive interactions increases with age up to 30 days post-emergence (Figure 9.4; Cole & Noakes 1980).

After a variable period in fresh water, during which they continue to fight over food and sometimes to defend territories, young salmon undergo parr–smolt transformation and move into their sea phase, switching to a largely non-aggressive, shoaling life style. Once salmon mature and return to their natal rivers to breed, they change back to being aggressive, this time fighting over nest sites and mates. This is caused by the changes in hormonal status that accompany breeding, but it may also be a response to the fact that the fish now have something to fight over. Overall, in salmon as in other species of cultured fish, the incidence and level of aggressiveness changes during development, partly due to the general process of growth and maturation and partly due to habitat shifts and other changes that make fighting over resources more or less worthwhile.

### 9.3.2 Genes and aggression

It is a striking fact that salmon fry nip and chase each other effectively on the first occasion that they encounter rivals and that in many species of fish, species-specific aggressive behaviour develops more or less normally in fish reared in isolation, without the possibility of learning how to fight. For example, male cichlids (*Haplochromis burtoni*) that have been reared in isolation fight normally, reacting to attack-eliciting stimuli (the black bar below the eye, for example) in the same way as socially reared fish (Fernald 1980). In brown trout (Lahti *et al*. 2001) and coho salmon (Rosenau & McPhail 1987), population differences in aggressiveness are still seen in fish reared in identical conditions. Given such observations, aggression is sometimes described as ‘innate’, with the implication that its development is controlled by the programmed expression of particular genes during development.

Several kinds of evidence show that variation both in aggressive behaviour and in the signals displayed during fights do indeed depend on genetic differences between the fish concerned. For example, selective breeding from the extremes of the continuum of aggressiveness in wild-caught male sticklebacks (*Gasterosteus aculeatus*) produces lines with very different levels of aggression within a few generations, showing that genetic differences were responsible for at least some of the original behavioural variation (Bakker 1986). Strains of Siamese fighting fish (*Betta splendens*) selectively bred for cockfight-like contests are more aggressive than wild type fish in pairwise interactions with live opponents (Verbeek *et al*. 2007). Crossing experiments in swordtails (*Xiphophorus* spp.)

have shown that variation in the pattern of pigmented vertical bars, which deter territorial rivals, is inherited under the control of a several different genetic loci (Zimmerer & Kallman 1988). Males with bars modulate their aggression in response to the sight of such bars in an opponent; males without bars do not, so inherited differences in signals are linked to differences in response to them (Moretz & Morris 2003). Reciprocal crosses between strains of guppy implicate elements on the Y chromosome in the inheritance of strain differences in aggressiveness (Figure 9.5; Farr 1983).

There is some evidence for inherited differences in aggression in long-lived cultured species. For example, selection for high and low stress responsiveness in rainbow trout carries with it differences in aggression, with low responsive fish being more likely to win fights, suggesting that such differences have an inherited basis (Øverli *et al*. 2004). Experimental crosses show that hybrids between lake charr (*Salvelinus namaycush*), which are relatively non-aggressive, and brook charr (*Salvelinus fontinalis*), which are aggressive, have intermediate levels of aggression, suggesting that genes are responsible for the original species differences (Ferguson & Noakes 1982). As a final example, salmonids that have an extra copy of the growth hormone gene are more aggressive than normal fish, probably as an indirect result of increased feeding motivation (Hallennan *et al*. 2007). The existence of inherited differences in aggressiveness among cultured fish species offers the possibility of selective breeding for levels of aggression that are appropriate for fish culture, for whatever purpose.

### 9.3.3 Environmental effects

Although aggression often develops in a broadly normal way in isolated fish and inherited differences in aggressiveness have been demonstrated in several species, how much an individual fish fights is profoundly influenced by the environment in which it develops. Some such environmental influences may be of a very general nature, others are highly specific, but all combine to determine just how a fish behaves in a fight.

#### *General and indirect effects*

Life history events such as adoption of a particular mating tactic are often caused by size-dependent and condition-dependent switches acting at critical times during development (Chapter 10). For example, juvenile male Atlantic salmon that grow fast in any given spring are more likely to mature and fight for access to females than are slow growing fish of the same cohort (Thorpe *et al*. 1998). As a consequence, anything that alters the rate at which fish grow will eventually have consequences for their aggressiveness. There are other general effects on how aggression develops. For example, zebrafish (*Danio rerio*) reared under hypoxic conditions are less aggressive as adults than those reared in normoxia, even when the fish are no longer held at low oxygen levels (Marks *et al*. 2005).

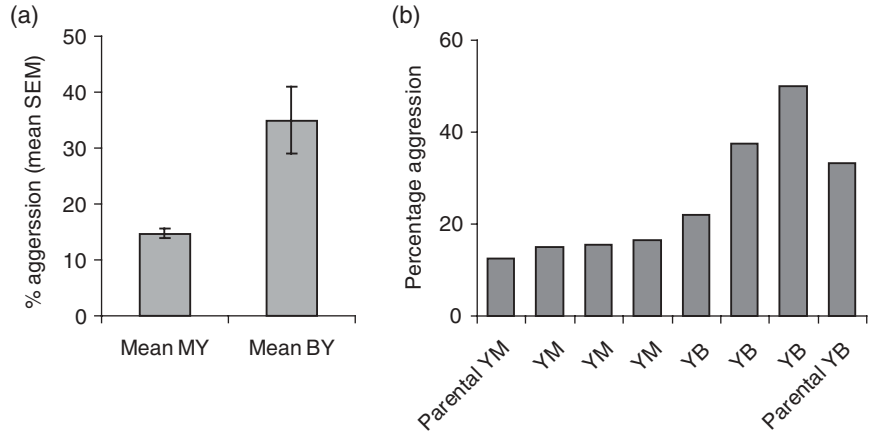


**Figure 9.5.** Evidence for effects of the Y chromosome on aggression. (a) Percentage of tanks in which aggression was observed in two parental strains of guppy, in F1 strain and a series of backcross strains. (b) Mean aggression percentage of encounters resulting in strains denoted MY (which have the Y chromosome from the least aggressive strain) and for those denoted BY (which have the Y chromosome from the most aggressive strain). Adapted from Farr 1983.

Some effects of the environment on the development of fighting are specific, but indirect. For example, nutritional status of female Atlantic cod (*Gadus morhua*) influences the size of their eggs and, through this, the size and age of their larvae at first feeding (Marteinsdottir & Steinarsson 1998; Chapter 2). Since size and prior residence are important determinants of the outcome of fights, such maternal effects are likely to influence how aggression develops in the young fish. Newly emerged coho salmon fry from crosses between captive-reared females and wild males tend to win fights against fry from the opposite cross. Captive-reared females produce paler eggs than do wild fish and, perhaps as a consequence, their fry are also paler, lacking melanin in their chromatophores. Since dominant salmonids are typically light and subordinates typically dark, it may be that through such maternal effects fry from captive-reared mothers continuously signal dominance to wild opponents (Berejikian *et al*. 1999).

### *Effects of experience during social encounters*

In addition to such general and indirect effects, how fish behave during fights can be strongly influenced by specific experience during previous aggressive interactions, often taking place early in life. For example, Nile tilapia fry reared for 9 weeks in small groups with companions that are unable to perform displays (because of a mutation-induced absence of the dorsal fin) are slower to engage in fights, probably due to lack of experience of normal display (Barki & Volpato 1998). Zebrafish reared as juveniles in groups composed of fish from two different strains, one more aggressive than the other, show more aggression (biting at a mirror image) than do those reared only with their own strain, even after subsequently being placed in pure-strain groups. This may come about through some combination of reduced familiarity and/or relatedness within mixed groups and social feedback causing aggression to escalate in mixed groups (Moretz *et al*. 2007a).

Experience during fights can modify aggressive behaviour on a shorter time scale throughout a fishes' life (Moretz *et al*. 2007a). Thus, when the same individuals fight repeatedly, the outcome may be experience-dependent changes in aggressiveness in the form of dominant-subordinate relationships. Even when fights are with different individuals, what happens in one fight can influence how likely fish are to fight on subsequent encounters and, if they do fight, exactly how they do so. In the mangrove-dwelling fish *Rivulus marmoratus*, prior experience of losing makes a fish more likely to retreat and less likely to initiate a fight in subsequent aggressive encounters. In contrast, prior experience of winning increases the likelihood that a fish will initiate a contest with attack rather than display (Figure 9.6; Hsu & Wolf 2001).

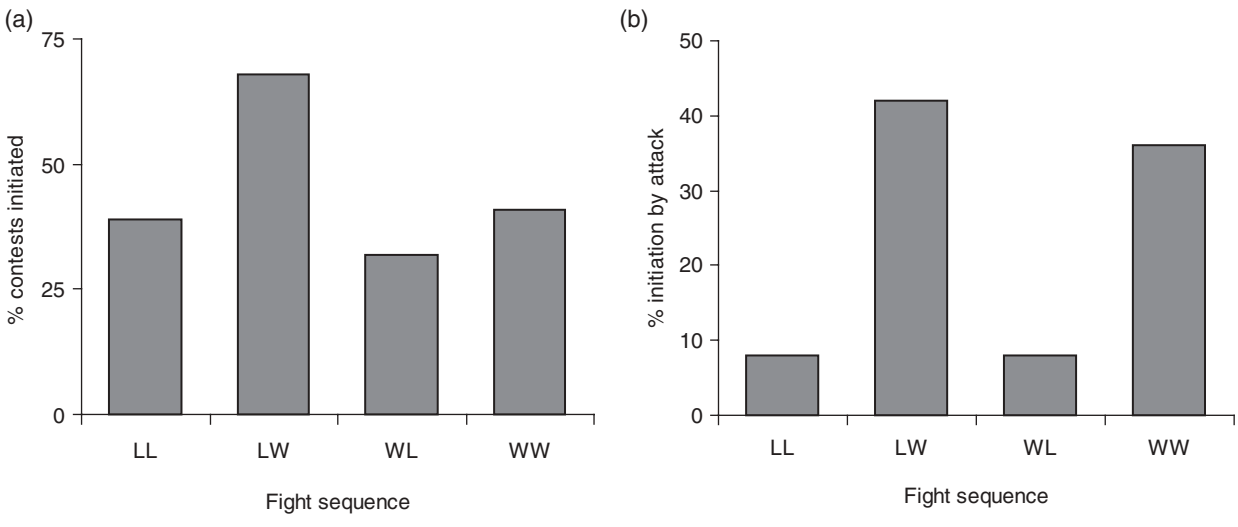


**Figure 9.6.** Effect of prior experience on aggression. (a) Percentage of pairwise contests initiated by a given individual *Rivulus marmoratus* and (b) Percentatge of interactions initiated by an attack rather than display, both in relation to its previous history of losing or winning fights. WW = won both previous staged fights. LL = lost both previous fights. WL = won the first and lost the second. LW = lost the first an won the second. Adapted from Hsu & Wolf 2001.

Knowledge of the status and fighting ability of familiar companions may be derived from observing them fighting other fish, as well as from direct interactions (Peake & McGregor 2004). For example, juvenile rainbow trout gain information about the fighting ability of potential opponents through watching pair-wise fights, being quicker to give up when paired against a fish that they have previously seen winning (Johnsson & Åkerman 1998). The effects of genes and environment on the development of aggression may not be independent, as certain genotypes may make developing fish particularly susceptible to specific environmental influences. For example, in Siamese fighting fish from strains with inherited low levels of aggression polarisation of behaviour between winning and losing fish is stronger than in fish from strains with higher base line levels of aggression (Karino & Someya 2007).

### 9.3.4 Summary of the development of aggression

Simple acts of aggression appear early in development in many species of fish, though fights tend to become more complex with age. The frequency of aggressive interactions may change at critical points during development, for example when fish move to different habitats and when they reach sexual maturity. Very young fish and those reared in social isolation often show species-typical aggressive behaviour, suggesting that development of these responses are strongly controlled by the fish's genes, and various lines of evidence have identified inherited differences in aggressiveness, between species, between populations and between individuals. At the same time, a variety of environmental factors influence the way aggression develops; these range from general effects such as food availability to specific learning processes occurring during fights. Genetic and environmental processes interact to determine how fish behave when they come into conflict, both during development and as adults. The fact that aggression is subject to so many inherited and environmental influences potentially offers the possibility of modifying this behaviour in cultured fish.

## 9.4 FUNCTIONS

In a functional sense, an encounter with a potential opponent may be seen as a series of decisions. This does not imply consciousness in the animals concerned, but simply that at several points in a fight an animal has alternatives, for example to initiate a fight or not, to escalate or not or to stop a fight or not. Each of these decisions has consequent costs and benefits for the animal concerned and the sum of the right decisions will lead to a higher fitness. The following sections describe the benefits that fish gain from winning fights, the costs they pay in the process and how the decisions they make during aggressive encounters reflects an adaptive balance between them.

### 9.4.1 Benefits of winning fights

Aggression is one way of coping with competition for limiting resources and the benefit that animals gain from winning fights is exclusive or preferential access to such resources. In wild animals, the disputed resource is often breeding opportunities and fish that win fights may gain direct access to fertile mates. For example, female pipefish (*Syngnathus typhle*) actively compete for access to males with empty pouches (Berglund & Rosenqvist 2003) and in wild male Atlantic salmon high levels of aggressiveness are associated with spawning success (Weir *et al.* 2004). Immature animals fight over a variety of resources. For example, during the winter juvenile rainbow trout fight over access to shelters, with larger fish usually winning fights and excluding competitors from shelters (Gregory & Griffith 1996). Since growth is a critical determinant of fitness, in immature fish a major benefit arising from winning fights is food, through direct access to individual food items, through ownership of a feeding territory or through dominant status. For example, in groups of Arctic charr, growth rate falls progressively down the dominance hierarchy and dominant charr have better nutrient reserves than do subordinates (Le Francois *et al.* 2005). In wild masu salmon also, dominant fish have higher daily growth rates than do subordinates (Nakano 1995). In tilapia species dominant social status brings with it preferential access to food (Nile tilapia; Vera Cruz & Brown 2007) when food is delivered from a point source, but not when it is dispersed (*Tilapi rendelii*; McCarthy *et al.* 1999). Compared to dominant fish, subordinate juvenile sea bream show lower food intake and slower growth (Montero *et al.* 2009). Such links between the outcome of fights, feeding and growth are of clear relevance in aquaculture, where fast, uniform growth is preferred.

### 9.4.2 Costs of fighting

The immediate costs of fighting include time taken from other activities, energy expenditure and the risk of injury; these often fall more or less equally on the fish that eventually wins and the fish that eventually loses. There are also longer-term costs in the form of prolonged physiological arousal especially during repeated defeats, which tend to fall more heavily on the loser.

Time spent fighting reduces time for other activities that are important for fitness, such as feeding, looking out for predators or caring for young; in other words cost takes the form of lost opportunities. Territorial coho salmon spend

more time fighting and have less time for feeding than do non-territorial fish (Puckett & Dill 1985). Male cichlids (*Nannacara anomala*) show less vigilance, allowing a predator to approach closer before detection when they are fighting than when they are not; the more intense the fight the closer the predator can approach (Jakobssen *et al*. 1995). Aggression interferes with tending young in species such as cichlids that show paternal care and it is probably for this reason that levels of circulating androgens, and with them levels of aggression, fall after mating in such species (reviewed by Oliveira *et al*. 2002).

Simply taking part in a fight, whatever its outcome, involves costs in terms of increased energy expenditure. In male cichlid fish (*Aequidens rivulatus*) fighting over breeding territories, respiration rate increases as encounters progresses in both participants, but particularly in loser (Figure 9.7a; Maan *et al*. 2001). In a different species of cichlid (*Tilapia zillii*) but in the same context, lactate accumulates and glycogen reserves are depleted during fights, again in both participants but particularly in the loser (Figure 9.7b; Neat *et al*. 1998). Such changes in metabolic status are not just short-term consequences of fighting, but involve real fitness costs. For example, in convict cichlid (*Archocentrus nigrofasciatus*) growth rates are slowest in social conditions where aggression is most frequent (Noël *et al*. 2005).

Although some fights are resolved by no more than an exchange of displays, in other cases they can escalate to intense circling and biting, with both participants running a risk of injury. The caudal and particularly the dorsal fin are often damaged during fight between juvenile rainbow trout (Abbott & Dill 1985). In juvenile Atlantic salmon, although aggressive fish grow fast and migrate to sea early, they suffer higher rates of fin damage than do their less aggressive companions (Nicieza & Metcalfe 1999). In *Aequidens rivulus* the number of injuries to mouth, fins, tail and flank increases in proportion to fight duration (Maan *et al*. 2001) and in *Tilapia zillii* scale loss and fin injury increase with fight intensity, especially in fish that loses (Neat *et al*. 1998). Fish may have adaptations that mitigate the cost of injury, such as the thick skin of adult male sockeye salmon (*Onchorhynchus nerka*; Johnson *et al*. 2006), but injury remains a real cost of fighting. In addition, because fish that lose fights experience elevated cortisol levels, the consequences of aggression include physiological activation, which may result in less efficient growth (Abbott & Dill 1989), as well as other adverse effects such as impaired immune function. Compared to what happens in natural conditions, such effects may be exaggerated in laboratory experiments, where fish are often in small tanks and cannot escape aggression (Sloman & Armstrong 2002). However, because cultured fish also cannot completely escape attack, most of the effects described above are likely to be relevant in aquaculture.

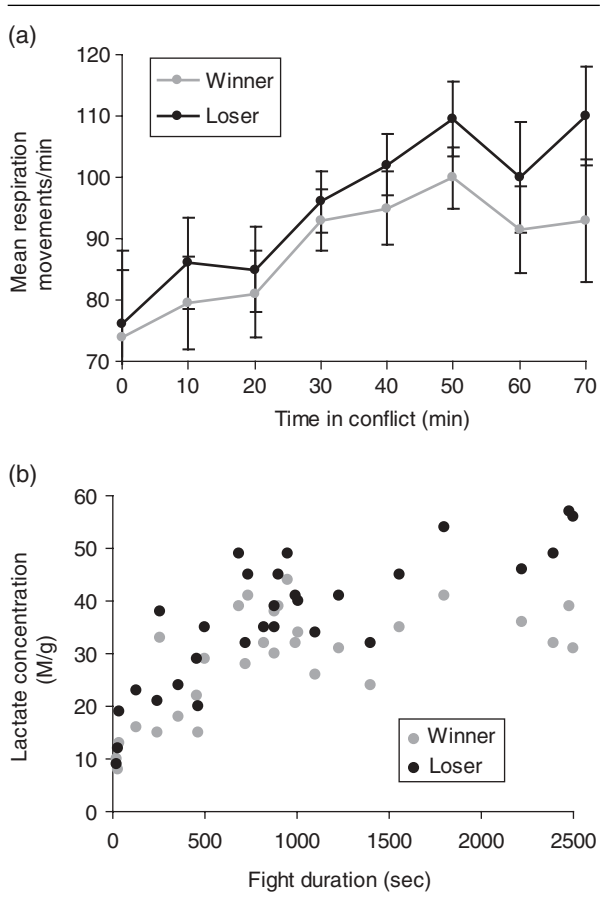


**Figure 9.7.** Costs of fighting. (a) Mean (±SE) rate of respiratory movements in the winners and loser of fights between male cichlids (*Aequidens rivulatus*) in relation to time in the fight. Adapted from Maan *et al*. 2001.( b) Lactate concentration versus fight duration in individual male *Tilapia zillii* that either won (grey circles) or lost (black circles) fights over breeding territories. Adapted from Neat *et al*. 1998.

### 9.4.3 Integrating benefits and costs

Because aggression involves costs as well as yielding clear benefits to winners and because both costs and benefits depend of the environment in which a fight occurs, animals often adjust their behaviour during a fight to according to the costs and benefits of the various options open to them. In functional terms how they make such adjustments determines whether an animal will defend a resource or not. According to one simple but influential framework, the

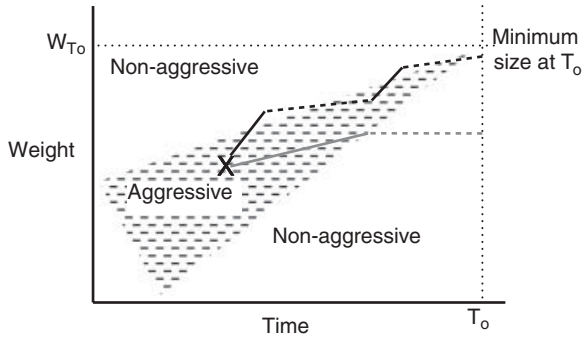


**Figure 9.8.** State-dependent dynamic model of changes in fighting and risk-taking tactics in smolting salmonids. As an individual fish grows from a certain size (X) in order to reach size W at time $T_0$, the growth trajectory is related to changes from aggressive, risk-prone behaviour (weight trajectory indicated by black solid lines) to non-aggressive, risk-averse behaviour (weight trajectory indicated by black dotted line). If growth falls under a threshold at which the size W cannot be reached (weight trajectory indicated by a grey solid line), the fish may give up its 'growth plan' and adapt a non-aggressive tactic (weight trajectory indicated by grey dotted line). Adapted from Damsgård & Dill 1998.

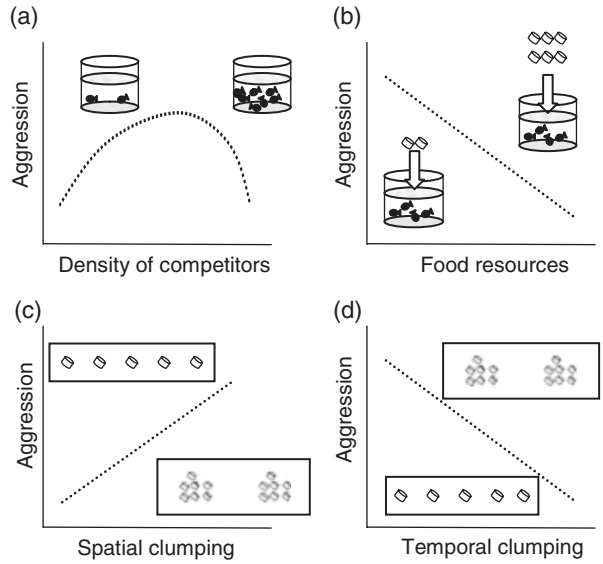


**Figure 9.9.** The economics of fighting. Expected aggression as a function of (a) Density of competitors, (b) Amount of food resources, (c) Spatial clumping of the food and (d) temporal clumping of the food.

theory of economically defendable resources, an individual will defend a resource if the net benefit gained from doing so (benefits minus costs) is positive (Brown 1964; Grant 1993, 1997). This implies that animals have and use information about the potential fitness costs and benefits of the particular decisions available to them during an aggressive encounter. In fish this is unlikely to be a conscious process, but instead is based on a continuous unconscious integration of information such as food availability and the competitive abilities of potential opponents. For example, coho salmon temporarily change both aggressiveness and risk-taking behaviour to meet deviation in feed availability (Damsgård & Dill 1998). Figure 9.8 shows a model based on such dynamic, state-dependent decision-making processes that can be used to explain shifts over time by individual fish between being aggressive and non-aggressive and hence day-to-day variation in rates of feed intake and growth.

The theory of economically defensible resources predicts that aggressiveness will be affected by any factor that alters the relative costs and benefits of fighting, influential variables including the density of competitors, the amount of the resource and its distribution in time and space. The relationships between these variables and expected levels of aggression have not been fully characterised, but sufficient is known to outline their general shape (Figure 9.9). As far as competitor density is concerned (Figure 9.9a), aggression is expected to rise initially as this increases, but above a threshold level, to fall again as the costs of defending the resource against many rivals start to outweigh the benefits. Empirical studies on both medaka and convict cichlid in which the ratio of competitors to resources are manipulated show that the relationships with aggression is indeed dome-shaped (Grant *et al*. 2000; Noël *et al*. 2005).

In contrast, the model predicts a simple negative relationship between the amount of food available and expected aggression (Figure 9.9b), as the benefits of defence are reduced when resources are abundant and there is plenty for all. In this case, empirical studies give complex results. Contrary to this prediction, cross-species comparisons of wild fish show that fish from productive habitats such as the coral reef are more aggressive than those from less productive marine and freshwater habitats (Grant 1997). Lower levels of aggression in poor habitats may simply indicate that, while many fish species have the ability to fight for limited resources, the resources are seldom worth fighting for (Barlow 1993). On the other hand, juvenile

brook charr from a river population with low food supply are more aggressive than similar population with high food supply (Dunbrack *et al*. 1996). In addition, several experimental studies confirm the prediction that a reduction in food levels is associated with an increase in aggression. For example, large dominant medaka chase their companions more when fed a limited ration; however, fish that are not fed at all have the lowest level of aggression, presumably because energy conservation has become a priority (Magnuson 1962).

In spatial terms, it is easier (and therefore less costly) to monopolise a resource that is clumped than one that is spread out, so the economical defensibility model predicts that aggression will increase with spatial clumping of food (Figure 9.9c). In contrast, the prediction is that aggression will decrease with temporal clumping (Figure 9.9d), because fish cannot physically consume a large number of rapidly appearing food items and therefore gain nothing from defending them. Using medaka again, levels of aggression are lowest when food is dispersed in space, but clumped in time and so cannot be monopolised in a cost effective way (Robb & Grant 1998). Drifting food in rivers is a natural example of a resource that appears in small amounts at intervals rather than being clumped in time; river dwelling fish that take such food can easily monopolise the best habitats (those that receive most food per time). In stream-dwelling salmonids, metabolic rate and thus food requirements scale to body mass and territory size increases in relation to body size to meet increasing energetic requirements (Keeley & Grant 1995).

Overall, predictions from the theory of economically defensible resources are confirmed reasonably well, though not perfectly, by empirical data on the behaviour of fish competing for food, suggesting that the benefits of victory are indeed traded off against the energetic costs of fighting as depicted in the model. One reason why the predictions are not met perfectly is that there are other costs of fighting, including increased predation risk, so the presence or absence of predators enters into the equation. In convict cichlids feeding at small food patches (but not at larger ones), levels of aggression decrease in response to an increase in perceived predation risk, manipulated by adding skin extract, or alarm substance (Chapter 8); as a consequence, the number of fish feeding at any given time increases and size variation within groups decreases (Kim *et al*. 2004). The fact that levels of aggression, and consequently rates of growth, are adjusted to costs and benefits in these complex ways offers potential for managing this behaviour among cultured fish.

### 9.4.4 Summary of the functions of aggression

The fish that wins a fight gains benefits in the form of exclusive or preferential access to resources that are critical for fitness, such as shelter, food or mating opportunities. At the same time, both participants in a fight incur costs, in the form of expenditure of time and energy and risk of injury or predation; some of these costs fall equally on both participants, but others fall particularly on the eventual loser. At various points in an aggressive encounter, fish have options such as to initiate or to avoid a fight, to escalate to intense fighting or to continue exchanging displays and to give up or to fight on. What they chose to do at such points is the result of an unconscious trade off between the probability and expected benefits of wining and the likely cost of fighting. Based on such costs and benefits, the theory of economic defensibility of resources predicts the level of aggression a fish should show at particular densities of competitors, levels of resource availability and patterns of resource clumping in space and in time. In general, these predictions are supported by experimental studies on a variety of species of fish, including several that are cultured, confirming that aggressive behaviour is finely tuned to its fitness consequences.

## 9.5 IMPLICATIONS FOR AQUACULTURE

There is nothing abnormal about aggression. Rather, it is a widespread adaptive response to competition for resources and consequently a common component of the natural behaviour of fish, including the species that are cultured. The previous sections in this chapter have described the mechanisms that control when and how intensely fish fight, the way in which genes and environment mould the development of aggression and how fish adjust their behaviour during aggressive encounters to the complex costs and benefits of fighting. These are key aspects of fundamental behavioural biology, but they also have a number of important implications when it comes to culturing fish. Some problems in fish culture arise from the high levels of aggression that can occur during production while the fish are being grown to the required size. Others arise from inappropriate aggressive behaviour when cultured fish are being put to use, whether as brood stock, for release into the wild, as ornamental fish or as subjects for scientific experiments. The following sections explore such problems, before discussing how knowledge of the fundamental behavioural biology of aggression might be used to solve them.

**Table 9.1.** Direct observations on the incidence of aggression among farmed fish species held at moderate densities under experimental conditions.

| Species/age | Approximate density | Approximate mean number of attacks | Reference |
|---|---|---|---|
| Juvenile sea bream (about 80 days) | 1.6 fish/ L | Nips delivered = 2/min for dominants & 0.6/min for subordinates | Goldan *et al.* 2003 |
| Adult rainbow trout | 10 fish/200L | Nips, attacks & chases/fish/min outside feeding period on 1 meals/day = 0.75 & on 3 meals/day = 0.30. Attach rates higher during feeding. Pectoral fins, caudal fins & central body targeted | Noble *et al.* 2007 |
| Adult swordtail | 2 adult males, 3 adult females and 6 juveniles/tank (915 × 330 × 350 mm) with clumped food. | One male clearly dominant in all groups, delivering 2 attacks/min to the subordinate male. | Magellan & Kaiser 2010 |
| Juvenile koi carp (5–6 weeks) | 20 fish/150 L | 1.3 attack delivered /fish/5 min. Higher during feeding Abdomen or fins targeted | Jha *et al.* 2006 |
| Juvenile goldfish (5–6 weeks) | 20 fish/150 L | ca 0.4 attacks delivered/fish/5 min. Higher during feeding. Abdomen or fins targeted. | Jha *et al.* 2005 |

### 9.5.1 The incidence of aggression in culture systems

The theory of economic defensibility discussed in Section 9.4.3 predicts that levels of aggression will be low when resources are abundant and since most cultured fish receive plenty of food, it might be expected that they would not fight much. A first point to establish is therefore whether and how much fish do actually fight in production systems. It is also important to know whether individual cultured fish differ in their ability to compete aggressively, since this could have a large influence both on production and on the welfare of individual fish. These are not easy questions to answer, not least because it is very difficult to see what happens to fish in intensive and some extensive husbandry systems (Chapter 3).

Direct observation aided by the use of underwater cameras has documented the incidence of fish attacking each other in conditions approximating to those found in production systems for a number of species; Table 9.1 summarises some of this information. Clearly, fighting can be common in cultured fish, even though levels vary between species. To give a few examples in more detail, between 30 and 60 days after hatching, larval Atlantic cod held at production densities show aggressive behaviour towards each other, in the form of simple nips primarily directed at smaller companions and towards the tail of the victim. Such attacks, which often elicit quick darts away on the part of the victim, occur at an average rate of 2.6 attacks per fish per hour, which multiplies up to a high rate of attack. Frequency of aggression is higher just before feeding than after feeding (Figure 9.10a; Forbes 2007). In contrast, in juvenile halibut (*Hippoglossus hippoglossus*) held in production-like conditions potentially damaging aggression (comprising nips and chases) occurs almost exclusively during meals (Figure 9.10b; Greaves & Tuene 2001). The halibut are more aggressive early in the feeding session, with many attacks being directed at fish that have successfully captured a pellet. Approximately 10% of the fish are responsible for approximately 60% of attacks. Aggression is commonest when the young fish are small, becoming relatively uncommon by the time they reach 2.5 kg (Greaves & Tuene 2001).

It is important to know whether all fish in a group are aggressive or whether there is a subset of particularly aggressive fish. With fish at production densities, it is very hard to collect information on the same individual fish on different occasions, but various sources suggest that not all fish are equally aggressive and that delivery of attacks is often polarised. For example, direct observation of larval yellow perch (*Bidyanus bidyanus*) held in mesh cages show that at some densities (25 and 50 fish/$m^3$), one or two particular fish are often chased continually during short (5 minutes) observation periods (Rowland *et al.* 2006). Using indirect evidence, compared to fish that grow well in production systems, adult Atlantic salmon that fail to grow over extended periods have a higher rate of turnover of brain serotonin, which is typical of subordinate fish

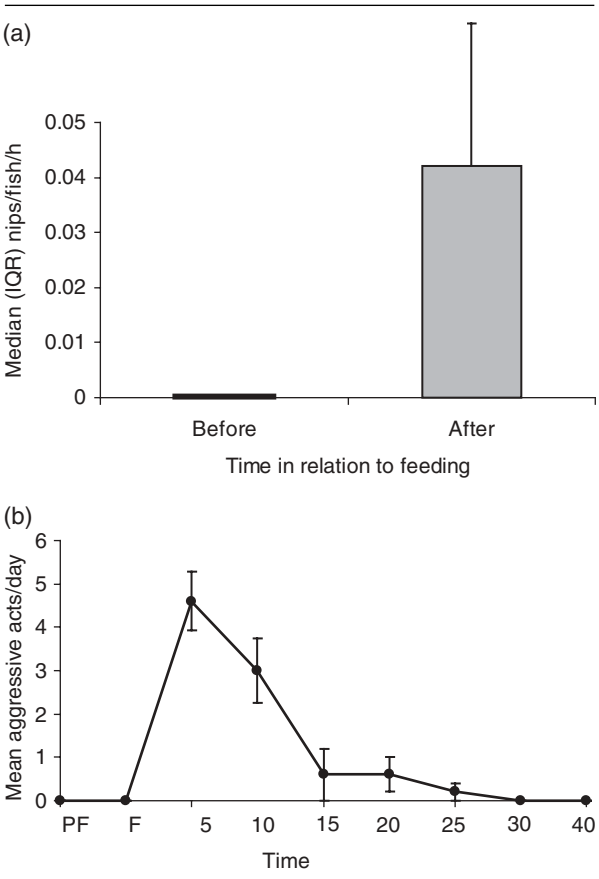


**Figure 9.10.** Incidence of aggression in relation to feeding in farmed fish species. (a) Median (IQR) number of nips per fish per hour in larval cod before and just after being fed. Adapted from Forbes 2007. (b) Median (IQR) number of aggressive acts per fish per day in juvenile halibut (mean weight = 45 g) in relation to time of feeding. PF: prior to feeding. F: feeding. Adapted from Greaves & Tuene 2001.

(Cubitt *et al*. 2008). Direct observation of salmon held at production densities, batch marked according to growth category, shows that non-growing fish avoiding areas where other fish are jostling for food (Figure 9.11; Cubitt 2002; Chapter 3).

Direct observation of aggressive interactions can be supplemented by information on the incidence, nature and location of injury, and in particular fin damage, in cultured fish (Figure 9.12). Fin damage is often used as an indicator of aggressive behaviour in cultured fish, with attack site being species- and context-specific. For example, salmonids often attack each other's caudal fin in reciprocal attacks (Moutou *et al*. 1998) and in rainbow trout both caudal and dorsal fins are targeted in non-reciprocal attacks (Abbott & Dill 1985). Dorsal fin damage seems to be the best indicator levels of aggression within groups of salmonids (Moutou *et al*. 1998). Several studies indicate that dominant fish are less likely to have damaged dorsal fins than their subordinate companions (for example, rainbow trout, Moutou *et al*. 1998), although MacLean *et al*. (2000) found that among juvenile Atlantic salmon held at high densities larger fish have more damage. It may be that large, dominant fish compete among themselves, gaining access to food but incurring fin damage, while less competitive individuals feed less and grow more slowly, but avoid injury (MacLean & Metcalfe 2000).

Evidence for polarised aggression among cultured fish also comes from estimates of percentage of a delivered meal eaten by identified individuals, using food labelled with X-ray dense opaque marker delivered over repeated days. In the case of *Tilapia rendeli*, the ranking of fish in terms of percentage the meal eaten is correlated to dominance rank on the basis of observed aggressive interactions when the fish are fed from a point source; the relationship disappears when the food is dispersed (McCarthy *et al*. 1999). The same approach has been used to examine dominance interactions in groups of rainbow trout (McCarthy *et al*. 1992) and greenback flounder (*Rhombosolea tapirina*, Carter *et al*. 1996).

### 9.5.2 Problematic consequences of aggression in aquaculture

The previous section has shown that, notwithstanding a relatively abundant supply of food, aggression does occur common in fish culture systems and is often polarised, suggestive of dominance–subordinance relationships. This can compromise the aims of fish culture, whatever its eventual purpose, in a number of ways. Problems arising from aggression among fish that are being cultured include uneven distribution of food, use of energy that could be put into growth, physical injury and mortality, acute and chronic stress and stress-related immunosuppressance. These are summarised in Table 9.2 and discussed further below.

#### *Uneven feed distribution*

The existence of hierarchies in fish held in production conditions with dominant fish gaining preferential access to food has been demonstrated for a range of species, mostly salmonids such as Atlantic salmon (Metcalfe *et al*. 1989; Kadri *et al*. 1996), Arctic charr (Jobling & Baardvik 1994; Damsgård *et al*. 1997) and rainbow trout (McCarthy *et al*. 1992; Moutou *et al*. 1998). For example, during compensatory growth (Chapter 7), dominant Atlantic salmon monopolise localised feeding areas and thus gain exclusive

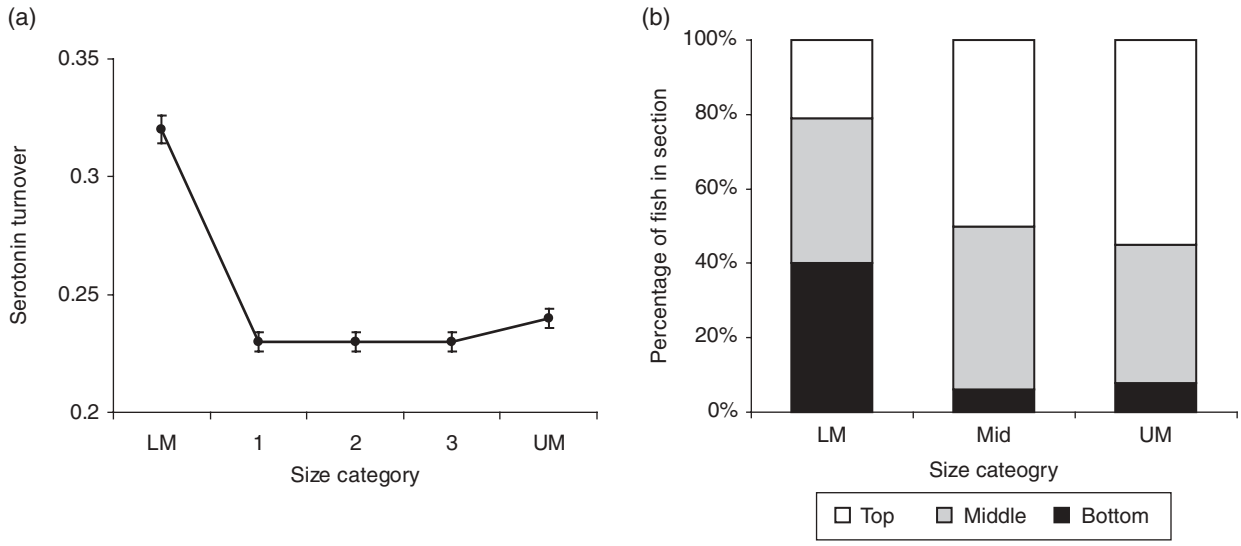


**Figure 9.11.** Social interactions in production cages. (a) Mean (±SE) rate of turnover of brain serotonin in adult Atlantic salmon growing at different rates in production systems fed a high food ration. LM and UM = fish in the lower and upper modes of the size distribution respectively. 1, 2 & 3 represent fish in the bottom, middle and top thirds of the remainder of the size distribution. Adapted with permission from Cubitt 2002. (b) Use of different tank positions (upper, middle and lower) in Atlantic salmon that had grown at different rates in production conditions. Adapted with permission from Cubitt 2002.

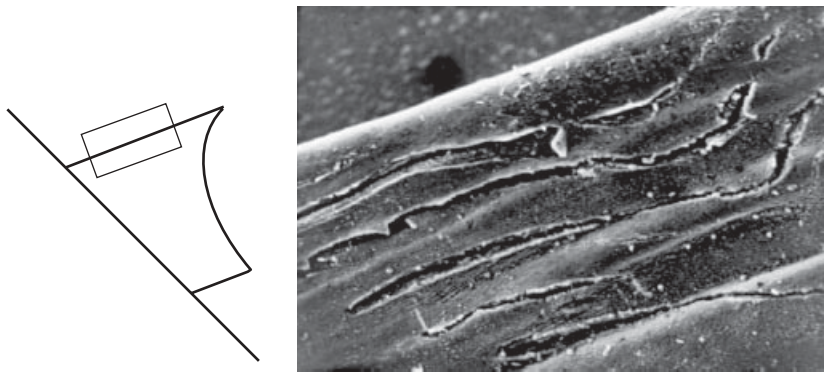

**Figure 9.12.** Aggression-induced fin damage in farmed fish. Scanning electron microscope of the dorsal fin of a farmed Atlantic salmon parr showing damage caused by biting attacks. Inset: schematic representation of the region of the fin shown in the micrograph. Reproduced with permission from J. Turnbull, University of Stirling.

access to feed (MacLean & Metcalfe 2001). Dominance-based access to food is also seen in other groups of food fish such as tilapias (*Oreochromis* spp.) and common carp (*Cyprinus carpio*) and in fish used for ornamental and scientific purposes (for example, zebrafish and medaka). As well as directly preventing a subset of fish from gaining access to food, one consequence of aggression is suppressed appetite in subordinate fish. For example, subordinate Arctic charr do not feed for many days after removal of dominant fish, indicating long and persistent appetite suppression; this can be related to the neuro-endocrine status of subordinate fish (Øverli *et al*. 1998). Uneven food intake and consequent

**Table 9.2.** Examples of potential consequences of aggression in fish culture.

| Consequences | Implications for production | Implications for welfare | Implications for the environment |
|---|---|---|---|
| Development of feeding hierarchies | Uneven distribution of food<br>Reduced average growth rates<br>Increased variation in growth & final size | None for dominant fish<br>Subordinates inhibited from feeding | Increased feed waste |
| Use of energy | Energy diverted from growth.<br>Impaired food conversion. | Not necessarily negative, provided all fish receive sufficient food. | Increased faecal waste<br>More feed required |
| Fin damage, other injuries & mortality | Lost production.<br>Reduced market value. | Short & possibly long term discomfort.<br>Reduced swimming ability.<br>Possible route for infection | Larger reservoir for infection of wild fish |
| Acute stress | Limited effects on production provided food supply is sufficient | Possible short-term increase in aggression.<br>Short term discomfort, including reversible physiological & behavioural coping mechanisms | No direct effects. |
| Chronic stress | May lead to reduced growth | Long term discomfort that may lead to irreversible coping problems | No direct effects<br>Increased faecal waste released<br>More feed required |
| Immune-suppression | More diseases, reduced growth & increased mortality | Negative impact through a higher incidence of disease. | Larger reservoir for infection of wild fish |

differences in growth represent problems for production, since cohorts of uniformly sized fish are easier to manage and to market. It also compromises the welfare of those subordinate fish that are unable or unwilling to feed.

***Use of energy, inefficient growth***

As discussed above, fighting incurs a significant cost in terms of increased energy expenditure, for example, making up 12% of the daily energy budget in territorial juvenile coho salmon (Puckett & Dill 1985). The costs of fighting are also apparent in fish held in groups. In small groups of Atlantic salmon there is no clear relationship between food intake and growth, perhaps because highly aggressive fish expend energy in territorial defence (Cutts *et al*. 1998). In tilapia hybrids (*Oreochromis mossambicus* × *O. hornorum*) fed an unrestricted ration, individual growth rates in larger fish are negatively correlated with their levels of aggression when food is delivered at a point source, though not when food is dispersed. This is probably because with a defensible food source larger fish spent time and energy fighting rather than feeding (Robinson & Doyle 1990). In brown trout, growth is reduced in subordinate fish as much as 8 months after an initial dominance test (Tiira *et al*. 2009), indication that growth effects of subordinates may last over long time periods.

***Fin damage and other injury***

In addition to depriving some fish of access to food and using up energy, aggression among fish in production systems can be a cause of skin and fin damage. Such

damage can directly reduce the value of the farmed product (for example, Atlantic salmon smolts with fin damage are less valuable than those with intact fins. Noble *et al*. 2011) and can also indirectly affect other production variables. Fast growth in production conditions may come at the expense of fin damage; for example, in 55 g and 250 g Atlantic cod held under production conditions, the incidence of fin damage is higher in fish that grow fast compared to those that grow slowly (Hatlen *et al*. 2006). Skin and fin damage increase vulnerability to pathogens, injured fins being a known route for entry of viral, bacterial and parasitic pathogens (El-Matbouli *et al*. 1995). Through various kinds of negative effects, aggression can cause high levels of injury and mortality; for example, aggression-induced mortality is common in juveniles of many grouper species (Sabate *et al*. 2009). As well as resulting in lost production and lower quality products, both the fin damage itself and any subsequent infections may compromise the welfare of the individual fish concerned through immediate noxious stimuli from tissue damage, compromised swimming ability and impaired health.

***Acute, chronic stress and immune-suppression***

Participating in a fight induces a physiological stress response, particularly in the fish that loses. Where this is acute and short lived, provided the fish receive sufficient rations, this is unlikely to have adverse effects. However, in production systems, fish that lose fights may be unable to escape from their victors, in which case they are likely to experience chronic stress. This in itself is a cause for concern from both a production and a welfare perspective, but can also have negative effects on many aspects of body function. Since chronic stress is known to suppress immuno-competance (Iwama *et al*. 1997), subordinate status in cultured fish may well compromise disease resistance. In addition, socially mediated differences in physiology may lead to variation in susceptibility for water-borne contaminants in aquaculture. For example, the accumulation of water-borne copper is higher in subordinate fish than in dominant fish, probably due to differences in sodium uptake over the gills (Sloman *et al*. 2003).

***Not all bad news***

It is worth pointing out that not all effects of aggressive interactions among cultured fish are negative. For example, although Lorenz's picture of an aggressive drive that inevitably accumulates with time since a fight and must find expression (Section 9.2.3) does not accurately depict the mechanisms that control aggression, it does draw attention to the fact that experiencing the sight, smell, sound and feel of a potential rival, as well as direct participation in fights, can have complex feedback effects. Such effects, including increased androgen secretion, are part of a priming process for effective resource defence and, in the case of mature fish, for full reproductive activity and may not necessarily be negative for the fish concerned. For example, damselfish will learn to swim through a simple maze for the reward of the opportunity to display to a rival behind glass (Rasa 1971), which suggests that the exchange of aggressive displays can be a rewarding experience. In addition, the fact that cultured fish show aggressive behaviour can be put to use. For example, it has been suggested that individual levels of aggression assessed in a simple mirror test might be used to predict general stress responsiveness, and hence general suitability for culture, in Nile tilapia (Barreto *et al*. 2009).

### 9.5.3 Effects of domestication and captive rearing on aggressive behaviour in cultured fish

In addition to the problems caused by aggressive interactions during the period that fish are being grown in culture, how fish fight can also lead to problems when the cultured fish are being put to use, whether as brood stock, for release into the wild, for ornamental aquaria or for scientific experiments. In many cases, the problems arise from the fact that wild and cultured fish may differ in their aggressive behaviour. As discussed in Chapter 1, cultured fish live in conditions that are very different from those experienced in the wild and some of the more striking differences, such as abundant, predictable food and protection from predators, are exactly those that are likely to influence patterns of aggression. Behavioural deficits in cultured fish may arise within a generation as a result of non-random mortality by behavioural phenotype or differential experience in wild and cultured fish. Over several generations, they may also arise through inadvertent domestication or in association with selection for production traits such as fast growth. Deficits may be in the form that aggression takes (cultured fish might simply not be able to fight effectively), in its frequency (cultured fish might fight too much or too little for fitness) and in how well cultured fish make the subtle assessments needed to optimise the cost-benefit ratio during fights. Current understanding of how genes and rearing environment interact to determine how fish behave can potentially help in generating appropriate mixes of behavioural phenotypes.

***Effects of domestication on aggression***

An important question for fish culture is whether, over successive generations, the process of domestication has altered the intrinsic aggressiveness of cultured fish; if this

is the case, given the problems caused by aggression in production systems outlined above, this could have significant implications for how easy it is to rear them. Certainly, cultured and wild-caught fish often behave differently during conflicts. For example, on the breeding grounds adult male Atlantic salmon from fish farms exhibit less combat and display behaviour than do wild-caught males and have difficulty winning access to mates. When they do fight, they are more often involved in prolonged reciprocal fights and so are more likely to be wounded (Jonsson & Jonsson 2006). First-generation hatchery reared Arctic charr have a lower incidence of fin damage and lower mortality than wild caught conspecifics from the same original location when the two categories are reared separately and at a moderately high stocking density (22 kg/m$^3$). When housed in mixed groups, hatchery reared charr suffer more fin damage, greater loss of condition and higher mortality, suggesting that aggression is directed selectively towards hatchery fish (Siikavuopio *et al*. 1996).

Simple comparison of farmed and wild-caught fish cannot tell us whether any differences in aggressive behaviour are inherited or whether they depend on the effects of captive rearing (Huntingford 2004). However, a number of studies have compared aggressive behaviour between juvenile fish of cultured and wild origin reared in standard conditions (so-called common garden experiments), with complex and variable results. For example, in pair-wise tests in simple tanks with a predictable food supply, farmed juvenile Atlantic salmon are marginally more aggressive than hatchery-reared fish of wild stock and tend to dominate them. In contrast, wild fish tend to win encounters in more complex, stream-like tanks when densities are low and food is unpredictable in space and in time (Figure 9.13; Einum & Fleming 1997; Fleming & Einum 1997). Juvenile Atlantic salmon from wild stocks adjust their aggressive behaviour according to prior residence, but fish of domesticated origin fail to do make this adjustment (Metcalfe *et al*. 2003). Newly emerged rainbow trout fry of wild origin are more aggressive than fry from a domesticated strain, but they also react differently to subsequent experience; domesticated fish become more aggressive when reared in a stream channel than when reared in a tank, but this rearing experience has no effect on the aggressive behaviour of wild fish (Berejikian *et al*. 1996). Higher levels of aggression in domesticated fish, or a tendency to dominate over wild counterparts, have also been reported for brown trout (Sundström *et al*. 2003) and coho salmon (Berejikian *et al*. 1999).

In contrast, lower levels of aggression in domesticated fish have sometimes been found in brown trout (Petersson & Järvi 2003), especially at high densities (Hedenskog *et al*. 2002), Arctic charr during feeding periods only (Brännäs *et al*. 2005) and European grayling, *Thymallus thymallus* (Salonen & Peuhkuri 2004). Variable effects of domestication on aggression may be the result of the species concerned or of differences in the conditions in which domestication takes place. For example, medaka fish selected for fast growth with abundant, clumped food are less aggressive than either those selected for fast growth with abundant, dispersed food or those selected for slow growth in either condition. This may be because when food is abundant but clumped, the energetic costs of fighting for it result in slower growth in aggressive fish (Ruzzante & Doyle 1991, 1993).

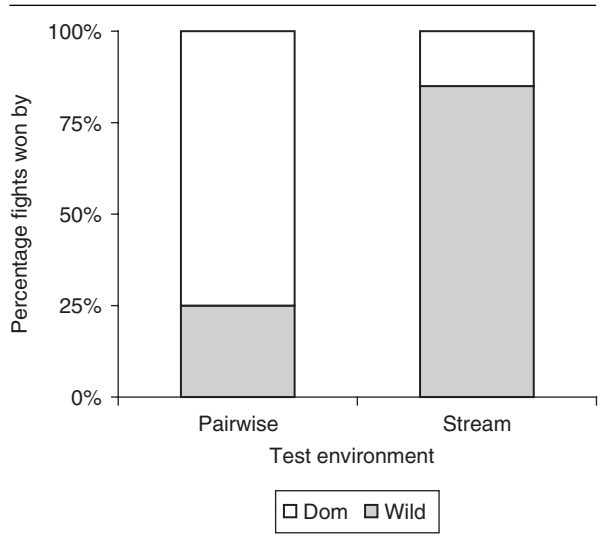


**Figure 9.13.** Differences between domesticated and hatchery-reared wild fish. Percentage encounters won by wild and farmed (Dom) Atlantic salmon in pairwise tanks tests and in complex stream-like tanks. From Einum & Fleming 1997 & Fleming & Einum 1997. Reproduced with permission from Huntingford 2004.

### *Effects of captive rearing on aggression*

A number of studies have demonstrated differences in aggression between fish of the same stock reared in the wild and in hatchery conditions. For example, juvenile brown trout reared in hatcheries initiate pair-wise contests sooner and fight longer and more fiercely than do fish of the same size captured in the wild. It seems that, through lack of experience of territorial interactions, hatchery-reared fish are poor at assessing their relative fighting

ability prior to a fight (Sundström *et al*. 2003). Such effects are known to be important in the development of aggression. Cichlid fish (*Aequidens rivulatus*) reared in small mixed-sex groups learn to use displays rather than overt attack while defending territories; fish reared in groups that are too large and dense for territories to be established fail learn this, use attack rather than displays when fighting and, as a consequence, sustain more injuries (Maan *et al*. 2001).

***Implications for fish culture***

Inappropriate levels of aggression may get in the way of successful mating when cultured fish are as brood stock. If cultured ornamental fish are more aggressive than wild fish, this may make it hard to maintain them in aquaria and if they are not sufficiently aggressive this may prevent performance of attractive displays. Where fish are reared for scientific purposes, high levels of aggressiveness in domesticated strains (as reported for zebrafish, for example by Moretz *et al*. 2007b) may restrict the generality of any findings in studies directly aimed at understanding aggressive behaviour. It may also compromise studies of other aspects of biology (immunology, for example) through the various adverse effects of aggressive interactions, including immune suppression in subordinate fish.

However, it is in the case of fish cultured for stock enhancement or conservation-based reintroduction that differences in aggressive behaviour between wild and domesticated and captive-reared fish are most likely to be problematic. Whether or not such programmes are appropriate is a matter of debate (Chapter 1), but where they are carried out it is important to consider whether the effects of abnormal aggressive behaviour in released fish may compromise their aims. For example, juvenile farmed Atlantic salmon may be inherently more aggressive than wild-origin fish (Metcalfe *et al*. 2003), but the hatchery environment reduces their ability to compete for territories and other resources with wild resident fish; releasing hatchery-reared salmon may therefore not be an effective conservation measure. An important point arising from what is known of aggression in wild fish is that the natural within-species variability in this behaviour exists because individuals with different behavioural profiles flourish in different environments. Therefore programmes designed to ensure that released cultured fish have an appropriate repertoire of adaptive behaviour should be aiming not for single species-typical norm, but for a species- and environment-specific mixture of aggressive phenotypes.

Abnormal aggressive behaviour in fish cultured for release may influence their interactions with wild populations. Cultured fish do not necessary out-compete their wild counterparts. For example, wild juvenile Atlantic salmon are able to appropriate shelters in winter, even when hatchery-reared fish out-number them by four to one (Orpwood *et al*. 2004). The fact that domesticated fish often grow faster than wild fish complicates the issue, since above a certain point size advantage is an important determinant of victory in fights. Although wild rainbow trout fry are more aggressive that domesticated stock and tend to dominate in pair wise interaction between evenly sized fish, a small size advantage (about 4%) overrides this effect (Berejikian *et al*. 1996). Thus, farm escapees may out-compete local fish in spite of showing less effective aggressive behaviour and even if they lose out in fights, these may still have adverse effects on wild fish though the various costs of aggression described above. The implications of differences in aggressiveness for the chances of and likely consequences of hybridisation between cultured and wild fish are discussed in Chapter 10.

### 9.5.4 Solutions: controlling aggression during fish culture

Having identified some problems for aquaculture that arise from fighting among farmed fish, it is possible to consider whether these problems can be solved for the farmer, the fish and the environment, based on what is known about the fundamental biology of aggression. There are two broad approaches here, which are not mutually exclusive. The first is to select the most appropriate fish to grow in culture and the second is to design husbandry systems and practices that generate aggression at an appropriate level. In both cases what is appropriate will depend on the purpose for which fish are being cultured. It is important to stress that the effect of any intervention will surely depend on the species, age and possibly the strain of the fish concerned and that it is highly unlikely that there will be any ‘one-size-fits-all’ solutions. The previous sections of this chapter have documented considerable variability in aggressiveness in wild fish, depending on species and on populations or strains within species, as well as reflecting natural individual differences. Given the existence of such variability, one way of solving the problems caused by aggression in cultured fish, whether these arise from high levels of aggression during culture or from failure to adjust levels of aggression to current circumstances in released fish, is to select and culture fish with appropriate levels of aggression.

### *Appropriate fish for food*

When fish are reared for food, problems arising from their natural aggressive behaviour can potentially be avoided by judicious choice of stock, farming only those species, strain or individuals that are naturally un-aggressive. As described in the introduction to this chapter, some species of fish are markedly less aggressive than others. For example whitefish (*Coregonus lavaretus*), a pelagic, schooling species, show relatively uniform growth and (on the evidence of variation in feed take and serotonin turnover rates) do not develop polarised feeding hierarchies even under food restriction (Jobling *et al*. 1999). African catfish (*Clarias gariepinus*) have a loose, non-linear hierarchy with a few despots, but no clear relationship between aggressive behaviour and feed intake (Carter & Davies 2004). Concentrating intensive production on such species might help to reduce the adverse consequences of aggression among farmed fish. In addition, some species, the Arctic charr for example, occur naturally in two distinct forms specialising on benthic and pelagic prey (Chapter 5); among the adaptations associated with this trophic polymorphism is a higher rate of aggression in benthic fish compared to the pelagic form, which is predisposed to school rather than fight. (Mikheev *et al*. 1996). In such cases, it would seem appropriate to base culture of the species concerned on the less aggressive form.

Applying this approach at the level of individuals, it might be possible to identify non-aggressive individuals and to use these either in full production or as a founder generation. Screening would need to be carried out as early in the production cycle as possible and would have to be economically feasible on a large scale. One suggestion is based on the link between standard metabolic rate and individual aggressiveness on the one hand and age of first feeding on the other. Fish with a low metabolic rate use up their yolk sacs more slowly and start feeding later than do those with a high rate (Metcalfe *et al*. 1995). This means that age of first feeding (which is easy to screen in large groups of fish) could potentially be used to predict aggressiveness in candidate fish for intensive culture (Hooglund personal communication). It is certainly the case that growth rates are equally high but less variable in juvenile Atlantic salmon with low standard metabolic rate than in fish with medium or high metabolic rates (Cutts *et al*. 1998). In yellowtail (*Seriola quinqueradiata*), a larval posture (called the J posture) that is a developmental precursor of later aggressive actions predicts dominance in schools of juveniles (Sakakura & Tsukamoto 1999). If simple methods for mass screening and separation could be devised, such early predictors of aggression could be used to identify suitable fish for culture.

Over a longer time period, selection for fish that grow fast but show low levels of aggression is also a possibility. For example, Ruzzante & Doyle (1991, 1993) were able to select for fast growth associated with low levels of aggression in medaka by giving them clumped but abundant food, thereby ensuring that the costs of fighting outweighed its benefits. A potential problem with an approach based on culturing only non-aggressive fish is the fact that in many species individuals that are un-aggressive tend also to show strong stress responses to a variety of challenges, so are likely to be particularly disturbed by husbandry practices. In other words, the existence of sets of covarying behavioural traits (or behavioural syndromes; Sih *et al*. 2004; Korte *et al*. 2005; Chapter 8) means that non-aggressive but unstressed fish will be rare. However, accumulating evidence suggests that boldness and aggression may be uncoupled (Bell 2005). In particular, the literature on domestication suggests that, whereas domesticated strains are usually bolder than their wild counterparts, they are not always more aggressive. One strain of rainbow trout examined by producing clonal lines (Lucas *et al*. 2004) has exactly the desired combination of behavioural traits (Figure 9.14). If the reasons for this could be identified, for example by more studies using model species, this information could help to generate welfare-friendly fish (un-aggressive but not easily stressed) for food aquaculture.

### *Appropriate fish for other purposes*

When rearing fish for release, the behavioural requirements are different. In this case, rather than producing only individuals with low levels of aggression (and ideally low stress responsiveness) what is required from effective culture is individuals whose behaviour is flexible and/or populations that, between them, encompass a range of behaviour phenotypes, ideally mimicking that for the species concerned at the proposed release site. As described above, inadvertent domestication over several generations often produces fish with inherited patterns of aggression that do not promote survival, growth or successful breeding in the environment into which the fish are released. In such cases, careful selection of un-domesticated stocks or individuals with appropriate potential is required. For example, it has been suggested that the Ω posture shown at metamorphosis by Japanese flounder (*Paralichthys oliveceus*), a candidate species for supplementation of wild populations but with high post-release mortalities, could be used to identify fish that are likely to survive well after release (Sakakura 2006). Whatever the source of fish reared for restocking, it might be advisable to provide rearing regimes that avoid inadvertent domestication, perhaps by

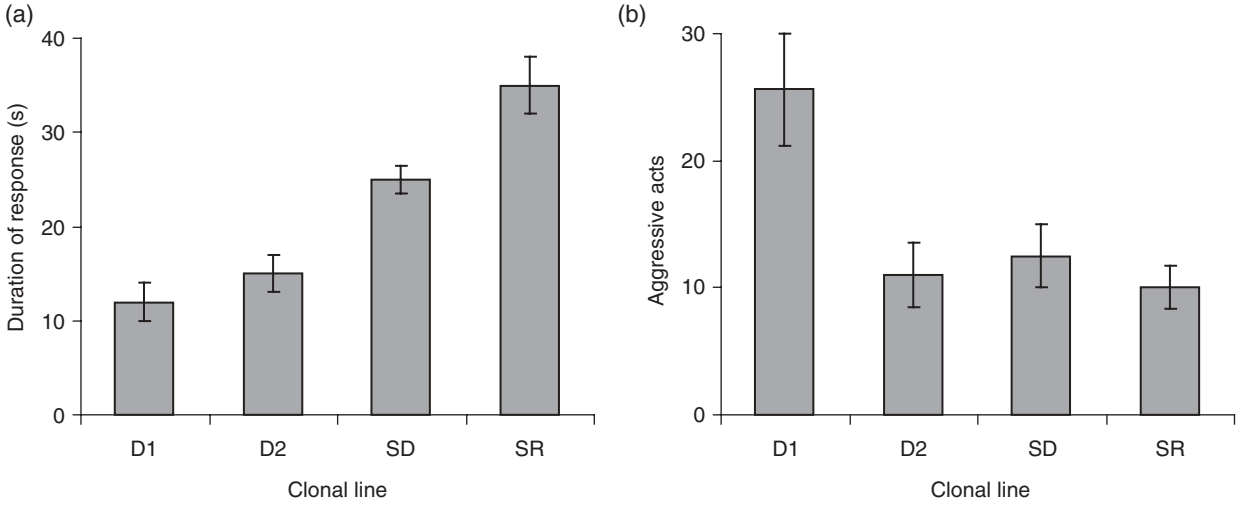


**Figure 9.14.** Uncoupling risk-taking and aggression. Mean (±SE) of (a) Duration of startle response to a light and (b) Number of aggressive acts per 20 min in pairwise encounters in rainbow trout from different clonal lines. D1 and D2 are derived from two domesticated lines, SD from a semi-domesticated line and SR from a sea ranched line. Line D2 combines a low startle response with low levels of aggression. Adapted from Lucas *et al.* 2004.

providing naturally non-aggressive fish with the opportunity to pursue alternative feeding strategies, as discussed below.

Where fish are reared for scientific purposes, the requirements for their aggressive behaviour are likely to be similar to those reared for release. In other words, at least if they are being used for behavioural biology and probably for other purposes as well, a natural spread of behaviour would make any findings more readily generalisable. Thus the same requirements for selection of stock and provision of rearing conditions apply as for fish cultured for release. When rearing fish for ornamental aquaria, what is appropriate will depend on the species concerned. In most cases, low levels of aggression and low stress responsiveness are probably best, so the same requirements would apply as for fish reared for food. However, in species where displays are part of the attraction, as least moderate levels of display are required. In addition, part of the pleasure of keeping aquarium fish is to watch fish breeding, and effective territorial behaviour might be required for this; in such cases, it might well be important to ensure a sufficiently complex rearing environment for effective territorial behaviour to develop.

### *Developing appropriate husbandry systems*

Another approach to solving the problems of aggression in aquaculture is to develop husbandry systems that generate appropriate levels of aggression, with what is appropriate again depending on the purpose for which fish are being cultured. In terms of causes, how fiercely fish fight is determined by the external stimuli to which a fish is exposed, in combination with its internal state. One possible way of controlling aggression in fish culture is therefore to adjust the sensory environment in which fish are reared. In functional terms, how fiercely fish fight is fine-tuned to the circumstances in which an aggressive encounter occurs, reflecting the variable costs and benefits of fighting. In principle, it should be possible to exploit this flexibility to manage aggressive behaviour in cultured fish. Since most cultured fish fight over food, patterns of feed delivery could be adjusted to reduce the benefit of fighting; other manipulations might be used to increase the perceived costs of fighting. Together, such changes would alter the economic defensibility of delivered food, tapping into natural behavioural processes and reducing the incidence of fighting.

### *Manipulating stimuli experienced by cultured fish*

Cultured species are often kept in groups of size and age matched fish at high densities, so are exposed to a multitude of aggression-related cues. Based on what is known about such cues, it is possible to devise husbandry practices to reduce aggression among cultured fish. For example, in the absence of landmarks, fish may abandon the attempt to establish territories, as in Arctic charr, which fight less in

plain tanks than in those with vertical stripes (Mikheev *et al*. 1996). Size grading is a common practice in aquaculture, aimed at improving growth rates and avoiding dangerous attacks by seriously large opponents. The behavioural literature suggests that fierce fights are more likely to occur between fish that are evenly matched for size, so grading to reduce aggression could be counterproductive. Certainly, large and medium-sized Arctic charr held in groups of equally sized fish show more aggressive interactions than do those in groups with a normal size distribution, though growth is unaffected (Brännäs *et al*. 2002). In this case, size grading does not improve growth, but does increase aggression.

Several authors have suggested that rearing fish in duoculture may improve growth and reduce levels of aggression by effectively diluting the cues that elicit aggression (Holm 1989; Nortvedt & Holm 1991). Mortality and fin damage in juvenile rainbow trout are dramatically reduced when the trout are held in duoculture with redside shiners (*Richardsonius balteatus*), subordinate trout taking refuge from dominants within the shiner group (Tinus & Reeves 2001). Not surprisingly, the effectiveness of duoculture is dependent on the species concerned. For example, Atlantic salmon feed less, grow less well and have more fin damage when reared in duoculture with brown trout than when reared in monoculture (Jobling *et al*. 1998), as do goldfish (*Carassius auratus*) reared in duoculture with koi carp (*Cyprinus carpio;* Jha *et al*. 2006), because they are attacked by the trout and koi respectively.

As described in Section 9.1.3, darkened colour of the eye and the body is part of a submissive display in several species of fish and has the effect of suppressing attack (Volpato *et al*. 2003). This means that any husbandry practices that, for whatever reason, result in pale coloured fish may promote aggression. For example, levels of aggression in captive-reared coho salmon fry are higher than in wild fish, probably because they have pale bodies and do not signal submission effectively. Their pale colour seems to be a result of low melanin deposition in the eggs and could perhaps be changed by providing brood stock and fry with melanin-rich diets (Berejikian *et al*. 1999). Husbandry practices that result in darker colour have the reverse effect; for example, Arctic charr kept on a dark background have darker bodies and reduced levels of aggression (Höglund *et al*. 2002).

Olfactory cues are also important in determining whether and how fiercely an opponent is attacked and this may influence what happens in culture. For example, recirculation apparently concentrates attack eliciting cues and increases levels of aggression in juvenile Atlantic salmon; in this case, use of flow through systems might prevent such effects (Griffiths & Armstrong 2000). In contrast, water-borne chemicals decrease levels of aggression in pairs of Nile tilapia, possibly because they allow recognition of familiar individuals; fish held in pairs fight more when a continuous flow of water removes such cues, (Giaquinto & Volpato 1997), mainly due to increased aggressiveness in the subordinate fish (Gonçalves de Freitas *et al*. 2008). So, recirculation might decreases the problem of aggression, but large Nile tilapia can show growth retardation in recirculation systems, which allow waterborne substances to accumulate (Martins *et al*. 2009).

Moving away slightly from controlling specific external stimuli, because familiarity reduces levels of aggression in many species, it makes sense to keep cultured fish in stable groups; one reason why grading may temporarily increase aggressive behaviour is the fact that it disrupts previously stable hierarchies (Abbott & Dill 1985; Jobling & Wandsvik 1983). Juvenile brown trout captured in the wild and kept in small groups of familiar fish (caught in the same place) fight less and as a consequence respond more quickly to a simulated predatory threat than do those in groups with unfamiliar fish (caught at different sites. Griffiths *et al*. 2004).

Another factor that has a marked influence on fighting in wild fish and that could potentially be used to manage this behaviour among cultured fish is the fact that many species show a strong prior residence effect. Ideally, therefore, when different groups of fish are combined in a new tank or cage, for example after grading or disease treatment, they should be placed simultaneously into an unfamiliar location. Another possible way of reducing aggression in cultured fish is to manipulate brain biochemistry directly, as shown by several studies in which dietary levels of tryptophan (the natural precursor of serotonin) are raised, thereby increasing brain serotonin levels and reducing aggression in rainbow trout (Figure 9.15; Winberg *et al*. 2001, Lepage *et al*. 2005) and Atlantic cod (Höglund *et al*. 2005) and cannibalism (groupers, *Epinephelus coioides*; Hseu *et al*. 2003).

### *Manipulating feeding regimes*

Studies of the causes of aggression show that nutrient status influences aggressiveness, with hungry fish being more likely to fight. Studies from a functional perspective show that fish (unconsciously) adjust their aggressive behaviour to the benefits to be gained by fighting. Both these areas of fundamental behavioural biology suggest that how much food cultured fish receive and how it is distributed in space and time are likely to have a strong influence

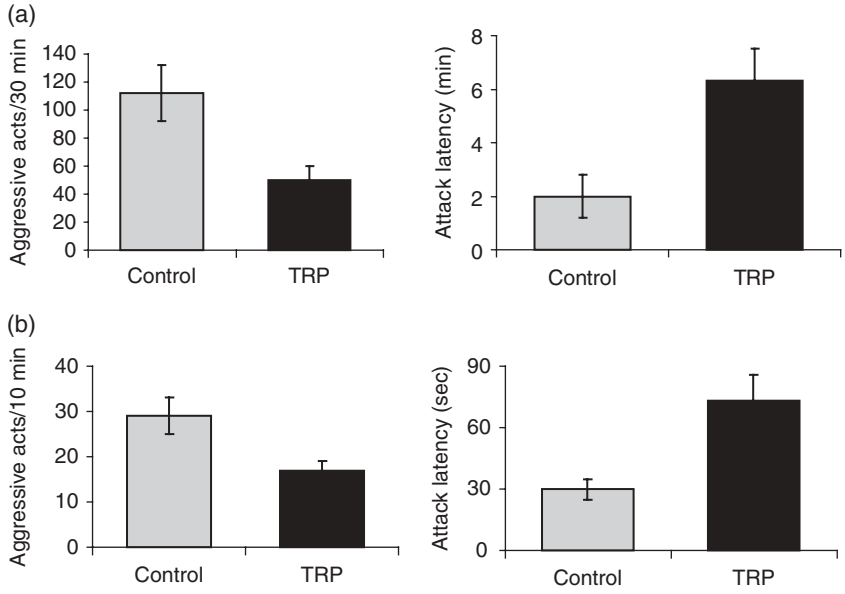


**Figure 9.15.** Reducing aggression in farmed fish by natural feed supplements. Mean (±SE) number of aggressive acts and attack latency shown in pairwise resident-intruder trials by (a) Juvenile rainbow trout and (b) Atlantic cod after several days of feeding either a control diet or a diet supplemented with tryptophan TRP, (a precursor of serotonin). Adapted from Winberg *et al.* 2001 and Höglund *et al.* 2005.

of levels of aggression in fish culture. Simply providing plenty of food is an obvious step to take and numerous studies have shown that cultured fish fight less when kept on high rations. Feeding hierarchies become less evident when rations increase in several species (McCarthy *et al.* 1992; Damsgård *et al.* 1997); for example, in juvenile rainbow trout, feeding hierarchies are less polarised and fin damage is reduced in fish on high rations (Moutou *et al.* 1998). Food-deprived Atlantic cod show a high frequency of attacks, with resulting damage to the dorsal and pectoral fins. When feeding recommences, aggression declines, healing takes place and fin damage decreases to control level within a few weeks (Hatlen *et al.* 2006).

In addition, food that is well distributed in space ceases to be economically defensible and several studies have demonstrated reduced aggression in cultured fish when food is well dispersed. For example, chum salmon (*Onchorhynchus keta*) show less aggression and more even growth when fed on dispersed rather than clumped food (Ryer & Olla 1995) and tilapia do not establish feeding hierarchies when fed from a dispersed as opposed to a point feeding sources (McCarthy *et al.* 1999). The timing of feed delivery can also be used to reduce fighting among cultured fish. For example, levels of aggression are lower during both feeding and non-feeding periods in rainbow trout given the opportunity to feed during three 2 hour meals per day compared to those given just one 3 hour meal, even though there were no differences in growth rates and feed conversion ratio (Noble *et al.* 2007).

Given the effects of ration and feed dispersal, a fruitful approach to reducing aggression in fish culture is to deliver feed according to current appetite of the fish concerned, rather than at prescheduled times. A variety of feeders developed for commercial production systems are designed to deliver food as long as any fish in the system are still ready to eat (Chapters 3 and 7). This reduces the benefits of defending the food source and offers subordinate fish the opportunity to feed when dominant fish are satiated. Several studies have demonstrated reduced aggression (measured directly from video footage or indirectly through measures of fin damage) in fish fed by to demand rather than by automated feeders. For example, compared to control fish, there is less aggressive competition for individual feed pellets in sea bream and Atlantic salmon fed to demand (Figure 9.16a; Andrew *et al.* 2003) and less fin damage in demand fed juvenile Atlantic salmon (Figure 9.16b; Noble *et al.* 2008).

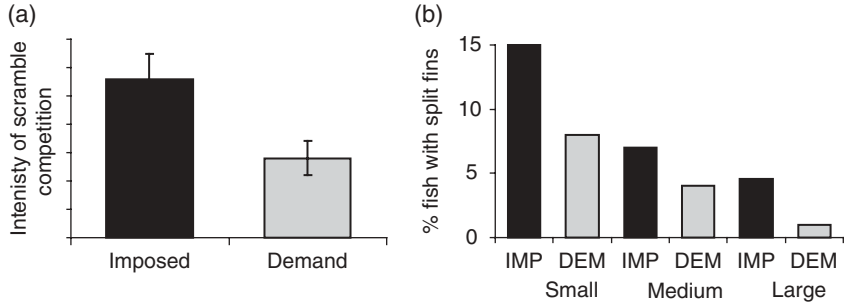


**Figure 9.16.** Reducing aggression in farmed fish by allowing fish to feed on demand. (a) Mean (±SE) of an index of scramble competition (the number of fish contesting each pellet) in sea bream on either an imposed or an on-demand feeding regime. Adapted from Andrew *et al.* 2002. (b) Percentage of fish with split fins in Atlantic salmon post-smolts of different sizes held under production condition on either an imposed (IMP) or an on-demand (DEM) feeding regime. Adapted from Noble *et al.* 2008.

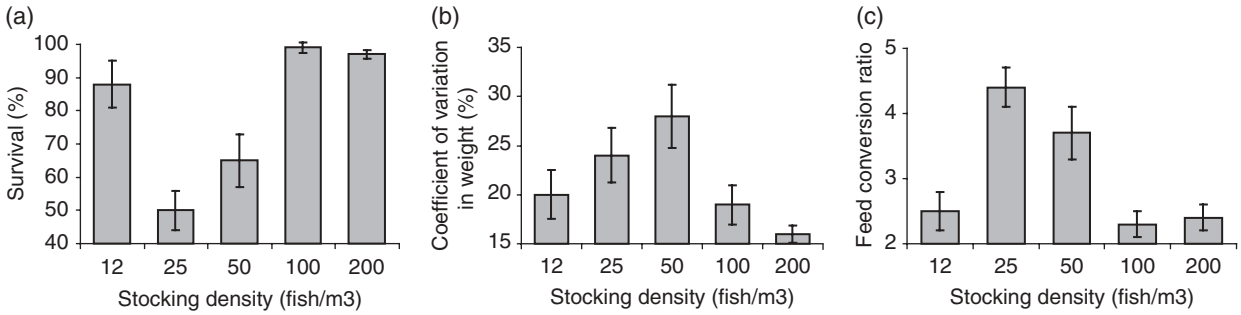


**Figure 9.17.** Mitigating the effects of aggression in farmed fish by altering stocking density. Mean (±SE) (a) Percentage survival, (b) Coefficient of variation in weight and (c) Feed conversion ratio in Australian silver perch fingerlings held in cages at 5 different stocking densities. Adapted from Rowland *et al.* 2006.

### *Increasing the costs of fighting*

The economic defensibility of food and hence levels of aggression in production systems can also be reduced by increasing the real or perceived costs of fighting. The numerous studies of the effects of stocking density on aggression in cultured fish can be interpreted in this context, given the dome shaped relationship between the number of competitors and levels of aggression (Section 9.4.3). For example, at low densities fish such as Arctic charr attempt to establish small territories and can be very aggressive; aggression decreases at higher densities, as the cost of fighting increases, the fish have fewer bite marks and growth is better (Brown *et al.* 1992). In sea run Atlantic salmon held at production densities in tanks, fish welfare (measured by an index combining body and fin condition, which contribute positively, with blood cortisol and glucose concentrations, which contribute negatively) is best in fish held at a density of 25 kg/m$^3$ compared to 15 kg/m$^3$ and 35 kg/m$^3$. Fish at the lowest density fight a lot, but at the highest density although levels of aggression are low, other adverse effects of crowding appear (Adams *et al.* 2007). Larval Atlantic cod also fight less at higher densities (Forbes 2007). In Australian silver perch fingerlings held in cages at four stocking densities, survival is lowest, variability in growth rates and feed conversion rations are highest (Figure 9.17) in cages at the intermediate densities. It is only at these intermediate densities that aggression is seen; this is frequent and intense in the period prior to feeding, with fish chasing each other relentlessly and with subordinates immobile at surface in corners with badly damaged fins (Rowland *et al.* 2006).

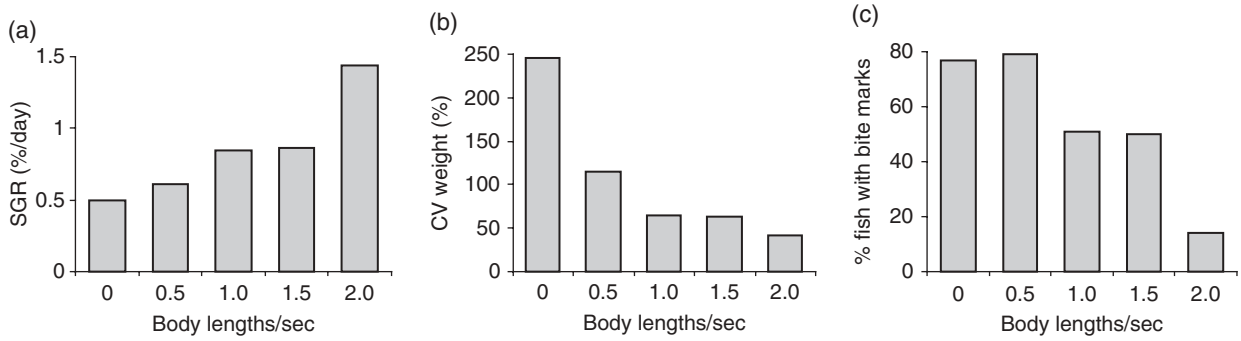


**Figure 9.18.** Mitigating the effects of aggression by altering current speed. (a) Specific growth rate (SGR %/day), (b) coefficient of variation in weight (CV weight %) and (c) aggression, indicated by the percentage of fish with bite makes in Arctic charr held at different current speeds. Adapted from Jobling *et al.* 1993.

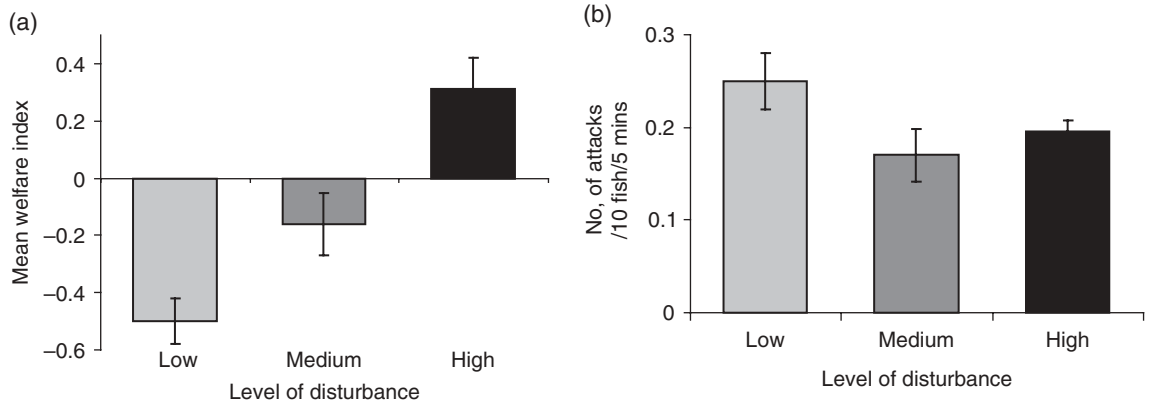


**Figure 9.19.** Unexpected effects of husbandry practice on aggression. Mean (±SE) (a) Integrated welfare score and (b) Number of aggressive interactions per fish/h in relation to degree of disturbance in Atlantic salmon held at production densities in sea water. Disturbance levels: low = tanks in the centre of a bock, disturbed once per day for cleaning; medium = tanks at edge of block disturbed by cleaning own and other tanks; high = as for medium, but adjacent to a screened corridor used regularly by farm staff. Adapted from Adams *et al.* 2007.

Stimulating fish to swim against a current can also increase the costs of fighting. A number of studies have demonstrated reduced levels of aggression as well as faster and more even growth in fish held at high densities in flowing water. For example, growth rates are higher and coefficient of variation in weight lower in Arctic charr exposed to a water current of 2 body lengths per sec than in those held at lower current speeds (Figure 9.18a, b; Christiansen & Jobling 1990). Some of these benefits of sustained swimming arise from reduced aggression (Figure 9.19c; Christiansen *et al*. 1992; Adams *et al*. 1995; Chapter 1), at least during feeding periods (Brännäs 2009). Reduced aggression may be responsible for the lower levels of cortisol found in fish swimming against a current compared to fish in tanks with low water current (Davison 1997). Sustained swimming and stocking density may interact to determine levels of aggression; for example, at the same specific water flow, a low water current leads to an increase in aggression in salmonids, while these fish can be held at high densities as long as the water current speed is high (Damsgård *et al*. 1997). The effects of sustained swimming against a current on growth rates depend in part on social rank (Brännäs 2009). They also depend on species and population of origin; for example, hatchery-reared grayling (*Thymallus thymallus*) originating from river populations show higher levels of aggression in flowing water, whereas aggression does not change with water flow in fish originating from lake populations (Salonen & Peuhkuri 2007).

A number of studies by behavioural ecologists have found lower levels of aggression in fish exposed to a predation threat. While it is neither desirable nor feasible to expose cultured fish to predators, a number of studies suggest that aspects of perceived predation risk can reduce aggression and improve production and welfare in fish held in culture conditions. For example, the presence of an older and larger conspecific reduces aggression and improves growth in juvenile Atlantic salmon held at high densities (Adams *et al*. 2000). In Atlantic salmon held at production densities in sea water, fish that are subject to relatively frequent disturbance during routine husbandry enjoy better welfare (again measured with a compound index) than those that are rarely disturbed (Figure 9.19a). This counterintuitive results can be explained by the fact that more frequently disturbed fish show less aggression (Figure 9.19b), perhaps because they perceived the disturbance as a low level predation threat (Adams *et al*. 2007).

### 9.5.5 Solutions: mitigating the effects of domestication and captive rearing

As well as helping in the identification of appropriate fish for culture, knowledge of the effects of genes and rearing environment on the development of aggression can be used to mitigate the effects of domestication and captive rearing. For example, deficits in aggressive behaviour in released fish could arise through differential mortality of behavioural variants during a single cycle of the captive rearing process. A possible solution here is to engineer cultured environments that allow fish from the whole spectrum of natural variability to flourish. For example, given several stations delivering feed at different rates, subordinate fish might be able to sneak feeding opportunities at sites that are not attractive to hungry dominants. Similarly, if food is provided on demand over 24 hours, subordinates might be able to feed at night (Alanärä *et al*. 1998).

In cases where behavioural deficits are the results of inappropriate individual experience during captive rearing, as when lack of opportunity to engage in territorial behaviour in conventional hatcheries prevents young fish from learning how to respond effectively to rivals, the solution is to ensure that the culture environment offers the necessary learning opportunities. For example, provision of in-water structures, overhead cover and underwater feeders stimulates tank-reared juvenile steelhead to defend territories and promotes the development of effective fighting. It also results in faster growth when the fish are subsequently stocked into quasi-natural streams than is seen in fish reared in standard tanks (Berejikian *et al*. 2000). Effective manipulation can be as simple as altering stocking density in hatcheries. For example, brown trout reared in hatcheries at a density equivalent to the highest seen in wild fish gain higher ranks when placed in small groups than those raised at a conventional hatchery density, which is much higher. They also grow faster, both before and after release into a natural stream, and survive better after release (Brockmark & Johnsson 2010). Beneficial effects are also seen in the case of trout reared at one third standard culture densities. When held in their rearing tanks, such fish show less fin damage and undergo smoltification more successfully than do those reared at standard densities. They also grow faster during a period of about 10 weeks after release into the wild (Brockmark *et al*. 2010). In both cases, the beneficial effect of lower rearing density is thought to come about through improved ability to establish stable territorial systems. It should be noted that in all these cases there may be a conflict between the need to reduce aggression to promote growth and welfare during the production phase and the need to offer opportunities for learning about aggressive interactions to promote effective behaviour on release.

## 9.6 SYNOPSIS

When a fish encounters a potential opponent, it received stimuli that provide information about the threat it poses and the probability of defeating it. Depending on the context in which the encounter takes place, such stimuli influence behavioural decisions both at the onset of a fight and as it progresses through escalation and to resolution. How a fish responds to such external stimuli is modulated by its nutrient reserves, its metabolic physiology, the hormones that are circulating in its blood stream and activity of various neurotransmitters in its brain. The causal link between physiology and its aggressiveness is a two-way process, because what happens to a fish during a fight has profound effects on its neuroendocrine status, including rapid changes in blood and brain biochemistry during the fight itself, medium-term changes in physiology and behaviour as a result of winning or losing and longer-term changes in life history processes. Simple aggressive behaviour appears early during development when young fish start to compete for food and the frequency of aggression and the repertoire of aggressive actions and displays often increases with age. How and how fiercely a fish fights is influenced by its genes and by the environment in which it develops. Levels of aggression are also adjusted to the benefits fish stand to gain from winning and the costs

they are likely to incur in the process; resources are usually only defended when the benefits outweigh the costs.

These fundamental biological facts about aggression in fishes pose problems when fish are cultured, both during the production phase when they are being grown to the required size/age and when they are being put to a specific use. Aggression-related problems during production include uneven access to food, variable growth, injury, chronic stress, associated vulnerability to disease and sometimes mortalities; these have implications for efficient production, for fish welfare and for the environment. Problems can also arise from the fact that the aggressive behaviour of cultured fish is often very different from that of their wild counterparts, both because of environmental differences experienced during the development of the young fish of a single generation and because of inadvertent domestication over a number of generations. Understanding the biology of aggression potentially allows such problems to be mitigated if not solved. In some cases, this can be achieved by directing fish culture towards those species, strains and individuals that are the most appropriate for its specific purpose. In other cases, it can suggest husbandry practices that allow farmers to manage the level of aggression shown by their stock, reducing it when fish are produced for food and producing an appropriate range of aggressive phenotypes when fish are farmed for other purposes.

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# 10
# Reproductive Behaviour

*Ian A. Fleming and Felicity Huntingford*

**Abstract:** This chapter documents striking variability in life history traits and reproductive behaviour among fishes, before giving an account of the mechanisms that control these traits, including the stimuli that promote or suppress reproductive behaviours and the neuroendocrine process that generate them. The development of reproductive behaviour under the combined effect of genes and environmental influences is then described, as are the complex costs and benefits of different life history patterns and breeding behaviour and how these are traded off to maximise fitness. Reliable provision of abundant, good quality fry represents a major bottleneck in the culture of many fish species and information is provided on how breeding is managed in fish culture and on problems that can arise from the expression of natural reproductive behaviour in this context. These problems can be overcome by provision of appropriate physical and social environments, based on knowledge of the natural behaviour of the fish concerned. Domestication selection acts particularly strongly during reproduction, raising concerns about the potential impact of cultured fish on wild populations, and an account is given of how brood stock management could be adapted so as to expose cultured fish to the potential benefits of natural and sexual selection.

**Keywords:** alternative reproductive tactics; courtship; fertilisation; life history patterns; mate choice; mate competition; mating system; modes of reproduction; parental care; reproductive hormones; sex differentiation; sexual selection; sexual maturation; sperm competition.

## 10.1 INTRODUCTION

The properties of animals that determine their overall reproductive success include morphological features, such as the intricate pouch in which male seahorses brood and feed their developing embryos, and behavioural features, such as the complex courtship that may result in a female seahorse depositing her eggs in a male's pouch. Traits that promote or hinder reproductive success extend well beyond the act of breeding itself and include events occurring throughout life. Therefore, to be properly understood, reproductive behaviour must be seen in the context of the general life history of the animal concerned. This chapter briefly documents some important aspects of the life history and reproductive biology of fishes, before looking specifically at their reproductive behaviour. It covers the mechanisms that control how fish behave when they reproduce, the developmental processes that influence the breeding behaviour of adult fish and the consequences for fitness of showing different patterns of reproductive behaviour. Wherever possible, examples are taken from fish that are cultured for a variety of purposes, including provision of food, use in the ornamental trade or scientific

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research and for release into the wild for supplementation or reintroduction programmes.

Obtaining a sufficient and predictable supply of good quality fry for rearing is a major hurdle in the development of effective culture for many species of fish. Many of the challenges that make this difficult to achieve, as well as many of the potential solutions to the problems they pose, lie in the natural reproductive behaviour of the fish concerned. Whatever the purpose for which fish are cultured, reproduction and the behaviour that accompanies it determine how easy it is to generate sufficient eggs and fry of appropriate quality. Where fish are cultured for supplementation to support fisheries, their reproductive behaviour after release is important because this will influence the sensitive issue of their impact on wild populations and, arguably, they should not breed at all. In contrast, where endangered species are cultured for the purpose of conservation, effective breeding is essential if re-introduced populations are to be self-sustaining. Where fish are cultured for the scientific study of reproductive behaviour, it is important that they show normal responses and in the case of ornamental fish, watching fish courting and breeding is part of the motive for keeping and therefore for culturing fish. Where fish are cultured for food, there is the additional point that maturation interferes with growth and flesh quality, so farmers prefer to suppress it. The second half of this chapter addresses all these issues, reviewing how reproduction is managed in culture systems, identifying problems for farmers that arise from the natural reproductive behaviour of fish and finally describing some behaviourally-based solutions to these problems.

### 10.1.1 The reproductive biology of wild fish

#### *Variable life history patterns in fish*

As described in Chapter 2, life histories and reproductive biology are highly variable among fish, both between and within species, and this variability forms the background against which reproductive behaviour is best considered. Variable reproductive biology has implications for fish culture, because it means that techniques for producing viable eggs and fry that work well for one cultured species may not work at all for others. The age and size at which fish breed for the first time, how many times they breed and the number and size of the gametes (particularly eggs) they produce are aspects of life history that are particularly important for aquaculture. The occurrence of metamorphosis and migration, important aspects of the life history of many fishes, are also critical for fish culture and these have already been discussed in Chapter 4.

#### *Patterns of sexuality*

Most fish reproduce sexually by the fusion of male and female gametes, but in a very few cases this has been secondarily lost. For example, in the Amazon molly (*Poecilia formosa*), a species used in the ornamental fish trade as well for scientific research, females reproduce by parthenogenesis (Hubbs & Hubbs 1932; Woodhead & Armstrong 1985). The species is of hybrid origin and females use sperm from males of one of the ancestral species to trigger embryogenesis, without using any of their genetic material (Schupp & Plath 2005). In most species of sexually reproducing fish the sexes are separate, but hermaphroditism occurs in several groups of fish. In simultaneous hermaphrodites, such as several species of seabass (Serranidae), fish have male and female gonads that are functional at the same time and mating commonly involves egg-trading, with pairs of fish taking it in turns to spawn as male and female (Petersen 2006). Many hermaphroditic fish show sequential hermaphroditism (Forsgren *et al*. 2002). The commonest form is protogyny, in which fish breed as females first and then change to males; examples include labrids, such as the cleaner wrasses *Crenilabrus melops, Ctenolabrus rupestris* and *Labrus bergylta* that are used in salmon aquaculture for sea louse control, and groupers, such as *Epinephelus* spp. that are farmed for food. Protandry, in which fish develop as males before changing to females, is less common, but is seen in the anemonefish (*Amphiprion akallopisos*), an increasingly important species in the ornamental fish trade (Nakamura *et al*. 2005), and the Pacific threadfin (*Polydactylus sexfilis*), a candidate for supplementation programmes in the United States.

#### *Sex differentiation*

Mechanisms of sex determination are highly variable in fishes (Mittwoch 1996), in striking contrast to the conservative nature of sex determination in mammals and birds (Mank *et al*. 2006). In some fish species, for example Nile tilapia (*Oreochromis niloticus*), sex determination follows the mammal-like XY system; others, including the closely related blue tilapia (*O. aureus*), show bird-like ZW sex determination (Devlin & Nagahama 2002). In spite of such genetic influences, sex differentiation is labile in many fish species and several environmental factors, including salinity and pH, may influence gonad differentiation and the phenotypic sex expressed by a fish (Devlin & Nagahama 2002; Evans & Claiborne 2006; Kah *et al*. 2010; Chapter 2). For example, in several species of cichlids and atherinids the proportion of males is increased when the developing young are exposed to high water temperatures, with genetic females

developing to reproduce as males; conversely, the proportion of females increases at low environmental temperatures, as genetic males develop into functional females. However, in other species, including channel catfish (*Ictalurus punctatus*), which are cultured for food, high temperatures produce female-biased sex ratios (Baroiller & D'Cotta 2001). Effects of temperature regimes on gender differentiation can be subtle and complex. For example, in Senegal sole (*Solea senegalensis*), juveniles exposed for 97 days after hatching to a temperature regime that is higher (22 °C) during daytime than at night (19 °C) grow faster than do fish exposed to the converse regime (higher temperature at night rather than during daytime) or those held on an unchanging intermediate temperature. They also show a strongly female-biased sex ratio (72% females), in contrast to the other two groups, which produce 83% and 60% male fish, respectively (Blanco-Vivas *et al*. 2011).

The mechanisms that control gender in fishes are important in fish culture, because they determine the ease with which sufficient fish of a particular gender can be produced. Differentiation of the gonad primordia into ovaries is often dependent upon the presence of oestrogens, the female sex hormones (Chapter 2). The synthesis of oestrogens from androgens, the male sex hormones, is catalysed by the enzyme aromatase (technically, cytochrome P-450 aromatase) and activity of this enzyme appears to be essential for sex differentiation in the female direction (Devlin & Nagahama 2002; Kah *et al*. 2010). In some fish species, sex-reversal of larvae and early juveniles from genetic females to phenotypic males, for example on exposure to high temperature, seems to be the result of reduced aromatase activity as a consequence of suppression of aromatase gene expression. This indicates that aromatase expression and suppression probably play a central role in environment-dependent sex differentiation.

Such a role is supported by work on zebra danio (*Danio rerio*), in which the gonads initially appear as undifferentiated ovarian tissue. In males the ovarian tissue degenerates by 30 days post-hatching and testicular differentiation and development of spermatocytes (sperm-producing cells) occur. In females the ovarian tissue continues to develop, presumably under the influence of the oestrogens produced by the action of the enzyme aromatase on androgens, ovaries differentiate and oocytes (egg-producing cells) grow and eventually mature. However, when exposed to high temperature during early development, genotypic females develop testes, becoming sex-reversed, probably through temperature-induced suppression of aromatase gene expression and/or inhibition of the activity of the enzyme. Disruption of the aromatase system during the critical period of sex differentiation may reverse the process of gonad development, producing fish that are either genetic females but phenotypic males or genetic males but phenotypic females. These complex processes leave ample scope for sex ratios to be manipulated (intentionally or unintentionally) in fish culture.

#### *Methods of fertilisation*

In most species, fertilisation is external, with eggs being shed into the water, where they are fertilised by sperm released from nearby males. In some cases, the eggs are deposited in nests or crevices where fertilisation occurs, as in the foam nests of the Siamese fighting fish and the gravel nests of salmonid fish. In sea horses, clutches of 100 or so eggs are fertilised externally by small numbers of highly fertile sperm before being sequestered in the male's pouch (Van Look *et al*. 2007). In many cichlids, including Nile tilapia, fertilisation takes place inside the mouth of the female (Barlow 2000). True internal fertilisation involves transfer of sperm into the female's reproductive tract by means of an intromittent organ or gonopodium; this occurs in several ornamental species, including guppies (*Poecilia reticulata*) and swordtails (*Xiphophorus* spp.). For very many species of fish, including a number of candidates for culture, exactly how fertilisation takes place is not known for certain.

### 10.1.2 The reproductive behaviour of wild fish

Spawning is just one component (albeit a pivotal one) of the behaviour associated with reproduction. Depending on species, fish may have to migrate to and locate suitable breeding sites, establish and defend breeding territories, prepare spawning sites, compete for and court potential mates and show parental care. Together, all these behavioural traits will determine how difficult it is to provide the correct conditions for breeding in self-sustaining aquaculture.

#### *Mating systems*

The social and competitive context in which breeding takes place is sometimes referred to as the mating system for the species concerned. There are a number of different ways of defining and classifying mating systems and the one used here is based on how many sexual partners a fish has in a particular breeding season and the nature of the pair bond between them. According to this scheme, in promiscuous mating systems animals of both sexes have multiple partners within a single breeding season, with no prolonged association between males and females. This is common in fishes, particularly in group-spawning pelagic fishes such as Atlantic cod (*Gadus morhua*; Nordeide & Folstad 2000),

a species cultured for food, and in schooling fishes such as zebra danio (Lawrence 2007), a species used in laboratory research and in the ornamental trade. Where members of one sex have more or less exclusive mating access to several members of the opposite sex within a single breeding season and there is a relatively close association between partners, the mating system is said to be polygamous. When males have exclusive mating access to several females, the term polygyny is used; polygyny occurs in many species of wrasse, including bluehead wrasse (*Thalassoma bifasciatum*; Warner 1990) and in dwarf cichlids (*Apistogramma* sp., see Yanong 1996). Less commonly, one female has exclusive mating access to several males within a breeding season, as in anemone fish (*Amphiprion* spp.; Moyer & Sawyers 1973), in which case this is called polyandry.

Polygyny includes the special case of lekking, in which breeding males congregate and defend small territories on which they display to visiting females. In the bower-building Lake Malawi cichlid (*Cyrtocara eusinostomus)*, males congregate in huge colonies of up to 50000 fish and build sand pyramids above which they display to visiting females (McKaye 1983). Lekking is observed in some cultured species, including the Mozambique tilapia, in which males aggregate in dense groups to establish temporary territories, dig spawning pits and court females. Females visit several males and, if courtship is successful, spawn in the pit of one selected male before collecting the eggs and sperm into their mouth and leaving (Oliviera & Almada 1999; McDonald *et al*. 2007). A form of lekking has been reported in other food fish, such as Arctic charr (Figenschou *et al*. 2004) and, possibly, Atlantic cod (Nordeide & Folstad 2000).

A monogamous mating system involves prolonged association between one male and one female, both with essentially exclusive mating access to the other; monogamy is rare in fish, but occurs in the angelfish (*Pterophyllum scalare*; Cacho *et al.* 2007), a popular aquarium species. Seahorses are strongly and famously monogamous, as evidenced in the Western Australian seahorse (*Hippocampus angustus*) in which paternity analyses using genetic fingerprinting has confirmed behavioural observations of strict monogamy (Jones *et al*. 1998). Monogamy can be facultative, depending on circumstance; for example, the seabass (*Serranus fasciatus*) spawns monogamously at low population densities, but mates polygamously at high densities (Petersen 1990).

### *Fighting over breeding opportunities*

Reproduction often involves competition for mates (usually but not always by males over females) and one way in which fish compete is by fighting. Where males fight over females, this often involves the development of sexually dimorphic traits, including large body size and specialised weapons in males. Male Mozambique tilapia, which fight over spawning territories, are larger than females and have more robust jaws that they use for mouth wrestling as well as for digging spawning pits (Oliviera & Almada 1999). During migration to their breeding grounds, mature male salmon shed their feeding teeth and grow a new set of long sharp teeth fused to their jaw. At the same time a large hook, or 'kype', develops at the tip of the jaw from rapidly-growing bone and cartilage, similar in composition to the antlers of deer (Witten & Hall 2002). Together with the sharp teeth, this forms an effective weapon that is used in fights over access to spawning females (Fleming 1996). In some species, females fight over breeding opportunities, as when female salmon fight over spawning sites (van den Berghe & Gross 1989) and female pipefish (*Syngnathis typhle)* fight over males with empty pouches (Berglund & Rosenqvist 2001).

### *Ornamentation and courtship*

Another way in which fish compete for and acquire mates is by developing ornaments that are attractive to members of the opposite sex. Examples of sexually dimorphic ornamentation include the breeding colours of many salmonids (Fleming & Reynolds 2004) and the elongated anal fin or sword in male swordtails, which makes them a popular aquarium species (McLennn & Ryan 1999). Females may also show sexual ornamentation, as in the case of pipefish females (*S. typhle*), which use their dark bars to display to potential mates as well as to deter rival females (Berglund & Rosenqvist 2001). Such elaborate ornamentation is often displayed to potential partners by means of more or less elaborate behaviour patterns, or courtship.

Courtship in many fish takes place in the context of a temporary association between ripe males and females. In salmon, females dig several nests sequentially within an area of gravel (referred to as a 'redd') using their tails. Large breeding males that have fought for a dominant position remain nearby and periodically approach the female with dorsal fin erect and may either vibrate their body next to the female or nudge her in her abdomen, moving back and forth across her back as she probes the nest for readiness with her anal fin. When the female is ready to spawn, she crouches down into the nest, thrusting her ovipositor to the bottom and begins releasing eggs. One or more nearby males also press down onto the nest, with bodies stiff and mouth open, before releasing milt (Jones 1959; Fleming1996; Esteve 2005). There are many other cultured species in which males and females associate together

briefly for the purpose of courtship and spawning, with males competing and females exerting choice; examples include Atlantic cod (Skjæraasen *et al*. 2008; Rowe & Hutchins 2004; Engen & Folstad 1999) and the Mozambique tilapia (Oliviera & Almada 1998).

In other cases, courtship is longer and marks the beginning of a more permanent association between partners. For example, in the dwarf seahorse (*Hippocampus zosterae*) the initial phase of courtship begins a day or so before spawning, when the courting pair undertakes an elaborate greeting dance, involving reciprocal quivering of their bodies. On the day of spawning, the male and female exchange signals that bring them close together, before swimming up into the water column and releasing eggs and sperm, which are quickly taken up into the male's pouch (Masonjones & Lewis 1996). The more or less complex courtship that precedes spawning in many species of fish is an important aspect of their reproductive biology that dictates their willingness to spawn in culture conditions.

### *Sperm competition*

Competition does not end once sperm have been deposited near a batch of eggs, because when sperm from two or more males are shed at more-or-less the same time, they compete for fertilisations. Sperm competition is widespread among fish and commonly results in the production of more and/or more active sperm. For example, male Arctic charr that are forced by subordinate status to mate in behaviourally-disfavoured roles produce more and more active sperm than do dominant fish (Rudofsen *et al*. 2006). Male sand gobies (*Pomatoschistus minutus*) courting females in the presence of a rival spread more mucus inside their nests than when courting on their own; the mucus contains sperm, suggesting that this is a response to sperm competition (Svensson & Kvarnemo 2005). In Atlantic halibut and Atlantic salmon, even when fertilisation is artificial, the sperm of certain males are more successful at fertilising eggs, probably because they are more motile and swim faster than do the sperm of their competitors (Gage *et al*. 2004; Otteson *et al*. 2009).

### *Parental care*

In many animals, parents interact with their offspring in various ways that enhance the offspring's development and survival, in other words they show parental care. Parental care is rare in fish and the majority of species show little more than judicious placement of eggs (Wootton 1990), which is convenient for fish farmers as it makes it easier to recreate conditions for successful development. Some form of parental care occurs in just over 20% of teleost families, male care being found in 11% of families, female care in 7% and biparental care in 4%. Many marine fish and some freshwater fish (silver carp, *Hypophthalmichthys molitrix*, for example) release eggs into the water column, allowing no opportunity for parental care. Other fish, including a number that are cultured, are substrate spawners, with eggs being released among rocks and gravel with no further parental care; these include dace (*Leuciscus leuciscus*) and striped bass (*Morone saxitalis*). In yet others, including the common carp (*Cyprinus carpio*), eggs are attached to vegetation.

Among those species that show parental care, the form it takes is variable, the commonest being egg guarding. Some Pacific salmon may defend their gravel nests for short periods after the eggs have been laid. A common form of parental care in fish is for breeding males to build nests in which eggs are deposited; the fathers then cares for the eggs by guarding, ventilating and cleaning them. For example, breeding males in corkwing wrasse (*Symphodus melops*) build nests of algae (Potts 1985) and in Siamese fighting fish (*Betta splendens*) build nests of mucus-based foam (Yanong 1996). More elaborate parental care may involve brooding and carrying the eggs on the skin (as in some catfish, Wetzel *et al*. 1997), in the mouth (as in the Mozambique tilapia) or in the gill cavity (as in the cave fish, *Typhlichythys subterranus*). In seahorses, the eggs are completely enclosed and nurtured within a brood pouch (Kvarnemo & Simmons 2004). In the discus (*Symphysodon discus*), developing eggs and fry are tended by both parents, which open the egg case, help the fry to emerge and feed them with mucous from their own skin (Schütz & Barlow 1997). In some cases, young are cared for not just by their parents, but also by helpers of the same species that do not themselves breed. The Lake Tanganyika cichlid *Neolamprologus pulcher* lives in small groups comprising a single breeding pair and up to 20 smaller, subordinate fish of both sexes. All group members participate in cleaning and defending broods of young produced by the breeding pair (Bender *et al.* 2008).

### *Alternative reproductive tactics*

Where competition for breeding opportunities is intense, males that are not physically equipped to win fights or to attract females may adopt alternative tactics for gaining access to mates (Oliviera *et al*. 2008; Chapter 9). For example, in the Mozambique tilapia, in addition to territorial males that dig spawning pits and court females, there are sneaker males that intrude quickly into the nest pit of territorial males when a female is

spawning and release sperm over her eggs. In addition, territorial males may court subordinate males, which respond with female-typical behaviour, allowing them to approach the nest without being attacked (Oliveira & Almada 1998). As described in Chapter 2, a proportion of young male Atlantic salmon mature as parr in freshwater without migrating to sea; these mature parr compete with adult males many times larger than themselves by hiding near gravid females and sneaking fertilisations (Jones & King 1952). The use of such males as brood stock for fish culture can have implications for genetic structure and may, for example, affect the success of hatchery programmes for supplementation or conservation of wild populations.

A particularly well-documented example of alternative reproductive tactics involves the bluegill sunfish (*Lepomis macrochirus*), which is sometimes cultured for supplementation programmes. In this species, large males establish territories, dig nests and actively court females; smaller males found near these territories act either as sneakers or satellites. Sneakers streak rapidly into and out of the nest, releasing sperm as a female lays her eggs, whereas satellites use female mimicry to steal fertilisations (Gross 1991). Small body size is important for sneakers, allowing them to gain proximity to females, but not for satellites (Stolz & Neff 2006a). Once near the eggs, sneakers release much more, faster swimming sperm than do parental males and can obtain equal paternity (Fu *et al*. 2001; Stoltz & Neff 2006b). There is a bias in fertilisation success towards parental males, suggesting that females may be exerting cryptic choice by selective use of sperm (Schulte-Hostedde & Burness 2005).

## 10.2 MECHANISMS

Adequate provision of fry for culture requires a regular supply of fully mature, fecund brood stock, which means ensuring that gonadal maturation is initiated and completed, ideally at a time that is suitable for the farmer or aquarist. This requires an understanding of, and the ability to control, the mechanisms that determine the size and age at which fish mature for the first time and their subsequent patterns of breeding. These are primarily matters for life history biologists and reproductive physiologists, but they are essential precursors to the proper expression of reproductive behaviour and define the conditions that must be met in fish culture before effective reproduction can be completed. This is a large and complex topic (see Hutchings 2002 for a review) and this chapter summarises only the points that are most relevant for how fish behave.

### 10.2.1 The control of maturation in fish

In general, fish start to mature once they reach a threshold size (Hutchings 2002), although the case of males that mature at a small size and use alternative mating tactics is more complex. One view of the control of age of maturity suggests that at certain key points several months before reproduction actually occurs, sometimes called 'developmental windows', maturation is initiated or not depending on an individual's condition with respect to achieved growth rates and/or accumulated nutritional reserves. Only if condition and/or reserves lie above a critical population-specific threshold do the physiological and morphological processes of maturation begin (Thorpe *et al*. 1998). Once fish are mature, the timing of breeding is often seasonal and the environmental cues and physiological processes that control breeding reflect this. In nature, fish tend to breed at a time that maximises lifetime fitness, usually ensuring that the resulting young will hatch into favourable conditions.

Mid- and high-latitude fish, such as salmonids, tend to show strong seasonal patterns of reproduction. In such species, gonadal maturation is under the influence of seasonal changes in several proximate cues, but most particularly in photoperiod, the most reliable cue of time of year. Effects of photoperiod often act on an endogenous circannual rhythm that causes fish to continue reproducing at approximately yearly intervals even when held under constant environmental conditions. The timing of breeding is controlled and can be shifted by alterations in photoperiod in many species of fish, including all the major farmed species. Temperature is also an important environmental cue, but its effects on the timing of reproduction are complex and often secondary to those of day length. At lower latitudes, reproduction tends to be timed with respect to seasonal changes in water levels (Lowe-McConnell 1986), but certain tropical species, including some of the farmed cichlids, spawn throughout the year. The reproduction of marine species may also be timed to the phases of the moon, with mating occurring at the high spring tides to promote subsequent larval dispersal (Therriault *et al*. 1996). Photoperiod and other influential factors control reproduction by promoting secretion of gonadotropin-releasing hormone (GnRH) in the hypothalamus, which in turn stimulates release of gonadotropic hormones from the pituitary gland, under the influence of which gonadal development occurs. Maturing gonads secrete various steroid hormones that stimulate secondary sexual characteristics (reviewed by Bromage *et al*. 2001).

### 10.2.2 The control of reproductive behaviour: external stimuli

Once fish are in breeding condition, the mechanisms that bring the sexes together for effective mating include external stimuli responsible for finding and attracting mates, choosing among potential mates and effecting fertilisation once a mate has been found and chosen. These are all important for fish farmers trying to manage the reproductive behaviour of their brood stock. For simplicity, each modality is illustrated in turn in the following sections, but multiple cues are often important (Rosenthal & Lobel 2006).

#### *Olfactory cues*

Water-borne scents are particularly important in controlling the timing and synchronisation of male and female spawning behaviour in fish. In some species, the scent of young conspecifics directs movement towards suitable breeding sites. For example, lingering scents from juvenile Arctic charr (*Salvelinus alpinus*), which are cultured both for food and for conservation, may attract mature adults to spawning grounds that have proved suitable in the past (Stacey & Sorensen 2006). Reproductive hormones or their breakdown products released in the urine and faeces provide information about the gender and reproductive status of potential mates and play a key role in coordinating the behavioural exchanges by which fertilisation is achieved. In goldfish, which are important both as an aquarium fish and in scientific research, breeding takes place within mixed-sex shoals and females release a cocktail of scents derived from reproductive hormones and reflecting her stage of maturation. The various components of this mixture stimulate males to produce sperm, to approach and inspect females and to attack rival males. At ovulation, females release a specific kind of lipid with hormonal effects (a prostaglandin) that attracts males, causing further sperm activation and triggering courtship. Similar effects, though less well documented, have been described for many other fish, including many cultured species such as the common carp, zebrafish and various salmonids (Stacey & Sorensen 2006; Lawrence 2007), as well as in Mozambique tilapia (Miranda *et al*. 2005) and African catfish (*Clarias gariepinus*; Resink *et al.* 1987, 1989).

#### *Visual cues*

Courtship and mating in fish includes the exchange of various visual cues, in many cases acting as indicators of species, gender and the quality of potential mates. For example, in two closely related, sympatric species of cichlids from Lake Victoria (*Pundamilia pundamilia* and *P. nyerere*) male colour patterns are clearly distinct, with *P. pundamilia* males being grey–blue and *P. nyerere* males having red backs and yellow sides. Males of the two species court females indiscriminately, but females show a strong preference for males of their own species (Mann *et al*. 2006). In swordtails, females prefer males with large swords (Trainor & Basolo 2006). Males sometimes choose among females on the basis of colour; for example, in two spotted gobies (*Gobiusculus flavescens*), breeding females develop an orange belly, the colour coming partly from the pigmented eggs visible through the skin; given a choice, males prefer those with the most colourful bellies (Amundsen & Forsgren 2001; Svensson *et al*. 2005). Body size is also important in courtship; for example, in Banggai cardinal fish (*Pterapogon kauderni*), a mouth brooding cichlid, females are more responsive to the courtship displays of (Figure 10.1) and produce heavier clutches when paired with large males than when paired with small males (Kolm 2001).

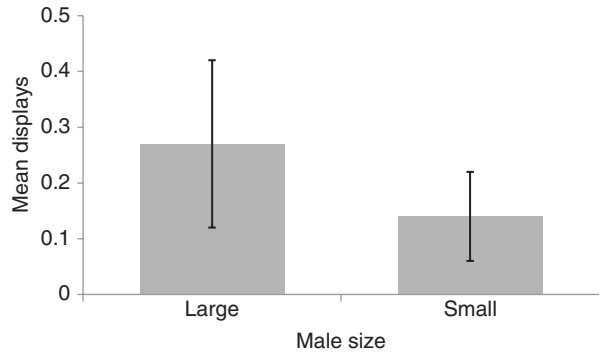


**Figure 10.1.** External stimuli and courtship. Mean (±SE) number of courtship displays performed by female Banggai cardinal fish paired with a large or a small male. Adapted with permission from Kolm 2001.

#### *Auditory cues*

Fish of many species produce vocalisations during courtship. For example, male Atlantic cod produce drumming sounds that attract females by vibrating their swim bladder during courtship. Courtship that is accompanied by sound production is more likely to result in spawning, so the sounds seem to be influencing the females' behaviour (Engen & Folstad 1999; Ripley & Lobel 2004). Just before spawning, the sounds change from 'grunts' to 'hums', suggesting that they may play a role in synchronising

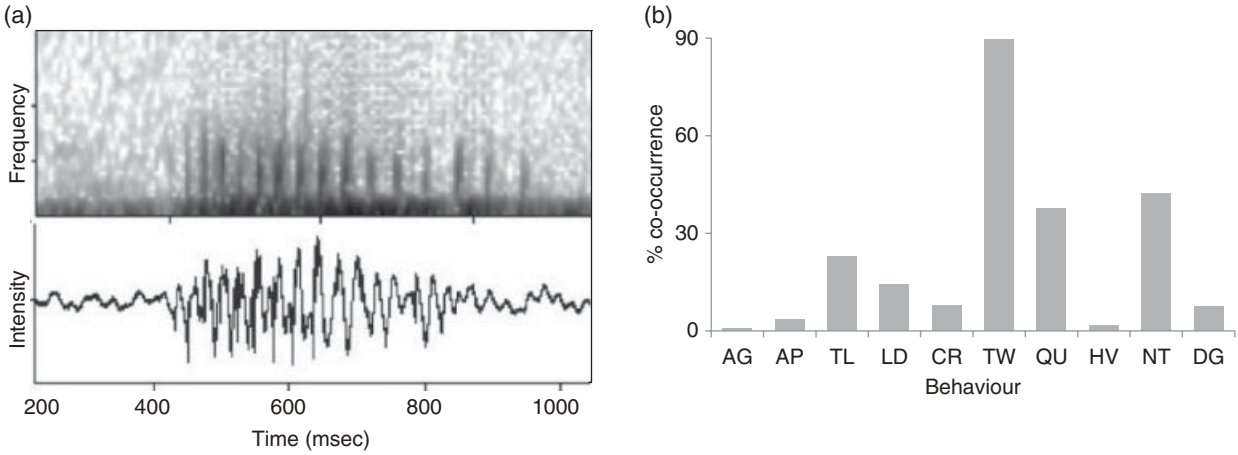


**Figure 10.2.** External stimuli and courtship. (a) Sonogram (top) and oscillogram (bottom, sound filtered through a 170 Hz high-pass filter) of a sound produced by a territorial male Mozambique tilapia during courtship. Reproduced with permission from Amorim *et al.* 2003. (b) Percentage co-occurrence of sound production and specific behaviour patterns in mixed sex groups of Mozambique tilapia. AG = agonistic behaviour. AP = approach female. LD = lead. CR = circle. TW = tail wagging. QU = quiver. HV = hover. NT = in nest. DG = dig. Adapted from Amorin *et al.* 2003.

gamete release (Brawn 1961a, b). Territorial male Mozambique tilapia produce sounds during courtship (Figure 10.2a), which are associated with particular behaviour patterns (Figure 10.2b) and may play a role in synchronising gamete release (Amorim *et al*. 2003; Longrie *et al*. 2009).

### *Tactile and electrical cues*

The later stages of courtship in many species of fish involve displays performed at close range, so fish may be exchanging tactile cues. In salmon (*Onchorhynchus nerka*), the male's quivering during courtship sends waves that are detected by the female using her lateral line; if lateral line function is blocked, courtship is inhibited (Satou *et al*. 1994a, b). In the yellowtail kingfish (*Seriola lalandi*), which is cultured for food, the male nips the female gonoduct and this stimulates spawning (Moran *et al* 2007). Electric organ discharge in weakly electric fish, which are popular as aquarium fish and used in scientific research, is both species-specific and sexually dimorphic (Bass & Zakon 2005). Members of the opposite sex are attracted to the discharge patterns of their own species, responding differently to male and female patterns (Kolodziejski *et al*. 2007) and also distinguishing between potential mates of different size on the basis of their electrical discharge (Curtis & Stoddard 2003).

### *External stimuli and effective spawning*

In nature, the complex exchange of signals that takes place during courtship, including the priming effects of olfactory cues on reproductive physiology and the role of auditory cues in synchronising spawning, is a key part of the mechanism that ensures successful production, release and fertilisation of eggs in wild fish. The extent to which breeding fish have access to such cues in captivity may well determine how easy it is to achieve effective spawning, recognised as a critical bottleneck in fish culture.

## 10.2.3 The control of reproductive behaviour: neuroendocrine processes

### *Gonadal hormones and sexual behaviour*

The hormonal processes that bring about the timely development of mature gonads and appropriate secondary sexual characters, described briefly above, also form a large part of the mechanism that controls the expression of reproductive behaviour in fish. Overall, they stimulate males and females to perform appropriate species- and sex-specific behaviour, but can also cause shorter-term changes during courtship.

There is a close association between plasma levels of reproductive hormones and reproductive behaviour in every teleost fish in which this has been examined

(Pankhurst 1995). In many species, seasonal changes in production and metabolism of sex hormones track the appearance and disappearance of sexual behaviour in both males and females. In addition, striking differences in hormonal physiology parallel gender differences in behaviour, as well as differences between males pursuing different mating tactics. For example, male Mozambique tilapia have much higher levels of the main circulating androgen in fish (11-keto-testosterone or 11KT) than do females, especially at the start of the nesting period when they are establishing territories and actively courting. In males, secondary sexual traits are typically suppressed or abolished by castration and reinstated by 11KT injections and frequency of courtship often correlates with individual 11KT levels (Oliveira & Canario 2001). Especially at the start of the breeding season, breeding females have elevated levels of oestradiol and testosterone, which is often present at higher levels in female fish than in males. Among other effects, oestradiol and testosterone make female fish more sensitive to courtship signals, enhancing their ability to detect and choose among potential mates.

Conversion of androgens to oestrogens within the central nervous system is an essential part of the mechanism by which androgens regulate reproductive behaviour in fish as in other vertebrates. Several species show gender-related differences in brain aromatase activity; for example, during the reproductive seasons, female goldfish have different patterns of steroid-induced aromatase activity than do males (Pasmanik & Callard 1988; Gelinas *et al*. 1998). In species with alternative reproductive strategies, the hormonal status of sneaker males largely parallels that of females; 11KT levels and the number and size of GnRH neurones in the brain are higher in territorial, displaying males than in sneakers (Oliviera 2006).

***Experience-mediated changes in endocrine status***

Reproductive experience can produce rapid changes in hormonal status. For example, following social stimulation by exposure to a rival, male cichlids (*Pundamilia nyererei*) have elevated levels of plasma 11KT and develop larger areas of red nuptial colouration (Dijkstra *et al*. 2007). In African catfish, 33 days exposure to water from mixed sex groups of adults promotes secretion of gonadotropic hormones and re-development of the gonads in post-ovulatory females (Van Weerd *et al*. 1990). Male Mozambique tilapia that have recently won fights against other males subsequently produce more sounds with longer pulse durations and lower peak frequencies when courting females, probably as a result of rapid changes in neuroendocrine status (Amorim & Almada 2004).

Experience-mediated changes in hormonal status play a role in sex change in several species. For example, in female-first (protogynous) hermaphrodites, such as the blueheaded wrasse, levels of 11KT increase and levels of oestradiol decline as females change into males. In the protogynous blue-banded goby (*Lythrypnus dalli*), brain aromatase activity is higher in females than in males. When resident males are removed from social groups of wrasse, levels of aggression increase in the dominant female, which changes sex 7–10 days later; this is accompanied by a 40% decrease in brain aromatase activity (Black *et al*. 2005). In male-first hermaphroditic species, the opposite changes take place. For example, the black porgy (*Acanthopagrus schlegeli*) acts as a functional male for the first 2 years of life, beginning sex change to female in year 3. Fish that are changing from male function to female function have higher levels of plasma oestrogen and lower levels of 11KT than do fish whose sex is not changing (Lee *et al*. 2001). Experience-mediated changes in production of reproductive hormones are important in aquaculture, because they are a key part of the mechanisms that bring fish into the precise physiological conditions needed for successful spawning. These mechanisms should be allowed to function if farmed species are to produce mature gametes.

### 10.2.4 Summary of the mechanisms that control the reproductive behaviour of fish

Once fish have come into breeding condition through the cascade of neuroendocrine events triggered by long photoperiods (in high latitude species at least), they produce signals in various modalities. These signals influence the behaviour of other breeding fish of the same species, attracting mates and possibly deterring rivals, allowing mate choice, synchronising the behaviour of males and females and facilitating spawning. The effects of such external stimuli interact with those of circulating hormones, particularly the gonadal steroids, to determine how fish behave. In general, the androgen 11KT promotes male typical behaviour and oestrogens promote female behaviour. Exposure to cues from mature conspecifics, particularly to scents derived from the gonadal steroids, modulates both endocrine status and subsequent behaviour. In species with distinct males and females, such feedback from behaviour to the neuroendocrine system serves to bring the fish into peak breeding condition, while in sequentially hermaphroditic species they can mediate sex change.

## 10.3 DEVELOPMENT

### 10.3.1 Ontogenetic processes

The behavioural aspects of reproduction, for example whether a fish shows female-typical or male-typical behaviour and among males which mating tactic is used, are determined early in life, through what are called organisational effects of hormones (Oliviera 2006). As far as the development of gender-specific reproductive behaviour is concerned, early exposure to oestrogens typically promotes structural and behavioural feminisation and early exposure to androgens promotes structural and behavioural masculinisation in many cultured fish species, including various tilapia species, rainbow trout and largemouth bass (Uguz *et al*. 2003). The midshipman fish (*Porichthys* spp.) provides a particularly well-studied case of different ontogenetic trajectories in males adopting different mating tactics. Genetic males that grow fast when young experience an early surge in androgen production, causing them to develop into territorial males and promoting development of the muscles and nervous system structures that control production of courtship song. Both genetic females and males that grow slowly when young fail to show an androgen surge and so do not develop enlarged muscles or produce courtship song; males in this category achieve fertilisations by sneaking (Bass *et al*. 1996). In other species of fish as well, the development of territorial and sneaker males diverges as a result of early hormonal differences (Oliviera 2006).

In parallel with the development of mature gonads, sexually dimorphic brains and secondary sexual characters, reproductive behaviour itself gradually takes on its adult form as fish mature. For example, courtship in adult zebrafish involves the female approaching the male, followed by a phase of parallel swimming, during which the female occasionally halts in front of the male, presenting her flank. Early in the courtship sequence, the male may touch the female and then swim round her in circles; later on, he shows more elaborate zig-zags until the female leads him to a suitable spawning area. Development of courtship in young zebrafish follows a similar sequence (Figure 10.3). Simple presentation of the flank appears at about 6 weeks after fertilisation, but more complex displays are not shown until later in development; the range of displays increases with age, until by 12 weeks most fish show the complete repertoire of effective courtship behaviour (Darrow & Harris 2004).

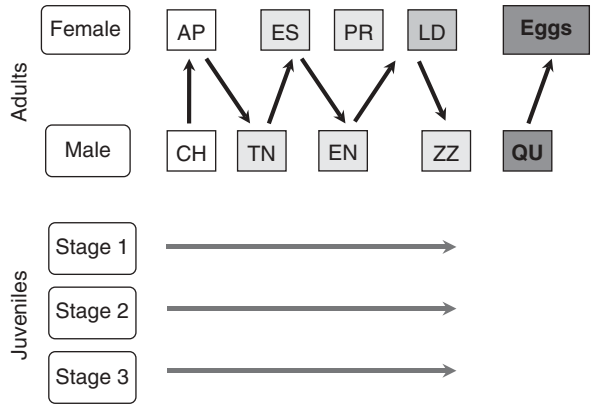


**Figure 10.3.** Development of courtship. Schematic figure of the sequence of behaviour patterns shown during courtship by adult male and female zebrafish, together with the behaviours performed by young at different stages of development. AP=approach. ES=escort. PR=present. LD=lead. Eggs=lay eggs. CH=chase. TN=tail to nose. EN=encircle. ZZ=zigzag. QU=quiver. Stage 1=6 weeks after fertilisation (wpf). Stage 2=9 wpf. Stage 3=12 wpf. Intensity of shading in squares represents increasing sexual motivation. Black arrows = frequent transitions. Grey arrows indicate the behaviour patterns performed by juveniles at different stages. Adapted from Darrow & Harris 2004.

### 10.3.2 Genetic effects

A number of lines of evidence suggest that the timing of life history events in fish is subject to genetic effects, often linked to inherited differences in growth rate. For example, the offspring of sneaker males in the bluegill sunfish grow faster and to a larger size during the yolk sac stage than do half-sibs sired by parental males (Neff 2004). Second-generation sea-ranched Atlantic salmon grow faster than do wild fish reared in identical hatchery conditions, both as juveniles and during the sea-going phase; they also reach sexual maturity earlier and show a higher proportion of early-maturing fish (Kallio-Nyberg & Koljonen 1997). Similarly, coho salmon (*Onchorhynchus kisutch*) transgenic for a growth hormone gene mature earlier than do non-transgenic fish (Bessey *et al*. 2004). In swordtails (*X. maculates*) and other poeciliids, age of maturity and reproductive tactics in males are controlled by a locus on the Y chromosome. Males with one genotype mature early (starting at about 5 weeks) at a small size and acquire matings by chasing females. Males with the alternative genotype mature later (at about 11 weeks) and at a larger size, acquiring mates by courting (Rhen & Crews 2002).

The fact that reproductive behaviour often develops normally in fish reared in isolation suggests strong genetic control of the behaviour concerned. For example, male Nile

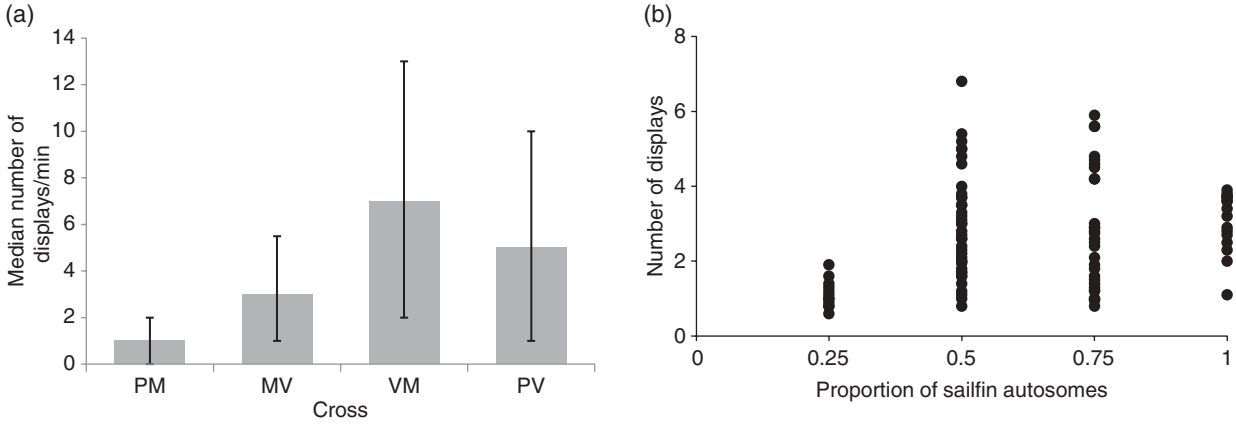


**Figure 10.4.** Genetic effects on courtship. (a) Median (±IQR) number of courtship displays per unit of time in pure lines and reciprocal hybrids between sailfin (*Poecilia velifera*) and shortfin (*Poecilia mexicana*) mollies. PM = pure shortfins. PV = pure sailfins. MV = crosses between a male shortfin and a female sailfin. VM = crosses between a male sailfin and a female shortfin. (b) Number of courtship displays per unit of time shown by fish from a variety of crosses in relation to the proportion of sailfin autosomes that they inherited. Adapted with permission from Loveless *et al*. 2009.

tilapia reared in isolation from the egg stage produce species typical sounds when confronting other males during nest construction (Longrie *et al*. 2008). More detailed evidence for the existence of genetic effects on reproductive behaviour comes from studies in which differences in behaviour are specifically related to differences in genetic make up. Significant heritability has been shown for both sexual ornamentation and courtship in a number of species, including guppies (Rodd & Sokolowski 1995). Reciprocal hybrids between sailfin (*Poecilia velifera*) and shortfin (*Poecilia mexicana*) mollies, both popular aquarium species, show courtship display rates typical of their father's species (much higher in sailfins). This suggests a Y-linked genetic effect on this aspect of reproductive behaviour, though autosomal genes are also involved in the inheritance of this trait (Figure 10.4; Loveless *et al*. 2009). In the pygmy swordtail (*X. nigrensis*), a Y-linked locus controls courtship behaviour through an effect on body size, with large males exclusively using frontal display during courtship and small males switching between frontal display and sneaking, depending on whether or not larger males are present (Zimmerer & Kallman 1989). Inherited differences in courtship colour, which are known to influence the behaviour of potential mates, have been documented in several species. In male guppies, attractiveness to females is a highly heritable character (Brooks 2000) and is at least partly dependent on Y chromosome-linked colour pattern traits (Hughes *et al*. 2005); these are also attractive to the keepers of ornamental fish.

### 10.3.3 Environmental effects

Many different kinds of experience acting on a variety of time scales influence the reproductive behaviour of fish. For example, the presence of larger members of the same species and sex suppresses gonadal development in male platyfish (*Xiphophorus maculates*; Sohn 1977), whereas exposure of young zebrafish to adults facilitates the development of courtship (Darrow & Harris 2004). Mate choice is shaped by early social experience and by various forms of learning. The inherited preference for conspecific males shown by females of two closely related sympatric cichlids from Lake Victoria (*P. pundamilia* and *P. nyerere*, see above) can be modulated by early interactions with parents. Females that have been cross-fostered onto mothers of the alternative species show more response to the courtship of heterospecific males than do those fostered onto females of their own species (Figure 10.5). Adult females show comparable colour differences to males of these two species, so this may be a case of sexual imprinting based on visual cues (Verzijden & Ten Cate 2007). Effects of experience on courtship may take the form of learning in a specifically sexual context. For example, adult male Trinidadian guppies can learn within a few days to distinguish between conspecific females and females of the closely related *Poecilia picta* (Magurran & Ramnarine 2004). Social learning can also influence mating preferences; for example, females of many species of fish prefer males with eggs in their nest, suggesting some sort of copying of mate

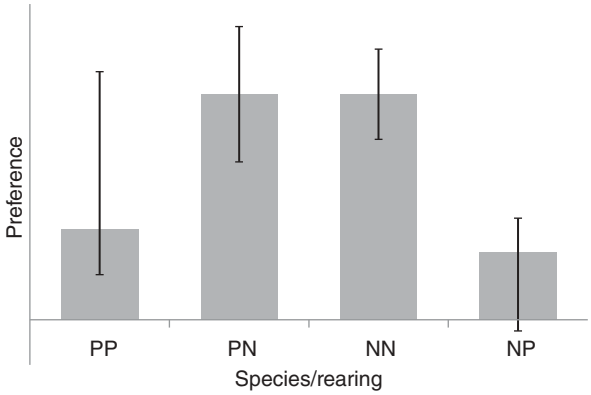


**Figure 10.5.** Effects of experience on reproductive behaviour. Median (±IQR) preference score for female cichlids of the species *Pundamilia pundamilia* and *P. nyererei* raised either by parents of their own species or cross fostered as eggs onto females of the other species. Preference is measured by subtracting the number of approaches made by each female to a male *P. nyererie* as opposed to a male *P. pundamilia* in a two choice test. PP = *P. pundamilia* females reared by their own species. NN = *P. nyererie* females reared by their own species. PN = *P. pundamilia* females fostered onto a *P. nyererei* mother and NP = the converse. Adapted from Verzijden & ten Cate 2007.

choice (reviewed by Brown & Laland 2003), while female gobies prefer to mate with a male whom they have already seen chosen by other females (Reynolds & Jones 1999).

### 10.3.4 Summary of the development of reproductive behaviour in fish

The early hormonal environment initiates development of the neuronal circuits that will eventually control the performance of gender-specific reproductive behaviour and in some cases the incidence of alternative reproductive tactics in males. In parallel with such processes, the elements of courtship behaviour gradually appear in the young fish, becoming increasingly complex and frequent with age, until by the time fish mature the full adult repertoire is in place. The ornamentation that fish display when breeding, the form of the behaviour patterns used in courtship and the responses of potential mates to them, all develop under the influence of the complement of genes that fish inherit from their parents. At the same time, reproductive behaviour can be modified by a variety of environmental factors, from general social conditions to learning during interactions with potential partners. The effects of inherited traits and individual experience on the development of reproductive behaviour combine to determine the behaviour of breeding adult fish. In the context of fish culture, they therefore determine how farmed fish behave when they come into reproductive condition and how easy it is to produce brood stock that can mate effectively.

## 10.4 FUNCTIONS

### 10.4.1 Natural selection, sexual selection and reproduction

Because selection acts strongly on traits associated with reproduction, understanding the consequences for Darwinian fitness of adopting particular reproductive options is of particular interest to evolutionary biologists. An important distinction to be made in this context is between naturally selected and sexually selected traits. Naturally selected traits are those that contribute to survival and to some aspects of reproduction, such as producing gametes in the correct season and ensuring that any resulting young survive. Sexually selected traits are those that contribute to fitness through improved competition for mates. Such traits include characteristics that allow animals to compete effectively by fighting off rivals of the same sex, the kype of male salmonids for example, and by being particularly attractive to potential mates, such as the bright breeding colour and the courtship sounds of male cichlids. While sexually selected traits increase the chances of obtaining mates, they may well reduce survival, as when visually hunting predators home in on courting fish. Natural selection and sexual selection may therefore be in conflict, although both contribute to overall Darwinian fitness and both must be considered for a full understanding of how selection has moulded the reproductive behaviour of fish. Such an understanding is potentially important for fish farmers as well as for evolutionary biologists, since over evolutionary time natural and sexual selection have produced fish with, in effect, the same aims as fish farmers, namely maximising the production of surviving, good quality young. In addition, the effects of natural and sexual selection on reproductive traits will almost certainly be altered by artificial culture, contributing to the process of domestication and to the tricky issue of the impact of farm escapees on native populations.

### 10.4.2 Differential selection on males and females

A central fact about the evolutionary biology of reproduction is that both natural and sexual selection act on males and females in very different ways. In brief and in general, compared to large, nutrient-laden eggs, sperm are smaller and cheaper to produce and, critically, take less

time to replace. Consequently, females invest more in each offspring than do males and their potential reproductive rate (the number of offspring that can be produced per unit time) is lower. This imbalance means that females with unfertilised eggs are often a limiting resource, male competition for females is often intense and males can generally maximise their reproductive success by fighting and showing elaborate courtship. On the other hand, female reproductive success tends to be limited by access to resources rather than to mates and they can maximise reproductive success by being choosy about which males they mate with (Forsgren *et al*. 2002). This explains why female choice is the dominant force in many mating systems and why males often provide services such as parental care and nest building (Barbosa & Magurran, 2006).

There are exceptions to this general rule of ardent males and choosy females, particularly in species in which males invest heavily in parental care, as in seahorses and some pipefish. In these cases, males mate selectively, choosing large females with well-developed ornaments. In contrast, females compete for access to males by means of a dominance hierarchy, with dominant females interfering with the mating opportunities of subordinates (Berglund *et al*. 1997) and chasing rival females away from males (Vincent *et al*. 1995). The fact that selection acts in such different ways on males and females has profound implications for many aspects of life history patterns and reproductive behaviour in fishes. Such effects are illustrated here with reference to the timing of key life history events, to courtship behaviour and to patterns of parental care. Although these may seem somewhat academic topics, they have implications for aquaculture, not least because the way in which natural and sexual selection have shaped reproductive behaviour can cause problems for broodstock management.

### 10.4.3 Functional aspects of the timing of life history events

The expression of life history traits, whether this be age of first reproduction, amount invested in each reproductive episode or number of reproductive episodes, is the result of a complex balance between the costs and benefits in fitness terms of the various options (Hutchings 2002). Age of first reproduction, and with it the adoption of alternative mating tactics, is of particular significance both for behavioural biologists and for fish farmers, so by way of illustration this trait is considered here.

The fitness consequences of maturing at a particular age depend on the relationship between body size and reproductive success, which is generally positive. For example, fecundity and egg survival in female coho salmon increase with body size, as do number of spawnings and number of eggs fertilised in males (Fleming & Gross 1994). Given such relationships, the benefits of maturing late include high fecundity in females and size-dependent competitive success in both sexes. The main cost of breeding at a larger size is that it takes longer to reach breeding age, so fish may die without ever breeding. Age and size at maturation represent a balance between these costs and benefits, which varies between species, populations and individuals in relation to local selection regimes. One influential factor is the rate of mortality in adults and juveniles; early maturation is favoured when variance in adult mortality is high and when adult survival rates are low compared to those of juveniles.

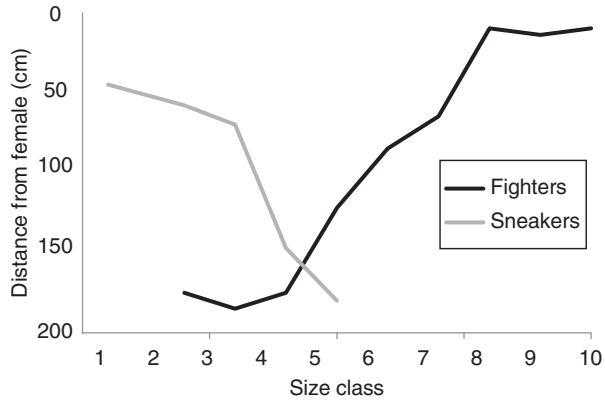


**Figure 10.6.** Balancing the costs and benefits of reproductive behaviour. An index of reproductive success (distance from mature females at the time of spawning) in relation to size class in adult male coho salmon (fighters) and jacks (sneakers). Adapted from Gross 1985.

The relationship between male size and reproductive success in coho salmon is complicated by the costs of fighting, especially at high spawning densities, which reduce the fitness of adult males that fight over females, regardless of male size. At high densities, or when levels of aggression are high for other reasons, small males that sneak matings (jacks) may gain higher fitness than males that mature as large adults (Fleming & Gross 1994). Figure 10.6 shows the relationship between body size and a proxy for mating success (proximity to a spawning female) in fish that sneak and fish that fight for mates. Fitness increases with body size in the large, 3-year old hooknose males, but decreases with size in the smaller, 2 year-old jacks, because it becomes more difficult for

larger jacks to hide from hooknose males (Gross 1985). Such differential size-dependent fitness is sufficient to maintain both mating types in a given population, at levels depending on environmental factors such as population density, sex ratio and levels of predation.

### 10.4.4 Functional aspects of courtship

The complex behavioural exchanges that take place before, during and after mating in many species of animals, including fishes, have long intrigued biologists. A satisfactory explanatory framework in functional terms arises from the fact that courtship confers various benefits on the performer and the recipient, that it also imposes costs, particularly on the performer, and that both costs and benefits are different for the two sexes. What actually happens can be seen as the result of both a trade off between the costs and benefits of courtship and a conflict between the sexes about the outcome that is optimal for fitness.

#### *Benefits of courtship*

Courtship fulfils a variety of functions. First of all, the colour patterns, displays, scents and sounds presented during courtship often serve to attract mates of the correct species. For example, some closely related sympatric species of Lake Malawi cichlid are distinguished by distinct colour patterns that are used in mate recognition; where colour patterns are similar in different species, their courtship sounds are distinct and breeding fish are attracted to the sounds produced by potential mates of their own species (Amorim *et al*. 2008). In the medium term, courtship serves to stimulate hormonal activity, helping to bring fish into peak reproductive condition and on a shorter time scale, helps to synchronise the behaviour of males and females so that successful fertilisation can take place. The complex exchange of chemical signals during courtship and mating in goldfish (see above and Stacey & Sorensen 2006) and of chemical, visual and tactile signals during courtship in salmon provide examples. Another important consequence of elaborate courtship is that it provides an opportunity for mate choice. The strong preferences that fish often show for particular traits in potential mates can promote fitness in two main ways. First, the preferred traits may reflect phenotypic qualities in potential mates that directly promote the fitness of fish making the choice. Second, preferences may be based on genotypes, with selected mates providing 'good' genes that will benefit their offspring indirectly.

Examples of attractive phenotypic traits include indicators of the availability of mature gametes, health status or probable quality of parental care. The commonly-observed preference of male fish for larger females, together with the fact that fecundity usually increases with body size, means that males choosing mates on the basis of size will tend to mate with females that have more eggs for fertilisation. Spawning male cod with large drumming muscles, and presumably the ability to produce loud sounds, have higher sperm counts than do males with smaller muscles (Rowe & Hutchings 2004). Male roach (*Rutilus* spp.), which are cultured for supplementation of natural populations, have breeding tubercles (small lumps on their skin) and males with more elaborate tubercles, besides having longer-lived sperm than those with fewer tubercles (Figure 10.7a; Kortet *et al*. 2004), may also have fewer parasites (Figure 10.7b; Wedekind 1992). Females that prefer males with more tubercles gain more sperm, from healthier mates. In a lekking cichlid species from Lake Malawi (*Copadichromis* sp.), certain features of the males' sand bowers are preferred by females and also predict male parasitic load; in addition, males that gain spawnings have livers that are well packed with nutrients. Together these results suggest that females choose mates that are in good condition, both in terms of energy reserves and in terms of parasite burden (Taylor *et al* 1998). As a final example, female angelfish (*Pterophyllum scalare*) mate preferentially with more experienced males, which provide more effective parental care than do inexperienced males (Cacho *et al*. 2006).

Moving on to mate selection on the basis of genotypic traits, if resistance to disease is inherited, as seems to be the case for some fish at least (Barber *et al*. 2001), the female roach that select males with more tubercles may in fact be selecting for good genes (genes for disease resistance) as well as for disease-free mates. Behavioural ecologists and evolutionary biologists have highlighted the trade off in many species between the role of carotenoids in maintaining sexually selected ornaments and in promoting health through their action as anti-oxidants and in immune defence. The interactions are complex, but by choosing brightly coloured males, fish such as female Arctic charr may be mating with males with inherited resistance to disease (Måsvaer *et al*. 2004). Sometimes compatibility of genes in potential partners, rather than possession of particular good genes, is important. For example, the major histocompatibility (MHC) gene complex controls natural resistance against pathogens and parasites and is involved in mate choice in several vertebrate groups. Given a choice of males, female sticklebacks (*Gasterosteus aculeatus*) choose mates so as to produce an optimal degree of MHC diversity in their offspring, basing their choice on olfactory cues (Milinski *et al*. 2005). Wild Atlantic salmon may also

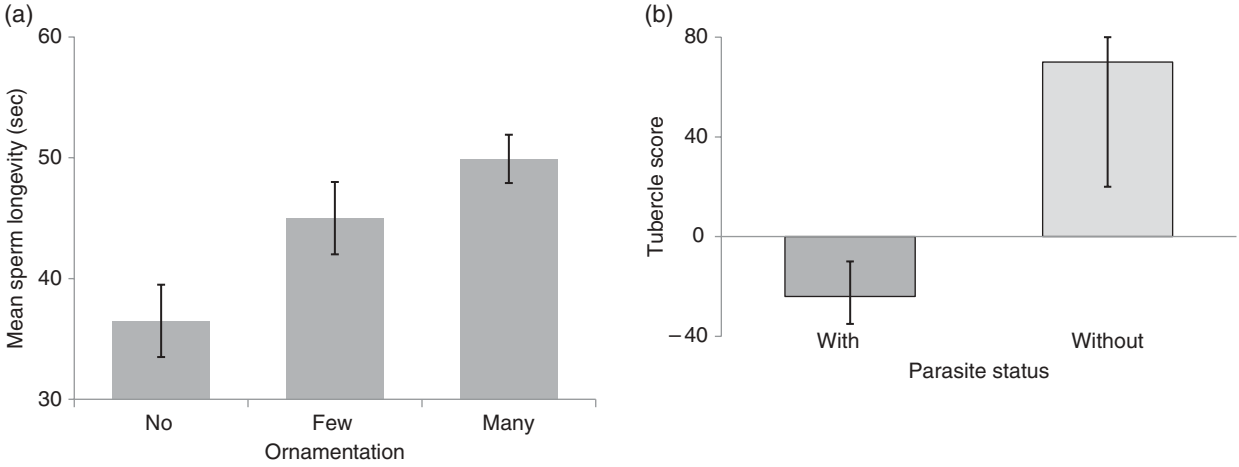


**Figure 10.7.** Mate choice for good quality gametes and disease resistance. (a) Mean (±SE) sperm longevity in male roach in relation to degree of ornamentation. No = no or very few breeding tubercles. Few = breeding tubercles clearly present. Many = many large tubercles. Adapted from Koetet *et al.* 2004. (b) Median, IQR and range for a compound score of tubercle development in male roach with or without the cestotode parasite *Diplostomum*. Adapted from Wedekind 1999.

choose those mates that maximise heterozygosity of their offspring at the MHC locus (Landry *et al*. 2001) and reduce their parasite loads (Consuegra & de Leaniz 2008).

Overall, an important function of elaborate courtship is that it allows fish to choose mates with both advantageous phenotypic properties and inherited fitness-related traits that can be passed on to offspring. Arguably, it might be beneficial for fish culture if brood stock are given the opportunity to exercise mate choice, or if fertilisation is artificial, for farmers to mimic the fishes' known preferences.

### *Costs of courtship*

Set against these benefits are costs, in the form of energy used both in developing secondary sexual traits and in performing courtship, increased predation risk and (for males) of the side effects of high androgen levels. An example of an energetically costly secondary sexual trait is the kype of breeding male salmon, which develops at a time when the fish are already nutritionally stressed by migration and anorexia (Witten & Hall 2002). In swordtails (*Xiphophorus montezumae*), males with elongated tails incur increased energetic cost of routine swimming (Basolo & Alcaraz 2003). Numerous studies show that breeding in general is expensive in terms of nutritional status and survival. This is seen in an extreme form in the salmonid fishes, many of which breed once and then die having completely depleted their nutrient reserves (Fleming 1998). In the cardinal fish (*Apogon notatus*), females court more actively than do males, which invest heavily in parental care, and females also suffer greater loss of energy reserves during the breeding season, reflecting the energetic costs of courtship (Okuda 2001). A cost of courtship in the form of increased predation risk has been documented for guppies, in which predators home in on courting males (Endler, cited in Magnhagen 1991), and for Pacific salmon, which are targeted by bears when spawning (Quinn *et al*. 2001). The increased levels of testosterone often found in breeding male fish increases energetic requirements, as well as suppressing immune function and decreasing resistance to parasitic disease (Miles *et al*. 2007).

### *Balancing the costs and benefits of courtship*

How fish behave during courtship interactions represents a balance between such costs and benefits. For example, male bicolour damselfish (*Stegastes partitus*) pay more attention to large than to small females. When in the presence of a predator, either of adult fish or of eggs, males courting a small female reduce levels of courtship compared to control fish; however, males courting a large female reduce courtship less in the presence of a fish predator and not at all when confronting an egg predator. (Figure 10.8; Figuera & Lyman 2007). When courting in the absence of a predator, male pipefish (*Syngnathus typhle*) prefer more active females, but when courting in the presence of a predator this is reversed, with less active

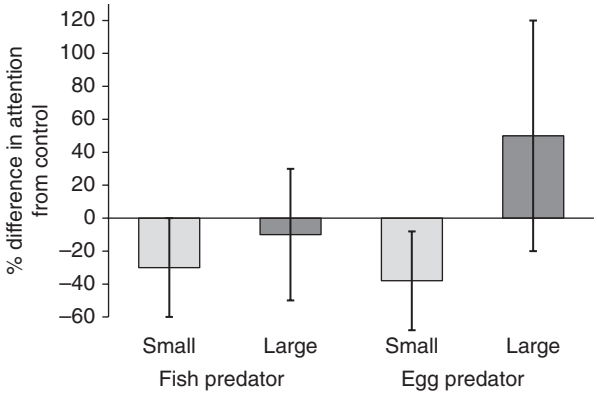


**Figure 10.8.** Costs, benefits and trade-offs during courtship. Mean (± 95% CI) difference from control fish in attention paid to a female by male bicolour damselfish courting either a large or a small female in the presence of a fish predator and an egg predator. Reproduced with permission from Figuera & Lyman 2007.

and therefore less conspicuous partners being favoured (Billing *et al*. 2007). Breeding may be balanced against predation risk on a longer, microevolutionary time scale; for example, in guppies, males from sites with a high level of predation have less conspicuous courtship colours than do those from low predation sites, trading off courtship success against survival (Millar *et al*. 2006).

### 10.4.5 Functional aspects of parental care

Most species of fish show no parental care, suggesting that this is the ancestral state, with fish investing instead in producing large numbers of offspring. This is the case for mass spawning species such as cod and for many coral reef fishes (Breder & Rosen 1966). Set against this large number of offspring is the fact that without parental care survival of young is at the mercy of uncontrollable events and environments (Mullowney & James 2007). Whether natural selection favours the evolution of some form of parental care depends on the costs and benefits of caring for, as opposed to abandoning, eggs and fry (Reynolds *et al*. 2002).

The benefits of parental care are more or less obvious, since young that are cared for are more likely to survive and, in cases where they are fed by the parents, to grow well. The costs of parental care include energy expenditure, increased risk of predation and lost breeding opportunities. Nesting male rock bass (*Ambloplites rupestris*), particularly those with large broods, lose weight during parental care and as a consequence survive less well over the following winter (Sabat 1994). Male pipefish caring for developing broods are more susceptible to predation than are those without broods (Svensson 1988). Female mouth brooding cichlids (*Haplochromis argens*) that have completed a full cycle of mouth brooding take longer to spawn again than do females whose broods are lost, so caring for young means missed opportunities for breeding (Smith & Wootton 1994). For fish, the costs of parental care usually outweigh any benefits, which is why most species show no parental care. The costs of caring are often higher for female fish than for males; because growth is indeterminate in fish and fecundity increases with size, it usually pays females to feed and grow rather than take time out to care for an existing brood. Consequently, benefits are less likely to outweigh costs for females than for males and male uniparental care is the commonest form of parental care in fishes.

### 10.4.6 Summary of the functions of reproductive behaviour in fish

Because eggs are nutritionally expensive compared to sperm, selection acts differently on breeding males and females and this asymmetry shapes many aspects of the reproductive biology of fishes. In functional terms, the age and size at which fish breed for the first time depends on the gender-specific relationship between body size and reproductive success on the one hand and age-dependent mortality rates on the other. Weak size-dependent success and high juvenile mortality favour early maturation and, in males, the adoption of alternative mating strategies. Once fish are in reproductive condition, the elaborate courtship seen in many species of fish serves a number of functions, including attracting mates of the correct species, fine tuning hormonal status and synchronising the behaviour of males and females so that fertilisation can be achieved. Courtship also creates the context in which fish, usually females, can chose among potential mates. Choice may be on the basis of phenotypic traits such as gamete number and quality and disease status that directly benefit the choosing fish and/or its young. It may also be on the basis of inherited traits such as disease resistance or compatible genotypes, both of which improve the genotypic quality of any resulting young. In addition to such benefits, elaborate courtship also involves fitness costs, in terms of increased energy expenditure and increased predation risk. Likewise, although parental care yields obvious benefits in terms of offspring survival and growth, this too carries costs in the form of energy expenditure, risk of predation and also lost breeding opportunities. The amount of courtship fish show

and the investment they make in parental care depends on how such costs balance out against benefits in both sexes.

## 10.5 IMPLICATIONS FOR AQUACULTURE

The implications for aquaculture of the complex and variable life history patterns and reproductive behaviours described in the previous sections depend on the purpose for which fish are being farmed. The requirements of the reproductive process when fish are produced commercially for consumption, used to supplement recreational harvest or to restore natural populations, or bred for the ornamental fish trade or scientific research are different and may be in conflict. Reproduction is a complex process, sometimes poorly understood in currently farmed fish species, and has not been fully described in many new species being developed for aquaculture. The lesson gained from experience with fish species that are well established in culture is that a solid understanding of reproductive biology is essential for controlled approaches to the management of reproduction. The following sections start by describing what actually happens in fish culture with respect to breeding and reproductive behaviour, focusing on the methods used to delay or prevent maturation during on-growing and how spawning is managed once the fish are allowed to mature. Some problems that can arise in aquaculture as a result of natural breeding behaviour of fish are explored, such as occur when fish are being grown to a required size, when they are being used as brood stock for fry production and also when cultured fish are released into the wild. Finally, some strategies that can be used to solve these problems are discussed.

### 10.5.1 Management of reproduction in cultured fish

#### *Suppression of reproduction in fish farmed for food*

In many species of cultured fish, both those reared for food and sometimes those reared for supplementation programmes, early maturation is considered undesirable. Where fish are reared for food, this is because growth rates fall and flesh quality deteriorates as maturing fish put resources into developing gonads rather than muscle, using up stored lipids, carotenoids and protein (Roth *et al*. 2007). The timing of reproduction in farmed fish can potentially be managed on the basis of what is known of the mechanisms that control life history events in wild fish. For example, maturation can be suppressed by altering photoperiod, tricking fish into behaving as though it were winter (Bromage *et al*. 2001). Another strategy is to reduce feeding and growth at critical times, tricking fish into behaving as though growth conditions were poor (Rowe and Thorpe 1990; Thorpe 2004). A third approach to controlling maturation is sterilization, for example through induced triploidy (Benfey 2001; Oppedal *et al*. 2003; Trippel *et al*. 2008), as described in Chapter 2. Finally, where variation in life history traits has some genetic component, selective breeding for delayed maturation is a possibility (reviewed in Gjedrem & Baranski 2009).

#### *Management of spawning*

Whatever the purpose for which fish are cultured, for this to be sustainable at some point it is necessary for some of them to provide fry for future production. Methods used for breeding fish for culture almost invariably interfere with the reproductive behaviour of the species involved, which as described above often includes competition and the opportunity for mate choice. These are critical where fish are cultured for release into the wild, but are also important when all that is required is for young fish to be grown to harvestable size in production systems. There are a number of ways of producing fish fry for culture; details depend on the species concerned, but in general these are artificial fertilisation, artificial pairing of single males and females, formation of small spawning groups, spawning within larger groups and capture of wild larvae for rearing. Table 10.1 summarises the way spawning is managed in the 10 important spotlight species that have been featured throughout this book.

The most intrusive way of breeding captive fish completely removes mating decisions from the fish, because fertilisation is undertaken artificially. Hatchery personnel choose pairs of fish, brought into reproductive condition in various ways, to be mated and then strip and mix the gametes. This method is used extensively for salmonids, but many cultured species will on occasion be spawned this way (Pillay & Kutty 2005), including red drum (Lee & Ostrowski 2001) and various ornamental fish (Yanong 1996). This method offers humans a high level of control over matings, which is important for selective breeding programmes and for some scientific research programmes, but takes no account of the behavioural biology of the species concerned.

Another commonly-used form of fish breeding for culture involves the artificial pairing of mates in enclosures or tanks; spawning takes place spontaneously, usually after some sort of courtship. This method is often used for food fish, such as tilapia (Nandlal & Pickering 2004) and channel catfish (Tucker & Robinson 1990), and is also one method of producing fertilised eggs in fish cultured for the ornamental trade (Yanong 1996). For example, many neon tetras are raised on farms in Southeast Asia, where

**Table 10.1.** Natural reproductive biology and usual regimes for obtainng fry for cultured fish in the 10 spotlight fish species.

| | | Natural reproductive biology | | | Usual stock rearing regimes | |
|---|---|---|---|---|---|---|
| | Age of maturity | Mating system & courtship | Fertilisation & egg deposition | Larval development | Fertilisation | Egg and larval rearing |
| Atlantic salmon | 3–7 years | Promiscuous Simple courtship. | Relatively large eggs deposited in gravel nests in fresh water. Sperm released over eggs. | Eggs hatch in spring. Fry 15–25 mm. Larvae emerge once yolk is used up. Feed on small zooplankton. | Artificial feritlisation using eggs & milt stripped from mature fish. | Eggs hatched in trays & fry are reared in tanks with water flow. |
| Rainbow trout | 3–4 years | Promiscuous. Simple courtship. | Relatively large eggs deposited in gravel nests in fresh water. | Eggs hatch after about 40 days at about 15 mm. Larvae emerge once yolk is used up. Feed on small zooplankton. | Artificial feritlisation using eggs & milt stripped from mature fish. | Eggs & fry reared in troughs and raceways with water flow. |
| European seabass | 2–4 years | Promiscuous. Simple courtship. | Small pelagic eggs released into & fertilised in the marine water column | Eggs hatch after a few days. Larvae about 4 mm. Migrate to shallow water a few weeks after hatching. Form shoals & feed on zooplankton. | Natural spawing in tanks with male:female ratio of 2:1. | Eggs incubated & larvae reared in open water systems with constant flow. |
| Nile tilapia | 5 mo. to 1 year | Lek mating system. Males dig pits & court females. | Medium-sized eggs laid in & fertilised in pit. Eggs taken up & incubated in the female's mouth. | Eggs hatch after 2–3 days & released 6–8 days later, when the yolk is exhausted. Females protect free-swimming offspring after release. | Usually natural spawning in artificial ponds or hapas. | Fry reared in hapas & ponds or in tanks following removal from females' mouth. |
| Pacific salmon | 2–7 years | Promiscuous. Simple courtship. | Large eggs spawned in nests in gravel. Fish typically die after spawning. | Young fish hatch at 20–30 mm & survive on the yolk sac until starting to feed on small zooplankton. | Artificial feritlisation using eggs & milt stripped from mature fish. | Eggs hatched in trays & fry are reared in tanks. |
| Seahorses | 4–12 mo. | Monogamous Complex courtship. | Female deposits 100–200 eggs in male's brood pouch. Eggs fertilised during transfer to pouch. | Eggs nourished through pouch wall for 2–4 weeks, after which young are expelled & feed independently. | Natural spawnings in small tanks with plant or rope holdfasts. Sex ratio = 1:1. | Young removed to nursey tanks on release. |

**Table 10.1.** *continued*

| | | Natural reproductive biology | | | Usual stock rearing regimes | |
|---|---|---|---|---|---|---|
| | Age of maturity | Mating system & courtship | Fertilisation & egg deposition | Larval development | Fertilisation | Egg and larval rearing |
| Koi carp | 1–5 years | Promiscuous. Simple courtship. | Females spawn several thousand small sticky eggs attached to underwater plants. Sperm released over eggs. | Eggs hatch after a few days to larvae of about 5 mm. Once they reach a size of 6–7 mm, larvae feed on small plankton. | Natural spawning in pools or ponds. Sticky eggs collected on brushes. | Eggs reared in tanks & fed on infusoria from a few days after hatching. |
| Zebrafish | *ca* 3 mo. | Promiscuous. Simple courtship. | Clutches of a few hundred eggs at a 2–3 d interval. Fertilisation external. | Eggs hatch after 2–3 days. Larvae capture prey by 5–6 days post-fertilization. | Natural spawning in small groups in mesh-based tanks with male:female ratio of 2:1. | Eggs fertilised in water column. Fall through mesh, avoiding cannibalism. |
| Guppy | 3–4 mo. | Promiscuous. Complex courtship. | Internal fertilisation. Sperm transfer during courtship. Fertilisation in ovarian cavity. | Live-bearer. Eggs incubated in ovarian cavity. Gestation 21–35 days. Young fish feed immediately on release. | Natural fertilisation. Gravid females & mature males held in pairs in tanks. | Released fry hide in gravel before being removed to separate tanks for rearing. |
| Clown-fish | Socially controlled protoandry | Polyandrous. | Adhesive eggs laid on coral near host anemone. Sperm released over eggs. | Eggs protected by male, hatch after 6–10 days & larvae disperse in plankton. | Natural fertilisation. Established mated pairs in tank with rocks on base. Females lay eggs on rock. | Males tend eggs until transferred to rearing tanks. Fry fed live rotifers. |

spawning is often managed by placing pairs of broodfish in tanks with a suitable spawning substrate; pairs can produce about 80 fry every 2 weeks over a period of a year (Chapman *et al* 1998). Zebra danio naturally spawn in shoals and most facilities for breeding these fish use pairs or small groups in a dedicated breeding tank, with a mesh base through which the eggs drop to avoid cannibalism (Lawrence 2007). Managing spawning in this way, especially with breeding fish in pairs, allows a high degree of control over crosses and is thus appropriate for selective breeding programmes and some fields of scientific research. However, compared to conditions in the wild, it allows little scope for natural mate choice.

Among the least intrusive forms of aquaculture breeding programmes are those that allow large groups of fish to breed in a sizeable but confined space from which offspring can be captured for grow-out elsewhere. The space concerned may be a tank, as in the case of marine pelagic spawners such as seabass, sea bream and turbot, or a pond, as in the case of milkfish (Lee & Ostrowski 2001), groupers (Yeh *et al*. 2003), Pacific threadfin (Lee & Ostrowski 2001), carp, catfish (Tucker & Robinson 1990) and tilapia (Nandlal & Pickering 2004). Such conditions allow for the expression of natural breeding behaviours and offer opportunities for the action of natural and sexual selection. For example, Nile tilapia in breeding ponds show territorial behaviour and reproductive competition. Marked variation in male mating success is observed, with 33% of males (usually among the largest in the group) fathering more than 70% of the young (Fessehaye *et al*. 2006). Most commercial cod hatcheries use spontaneous mass spawning in large tanks. There is little capacity for humans to control crosses, but good capacity for the fish to choose their mates, reflected in uneven contributions to the next generation, with 10% of the cod spawning in such a tank producing 90% of the fry (Herlin *et al.* 2008). Finally, for several species of cultured finfish, provision of stock relies almost completely on the collection of larvae or juveniles from natural sources; species sourced in this way currently include eels, grouper, tuna, milkfish, grey mullets and many ornamental fish. Only about 20% of the 1000 or so coral reef fish species that are collected for the aquarium trade have been successfully cultured in captivity, the rest being captured from the wild (Wittenrich *et al*. 2007). Culture of larvae or juveniles collected in the wild has the advantage that both sexual and natural selection will have been at work in the life histories of the fish concerned, but there is a danger of depleting wild populations in the process.

### 10.5.2 Problems in production arising from the behavioural biology of fish reproduction

A number of problems relating to production, to fish welfare and to environmental protection can arise in fish culture as a result of the behavioural biology of reproduction in fish. The problems can arise in the context of suppression of reproduction during on-growing and also of how brood stock are managed. Some of these problems and their implications are summarised in Table 10.2 and explored further, together with possible solutions, in the following sections.

#### *Suppressing sexual maturation*

Where the methods used by fish farmers to suppress maturation and breeding in their stock fail and some fish reach maturity in production systems, a number of problems arise. For example, diets may no longer be adequate for the maturing fish's needs and maturing fish may start to fight. However, even if successful in achieving their main aim, the various methods for suppressing reproduction can bring their own problems. For example, the induction of sterility by induced triploidy can have associated negative effects on the fish concerned, including reduced immunocompetence and morphological deformities (Benfey 1999). The use of light in farm cages to suppress breeding can cause disturbance to the fish being cultured (Trippel & Neil 2003; Wargelius *et al*. 2009), as well as to fish and other organisms outside the cages and can also attract sea-lice (Chapter 4). Reduced feed delivery at critical times aimed at suppressing gonadal development could increase aggression, causing stress and impairing fish welfare (Chapter 9), although on the plus side, it might result in lower levels of nutrient release into the local environment. In the case of selective breeding for delayed maturation, the inevitably low numbers of breeders used in each generation increases the potential for inbreeding and inbreeding depression, primarily through increased expression of deleterious recessive alleles. Any genetic changes arising from selective breeding also potentially raise problems in the case of farm escapees, which may compromise the performance and genetic integrity of wild stock (see below).

For several methods of controlling reproduction, a paradoxical problem for farm management arises because growth rate is one of the variables that controls the onset of reproduction. The proportion of early-maturing fish is higher in populations with fast growth rates, whether this comes about through selective breeding or high food availability, and the requirement for rapid growth must therefore be balanced against a preference for deferred maturity. In salmonids, the consequences of selection for fast growth

**Table 10.2.** Some problems for fish culture from the natural reproductive biology and behaviour of fish.

| | Implications for production | Implications for welfare | Implications for the environment |
|---|---|---|---|
| Methods for suppressing reproduction | Artificial lighting may stress fish, cause high elective stocking density & attract parasites | Stress, high stocking densities & disease compromise health & welfare | Lights may stress wild fish, disturb their breeding & attract wild fish to farms, where they may feed & promote disease transfer |
| | Triploids may have health defects | Poor health is a welfare problem | Sterile, triploids pose less of a threat to native populations than do fertile fish. |
| Failure to suppress reproduction | Maturing fish show loss of growth & condition, increased aggression, stress and lost production | Inability to breed in mature fish & aggression-induced stress & injury may compromise individual welfare | May allow reproduction within cages & escape of fertile embryos into the environment, raising concerns about impacts on wild populations. |
| Method of obtaining fry | Artificial fertilisation & pairwise mating facilitate selective breeding for production traits | Artificial fertilisation requires handling & causes stress<br>Maturation without the opportunity to court & select mates may compromise welfare | Removal/relaxation of sexual & natural selection can cause domestication, with potential negative impact on wild populations after release/escape |
| | Capture of larvae from wild | Capture of larvae from the wild results in stress at capture and transport | Acquiring wild-caught larvae puts wild populations at risk |

are evident in terms of early smolting, which is advantageous for rearing fish for food, but also in early maturation, which is disadvantageous (Refstie & Gjedrem 2005).

***Broodstock management and provision of fry***

Provision of good quality fry on a sufficient scale at an appropriate time is a major bottleneck for effective culture for many species, whether the aim is to culture fish for food, for the ornamental trade or for conservation. Where fry are produced by natural fertilisation between freely interacting fish, establishment of culture conditions in which successful spawning occurs is a major challenge; accommodating the natural reproductive behaviour of cultured species can help the fish farmer in this context.

***Getting cultured fish to breed***

For many candidate culture species the challenge is simply to get fish to breed. Achieving this depends on, among other things, good nutrition, appropriate environmental conditions for gonadal maturation and/or effective artificial manipulation of endocrine status. Behavioural interactions can also influence the extent to which eggs ripen, are spawned and are fertilised in culture systems. Failure to allow for such social processes can compromise the provision of fry for fish culture, even when appropriate physical conditions such as temperature and photoperiod have been provided. For example, in groupers (*Epinephelus tukula*), which are protogynous, dominance interactions determine whether and which females change into males, so natural aggressive interactions among female broodstock can interfere with production of sufficient males for captive breeding (Yeh *et al*. 2003).

In terms of reproductive behaviour itself, as described above, courtship in many species of fish is long and elaborate and in nature serves a number of important functions, including fine-tuning the fish's endocrine state and synchronising gamete production and release. Cultured fish inherit the mechanisms that, in nature, produce such beneficial effects and if the conditions in which brood stock are held do not allow these to be expressed, spawning may be prevented or compromised. In pairs of Nile tilapia held without visual contact, males have smaller gonads relative to their body size and show less courtship and females spawn less than do those allowed visual contact (Castro *et al*. 2009). The fact that fish balance the costs of courtship adaptively against its benefits means that spawning may be suppressed in unfavourable, stressful conditions. In a culture context, cod that are stressed show

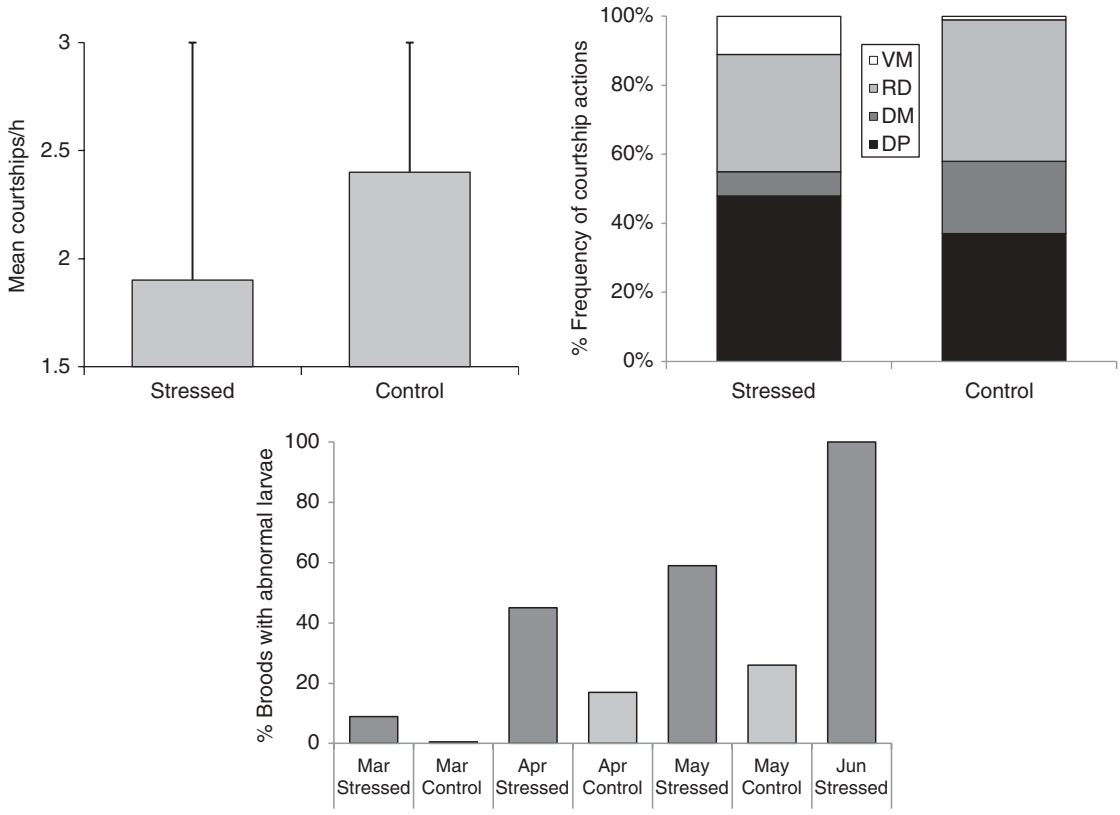


**Figure 10.9.** Effects of stress on courtship and reproduction. (a) Mean (±SE) number of courtships per hour, (b) Percent frequency of different courtship actions and (c) Median % batches with abnormal eggs at a series of sampling points in cod that had been stressed (chased, captured and confined) and control, unstressed fish. No control sample was provided for the June sample. VM = ventral mount. RD = roll down. DM = dorsal mount. DP = dorsal prod. Adapted from Morgan *et al.* 1999.

less courtship (Figure 10.9a) and an abnormal balance of different behaviour patterns (Figure 10.9b) than do unstressed fish (Morgan *et al.* 1999). Another aspect of reproductive behaviour that serves a clear function in nature is fighting over breeding opportunities, as seen in many cichlids and in Siamese fighting fish, for example; this too can cause problems when fish are cultured, since breeding males may attack rival males (Yanong 1996).

### *Obtaining good quality fry*

Even for well-established cultured species where effective methods exist for getting fish to spawn naturally or artificially there can still be problems in obtaining fry of an appropriate quality in sufficient numbers. Whatever the purpose for which the fish are being cultured, fry need to be healthy, of a good size and capable of feeding and growing well in culture conditions. As well as showing less courtship, cod that are stressed also produce more deformed larvae than do unstressed fish (Figure 10.9c; Morgan *et al.* 1999). In addition, when fish are being reared for release, whether to supplement natural populations or for reintroduction of endangered species, being of appropriate quality also means that the released cohorts are 'genetically representative of the target population' (Le Vay *et al.* 2007). This requirement is discussed further below.

Rearing good quality fry in culture conditions may include provision or replacement of parental care. In well-established food aquaculture species, natural patterns of parental care are not necessarily relevant for efficient rearing, since fry are reared in hatcheries under well defined procedures. However, in some such cases, rearing procedures include elements of natural parental care, such as provision of suitable spawning sites for cyprinids or allowing tilapia fry to be brooded in their mother's mouth for a few days before harvesting them (Yanong 1996). Patterns of parental care may also be important for some

cultured ornamental species. For example, the Oscar (*Astronotus ocellatus)* is a popular ornamental cichlid that shows biparental care, both parents guarding the eggs until hatching and then moving the fry to a shallow pit, where they remain for a further 6 or 7 days. Providing fish with the opportunity to show these behaviour patterns is important for successful breeding in captive conditions (Mills & Vevers 1989). Nutrition is provided to larval seahorses by their father's pouch and to larval killifish (*Heterandria formosa*) by their mother's oviduct. There is no substitute in either case and the natural period of gestation simply has to be incorporated into the procedures for fry culture (Faleiro *et al*. 2008; Yanong 1996).

### 10.5.3 Problems arising from domestication and captive rearing

#### *Domestication, captive rearing and fish reproduction*

As discussed in Chapter 1, generations of fish culture can result in inherited differences between wild and cultured fish through a process of domestication, either inadvertently or as a consequence of selective breeding for desirable production traits. How cultured fish breed naturally and how they are allowed to breed in culture are both extremely important in this context. Removal, relaxation or alteration of natural and sexual selection during fry production, as well as intentional selection for desired traits, are key components of the process of domestication and reproduction is the life history stage at which domestication selection is most intense. Life history traits and the behaviour associated with reproduction are among the characters that might be modified by domestication and this can pose problems, whatever the purpose for which the fish are being cultured. In addition, because domestication distorts the natural gene pool, this is a problem in itself when fish are reared for release. On top of such effects of domestication, raising fish in culture can also alter their reproductive behaviour through non-genetic effects of their developmental environment. Although the effects of domestication and captive rearing are different in their origin and their consequences, they are not always easy to separate, so are considered together in this section.

#### *Domestication, captive rearing and life history variables*

A number of studies have identified differences in life history traits between farmed and wild fish, though it is often not possible to distinguish between the inherited effects of domestication and the developmental effects of captive rearing. For example, compared to the population from which they were derived (Nova Scotia, Canada, in the early 1960s), farmed Atlantic salmon in Tasmania are now ready to migrate to sea (smolt) earlier, with 100% of farmed fish smolting at 1 year compared to 0% in the donor population. The male parr that mature do so at a younger age and farmed fish that are transferred to sea water mature more quickly than do wild fish, with most fish maturing at 2 years in the farmed population and most at 5 years in the donor population (Thorpe 2004). Over about some six generations, several life history traits have changed in native sea trout from a Swedish river taken into hatcheries as part of a sea ranching programme. These include an increase in smolt size, which could be due to improved rearing methods as the sea ranching programme has developed and/or to inadvertent selection for fast growth during the culture phase (Petersson *et al*. 1996).

#### *Domestication, captive rearing and sexually selected ornamentation*

Farmed and wild fish frequently differ morphologically in ways that have implications for their reproductive behaviour (Fleming *et al*. 1994; Fiske *et al*. 2005). For example, in cultured male Atlantic salmon both breeding colouration and the hooked snout or kype are less well developed than in wild fish (Aksnes *et al*. 1986), which can affect their competitive ability and reproductive success. Comparison of cod from the same stock reared in culture or captured in the wild shows differences in development of some of the secondary sexual characters used in courtship. Thus farm reared males have shorter pelvic fin for their body length than do wild fish (Figure 10.10a), while farm-reared females have less well developed drumming muscles than do wild females (Figure 10.10b Skjæraasen *et al*. 2008).

#### *Domestication, captive rearing and reproductive behaviour*

Farmed fish also differ from wild fish in their reproductive behaviour and these effects may be magnified in fish that have undergone directed selection for production traits (Fleming *et al*. 1996, Weir *et al*. 2004). For example, when Atlantic salmon are held in mixed groups of farmed (fifth generation) and wild fish captured during their spawning migration, farmed fish show several behavioural deficits that reduce their reproductive success (Figure 10.11; Fleming *et al*. 1996). Farmed males are less aggressive than wild fish, less able to gain access to mates and show less courtship. They take part in fewer spawnings and achieve only 1–3% the reproductive success of wild males. Farmed females show less digging, construct fewer nests and attract less courtship than do wild females. They are also slower and less efficient at covering their eggs and,

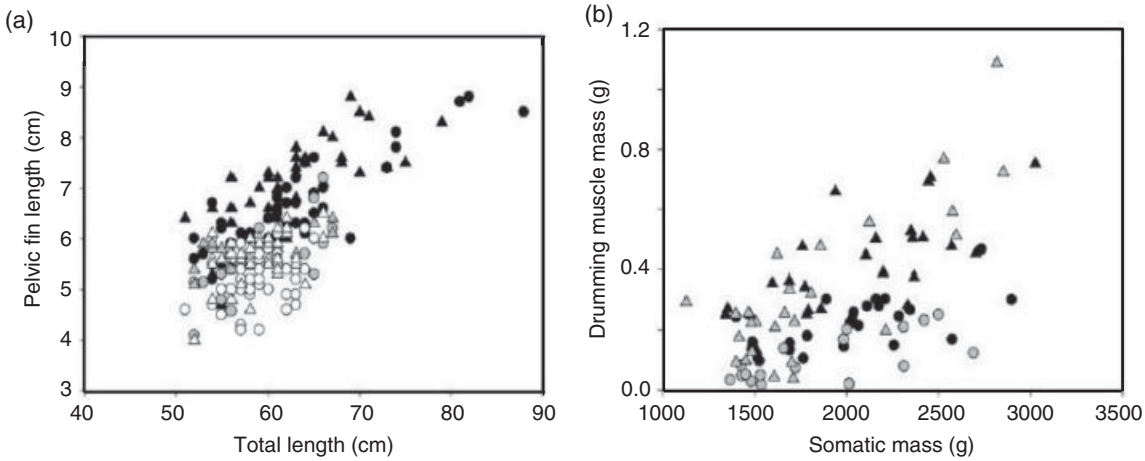


**Figure 10.10.** Differences in behaviourally-relevant reproductive structures in wild and farmed fish. (a) Pelvic fin length in relation to total fish length and (b) Drumming muscle mass in relation to somatic mass in male (triangles) and female (circles) cod from of wild (black) and farmed (grey and white) origin. Reproduced with permission from Skjæraasen *et al.* 2008.

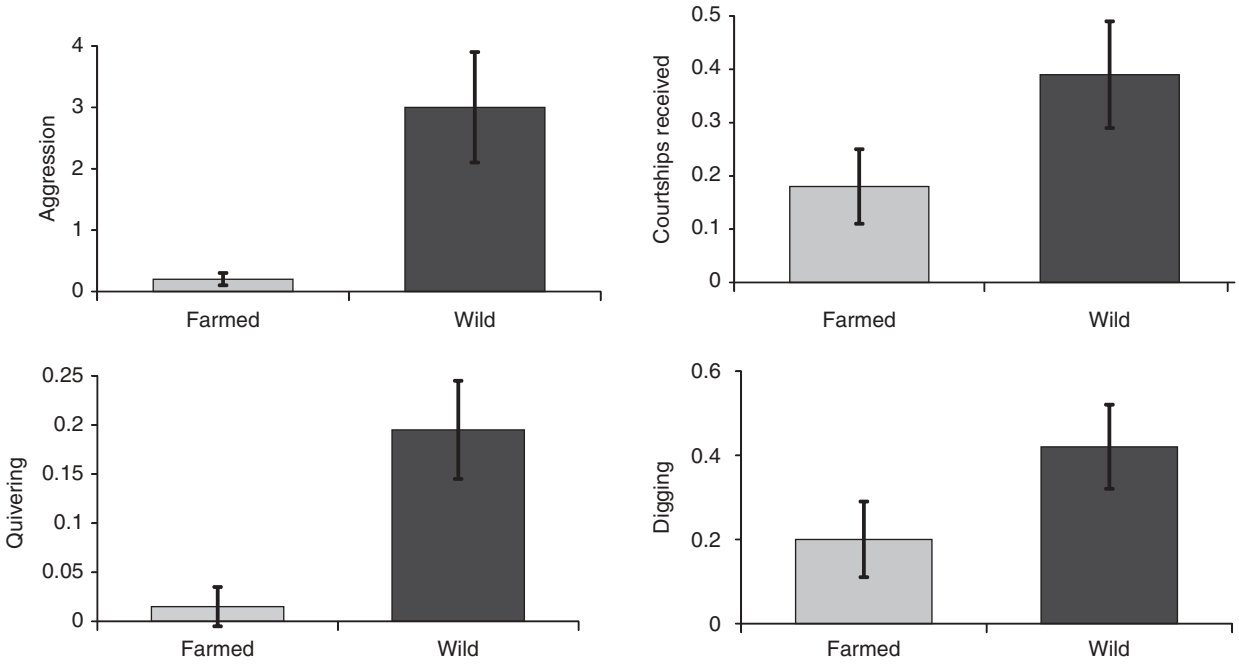


**Figure 10.11.** Behavioural differences between breeding farmed and wild fish. Mean (±SD) frequency of aggression and quivering in farmed and wild male Atlantic salmon and of digging and being courted in farmed and wild females in mixed group arenas. Adapted from Fleming *et al.* 1996.

overall, are considerably less successful than wild females in terms of egg survival (Fleming *et al.* 1996). Wild and farmed cod also differ in their behaviour in spawning aggregations, with wild males being found lower in the water column than either farm-reared males or females of both stocks. In addition, farmed fish remain in spawning

groups for shorter periods. All these differences are likely to reduce the relative reproductive success of farmed cod compared to their wild counterparts, but even so some hybridisation is likely and probably through farmed females mating with wild males (Meager *et al*. 2009).

Demonstrating an effect of captive rearing requires comparing the behaviour of fish from the same genetic stock reared either in the wild or in culture conditions. Wild and sea-ranched male Atlantic salmon of the same genetic stock show similar courtship behaviour, but sea-ranched males are out-competed by wild fish for the primary courting positions. In addition, they are more prone than wild males to get involved in prolonged aggressive encounters and, as a consequence, are more likely to be wounded and suffer higher mortality. Overall, sea-ranched males may achieve only 51% of the reproductive success of wild males. Sea-ranched and wild females are similar in their reproductive behaviour. Thus while early rearing environment has an effect on subsequent reproductive behaviour in males, it is of less importance in the development of female reproductive behaviour (Fleming *et al*. 1997).

Effects of rearing conditions on reproductive behaviour can also be seen in other species. For example, when held in groups wild male coho salmon tend to dominate captive-reared fish from the same stock. In general, large wild males occupy the more favourable position for spawning and small wild males occupy the best satellite position (Berejikian *et al*. 1997). In paired encounters also, wild males out-compete captive-reared fish and gain the dominant position for spawning (Berejikian *et al*. 2001). Wild female coho are much quicker to spawn in their first nest than are cultured fish of the same stock and captive-reared fish of both sexes tend to be the target of more aggression (Berejikian *et al*. 1997). The Mexican species *Skiffa mulitpunctata* is a popular aquarium fish that is endangered and being reared in captivity for conservation purposes. Fish reared in culture show more intense courtship than do those reared in more natural conditions in ponds and are also less alarmed by predators. These two traits may compromise their ability to reproduce successfully if released (Kelley *et al*. 2005).

### *Potential impact on wild populations*

Differences in behaviour between farmed and wild fish, whether the result of one generation of captive rearing or of many generations of domestication, can potentially cause problems for wild populations. For example, abnormal courtship and high levels of aggression in farmed fish may interfere with breeding in the wild fish with which they interact. An additional problem arises from the potential for genetic introgression into wild populations. The nature and extent of such effects will depend critically both on how farmed fish behave on the breeding grounds and on how distinct they are genetically from wild fish. Evidence from Atlantic salmon indicates that the spawning success of farmed fish is low, being 10–30% that of wild fish (Fleming *et al*. 1996, 2000), so interbreeding with wild fish will be relatively uncommon. However, despite such a bottleneck to invasion, mixing of wild and cultured gene pools will occur and research has shown that successful invaders can threaten the persistence of wild populations through both ecological and genetic interactions (Fleming *et al*. 2000; McGinnity *et al*. 2003; Hindar *et al*. 2006*)*.

Exactly how seed and fry are produced in fish culture is critical for how distinct farmed and wild fish are genetically (see below). Where artificial fertilisation is used, sexual selection, in the form of both competition for mating opportunities and the exercise of mate choice, is eliminated. Natural selection during the reproductive period is also altered, as the fish are exposed to relatively benign environments. The mixing of sperm from more than one male to fertilise eggs can introduce limited sexual selection through sperm competition and differential utilisation of sperm due to the properties of eggs and ovarian fluid (Campton 2004). However, since most selective breeding programmes for the genetic improvement of aquaculture strains favour pair spawning for the ease of tracking family performance, such methods for allowing natural selection are not always feasible. Artificial pairing eliminates the opportunity for sexual selection, but compared to artificial fertilisation, does involve a greater range of natural selection during breeding, because pre- and post-mating performance will influence offspring production and survival; for example, courtship interactions and synchronisation of gamete release will be critical to fertilization. Placing fish in small groups for spawning takes this further by introducing a degree of competition and mate choice, while using large numbers of spawners in extensive enclosures allows natural interactions within reproductive groups. However, such systems are generally impractical for selective programmes aimed at genetic improvement in production traits, which require keeping track of parents. Capturing fry for culture in the wild is dependent on the vagaries of natural recruitment processes and also impacts wild populations through the ‘mining’ of natural production.

## 10.6 SOLUTIONS

The previous section has already included some possible solutions to the problem of avoiding domestication selection in fish culture, showing that the problems in

aquaculture that arise from the natural reproductive behaviour of fish are not insoluble. In many cases the solutions lie in an understanding of the behaviour that causes the problems in the first place. This final section gives examples of how the effectiveness of fish culture can be improved by applying what is known and understood about the way breeding fish behave, often the combined result of careful research by biologists and the accumulated wisdom of and careful observations by the farmers concerned.

### 10.6.1 Research into the natural breeding behaviour of cultured and candidate species

One reason why provision of good quality fry on a sufficient scale and at appropriate times remains a barrier to the effective culture of many species is that there is simply insufficient knowledge of the natural reproductive behaviour of the species concerned. One important step in solving some of the problems outlined in the previous section is therefore to carry out more research. This is reflected in the scientific literature, reproduction coming a close second to feeding as a major topic for aquaculture research. An increasing number of papers are being published that document the reproductive behaviour of existing and candidate culture species, including potential food fish, ornamental fish and fish reared for conservation. To give just one example, the leopard grouper (*Mycteroperca rosacea*) is a candidate species for culture for food. Behavioural observations of captive fish held in large enclosures show that these fish spawn in aggregations of up to 700 individuals. Specific spawning events involve 6–40 fish and most take place in the evening, though courtship can be seen throughout the day. Mature males have relatively large testes (up to 7% of adult weight), indicating that sperm competition may occur (Erisman *et al*. 2007). Such studies provide a rich source of valuable information for behavioural biologists, but also contribute to the essential background information that is needed to establish culture of such species.

### 10.6.2 Providing the right physical environment for spawning

One result of such studies is that fish farmers know what physical environment they should provide for their brood stock. There are many examples of fish failing to spawn in culture because the physical environment does not provide some critical feature that they need, but successful spawning may only require provision of one or two essential factors. In pelagic spawners, it seems that spawning behaviour requires a critical volume or depth of water. The minimum holding volume for spawning is 4 $m^3$ for gilthead sea bream (*Sparus aurata* (Zohar *et al*. 1995), 10 $m^3$ for seabass (*Dicentrarchus labrax*; Carillo *et al*. 1995) and 50–100 $m^3$ for red sea bream (*Pagrus major*; Watanabe & Kiron 1995). Such minimum volumes may be necessary because fish are stressed in smaller water bodies and this interferes with spawning or simply because performing spawning behaviour requires a certain minimum space. In the New Zealand snapper (*Pagrus auratus*) and black bream (*Acanthopagrus butcher*) spawning involves circular chasing of receptive females on the tank floor by groups of males, followed by a rush to the surface where gamete release occurs. This can be facilitated by providing the fish with the space they need in which to perform these actions (Smith 1986; Pankhurst 1998). Given the priming effects of courtship on gamete maturation, conditions should allow for fairly long interactions, which may involve providing ample shelter for females so they can escape attacks, as in the case of bubblenest builders, such as the Siamese fighting fish (Yanong1996).

In addition to simply providing space, spawning may be improved by addition of specific environmental features. Cyprinids will spawn when provided with suitable spawning substratum; natural spawning occurs in aquatic vegetation and in captivity, floating bunches of synthetic yarn provide a suitable alternative. Killifish spawn readily in mop heads, especially green or dark coloured ones, which also provide good shelter for newly-hatched fry (Yanong 1996). Providing male Mozambique tilapia in spawning ponds with artificial nests increases seed output, especially at high densities, in water with good visibility and when the nests are small and placed deep in the water (Bhujel 2000; Figure 10.12a). Where Nile tilapia are spawned in tanks, the proportion of fish breeding is higher under blue light than under white light and males build larger nests, possibly because stress levels are lower in fish under blue light (Volpato *et al*. 2004).

### 10.6.3 Providing the right social environment for spawning

Knowing the natural mating systems and reproductive behaviour of cultured fish can also help farmers to provide the right social conditions for effective reproduction, increasing the probability that spawning will occur and promoting the production of healthy, fast-growing fry.

#### *Facilitating spawning*

Both number of potential mates and their sex ratios can influence the probability of effective spawning (Yanong 1996). For example, in Mozambique tilapia breeding in

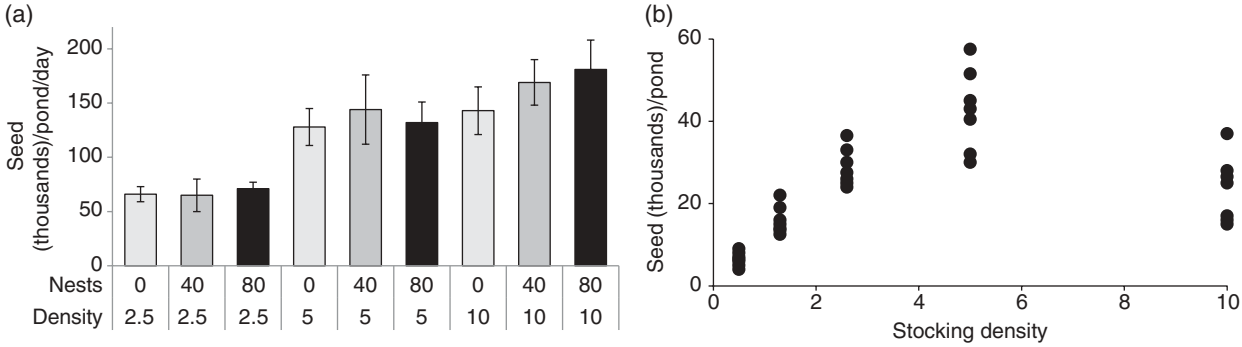


**Figure 10.12.** Providing the right physical environment for spawning. (a) Mean (±SE) seed output (number of eggs/pond/day) by Mozambique tilapia at three stocking densities (fish/m$^2$) in spawning ponds provided with differing numbers of artificial nests. Adapted from Bhajel 2000. (b) Mean (±SE) seed output (number of eggs/pond/day) in relation to stocking density (fish/m$^2$) in Mozambique tilapia. Adapted from Little 1992 in Bhujel 2000.

enclosed net units suspended within larger ponds (or 'hapas'), seed production peaks at a density of about five fish/m$^2$ and is higher at a male:female ratio of 1:2 rather than 1:3 (Bhujel 2000; Figure 10.12b). The size distribution among potential mates can also be important. For example, given the opportunity, seahorses (*Hippocampus guttulatus*) tend to mate with partners of a similar size to themselves; this maximises the reproductive potential of breeding pairs, since larger females produce more eggs and larger males have more space in their pouches to brood them. It therefore makes sense to give these fish access to potential partners of their own size (Faleiro *et al*. 2008). The circumstance in which pairs are established can also influence whether or not spawning occurs. For example, holding male and female of Nile tilapia in visual contact with each other for several days before pairing increases gonadosomatic index and promotes courtship in the males and spawning in the females (Castro *et al*. 2009). This is presumably the result of the influence of social interactions on neuroendocrine state (see above). In easily disturbed ornamental fish, such as angelfish and discus, pair-formation can be facilitated by housing fish with a non-aggressive, less-easily disturbed species prior to spawning. The presence and behaviour of the 'dither' fish have a calming effect, perhaps through some sort of social learning (Yanong 1996).

### *Improving fry quality*

Since fish have been equipped by natural selection with behavioural mechanisms for selecting mates that will produce good quality offspring, arguably obtaining fry that are satisfactory for culture might best be achieved by giving fish a large number of possible mates and letting them express their evolved preferences. Other ways of improving fry quality include reducing stress levels. As described above, unstressed cod produce fewer deformed fry than do stressed fish (Figure 10.9; Morgan *et al*. 1999 and see also Chapter 2).

### *Improving the ornaments of aquarium fish*

In the special context of aquarium fish, the ornaments that aquarists favour are often the ornaments that feature in mate choice in fishes. Techniques for improving these often draw on what is known about the mechanisms, development and function of such traits in nature. For example, testosterone-treated feed produces long-lasting increases in sword-length in female swordtails, making them more valuable (Yanong *et al*. 2006). The fact that courtship colouration, tail size and frequency of courtship in guppies are all inherited via the Y chromosome (see above) suggests that programmes of selection to enhance these desirable traits will only be effective if applied to males.

Carotenoid-rich diets have been use to enhance colouration in ornamental species; for example, male flame-red dwarf gouramis fed such a diet for 12 weeks develop brighter red colouration than males fed standard diet and are preferred by females (Baron *et al* 2008). However, the effects are not always simple or predictable and there are differences in the effects of carotenoid supplementation among individuals of the same sex and species. This can be explained in terms of a trade-off between the use of these pigments in ornamentation and health (see above). Male

Siamese fighting fish with redder colouration, which are preferred over blue males by females seeking mates, respond to a carotenoid supplement by allocating the pigment both to improved immune response and to enhanced colouration. Bluer fish on the other hand do not become more red when given the same supplement, but instead invest the pigment in their own health, developing greatly enhanced immunocompetence. (Clotfelter *et al*. 2007).

### 10.6.4 Avoiding domestication

Where fish are reared in culture as part of a captive breeding programme aimed at supplementing or re-establishing endangered wild populations, it is important to ensure that cultured fish are capable of reproducing successfully after release. There is argument about the desirability of captive breeding programmes, as opposed to other methods for protecting endangered species, such as moving endangered populations to new habitats (Fraser 2008). Here we consider how knowledge of the reproductive behaviour of wild fish might improve the effectiveness of such programmes, should these be considered desirable. In principle, improvements can be achieved both by careful choice of breeding programme to avoid domestication selection and by designing rearing environments that allow the development of full and effective reproductive behaviour.

From the perspectives of conservation genetics, breeding programmes should avoid domestication selection and produce new generations of fish with an appropriate spectrum of genotypes (Fraser 2008). It is not clear whether programmes aimed at supplementing or re-establishing populations of endangered fish species should attempt to maximise genetic diversity or to generate genotypes that increase the fitness of individual fish (Grahn *et al*. 1998; Neff & Pitcher 2005). For example, the many breeding programmes aimed at augmenting natural populations of threatened salmonids typically use artificial fertilisation techniques designed to maximize genetic diversity and minimise any reduction in fitness due to mating of related individuals (inbreeding depression. O'Reilly & Doyle 2007). Similar principles are applied to marine fish reared for stock enhancement (Le Vay *et al*. 2007). The issues are complex, but where the task is to conserve small, highly endangered populations or to establish new populations, there are a number of benefits of such an approach, including helping to retain genes that can persist in the new environment and increasing the ability of very small endangered populations to evolve in the face of environmental change (Fraser 2008). However, in hatchery programmes designed to enhance or rehabilitate existing populations, it may be more appropriate to increase the fitness of individual fish by exposing parents to sexual selection rather than simply maximising overall genetic diversity. This includes allowing them to express their natural behaviour with respect to competition for and choice of mates, whether this is on the basis of good genes, perhaps for fast growth or disease resistance, or of compatible genes, perhaps in the major histocompatibility complex (Neff & Pitcher 2005 and see above).

Several quantitative genetic studies have examined the contribution of natural patterns of mate choice, among other traits, to individual fitness in endangered fish. For example, in one study, survival to hatching was measured in whitefish (*Coreogonus* spp.) derived from all possible crosses between 10 males and 10 females and reared in a standard environments. Quantitative genetic analysis showed that survival was significantly influenced by additive genetic variance (reflecting the action of good genes), by sire/dam interaction effects (reflecting the action of compatible genes) and by the maternal environment effects (reflecting the influence of variable egg nutrition). These accounted for 3.5%, 19% and 81% of the total variance in early mortality, respectively; the effects of natural mate choice in this context are therefore small compared to that of egg nutrition, but are still not trivial (Wedekind *et al*. 2001). A similar study in young Chinook salmon also showed significant additive effects (good genes), interaction effects (compatible genes) and maternal environmental effects on survival (Pitcher & Neff 2007). A simulation model based on these data suggests that allowing female Chinook salmon to select their mates for good genes and/or compatible genes can potentially increase the survival of their young by up to 19%. Mate choice can be incorporated into supportive breeding programs, for example by using natural mating channels, so generating offspring that have benefited from sexual selection on their parents (Berejikian *et al*, 2004). Such examples show how understanding the natural behaviour of fish can be used to promote both efficient reproduction and appropriate genetic diversity in fish that are cultured for conservation purposes.

### 10.6.5 Mitigating the effects of captive rearing

As discussed above, captive rearing is known to impair reproductive behaviour in some species of cultured fish. Where the aims of culture require fish to show natural reproductive behaviour, as for some ornamental fish and for fish bred in captivity for conservation purposes, it might therefore be appropriate to modify the physical or social environment to avoid development of abnormal

reproductive behaviour. That such modifications can be effective is shown by the fact that housing zebrafish with adults facilitates the development of courtship. This may be because adults provide stronger courtship-eliciting stimuli than do younger fish, so the developing fish get more opportunity to practice the actions used in courtship (Darrow & Harris 2004). However, to the best of our knowledge, systematic 'life skills training' for reproduction has not been attempted in cultured fish, in contrast to many such attempts for foraging and antipredator behaviour (Brown & Day 2002; Brown & Laland 2001; see Chapters 5–8).

## 10.7 SYNOPSIS

As a group, fish show striking variability between species, between populations of the same species and within a single population in many aspects of life history and reproductive biology. This variability includes differences in age at first reproduction, in the social context in which mating occurs, in the behaviour that accompanies spawning and in the nature and extent of parental care given to the young. The mechanisms that control the timing of breeding and the behaviour that fish show before, during and after spawning are necessarily complex, since these are complex processes. As far as reproductive behaviour is concerned, the interactions between male and female fish during mating depend on a variety of cues that provide information on the species, gender, reproductive status and quality of potential mates. The effects of such external stimuli depend on levels of the circulating hormones, particularly gonadal steroids, that control reproduction and reproductive behaviour in fish. The actions of these hormones during development and in adult fish generate not only gender differences in behaviour between males and females, but also differences between males that adopt different reproductive strategies. Reproductive behaviour, including the performance of courtship and the expression of mate choice, develops gradually in fish, through the interaction of genetic influences and environmental effects acting on various time scales. Because of the differential costs of producing eggs and sperm, the selective forces acting on males and females can be very different and this is reflected in many aspects of fish reproductive biology, from the timing of first reproduction to performance of complex courtship displays and parental care. The behaviour shown by breeding fish is shaped by the costs and benefits of the different options available to them, by trade-offs between such costs and benefits and by conflict between males and females, whose fitness is often maximised by different outcomes.

Providing fry in sufficient numbers and of sufficient quality at appropriate times is a recognised challenge for sustainable fish culture. To achieve this requires fish to be raised to an age and size at which they are reproductively competent and then to be held in conditions that allow full gonadal maturation, release of eggs and sperm and effective fertilisation. It also involves keeping the eggs in conditions that promote survival, development and hatching into healthy fry that can feed independently. Depending on the species, a number of problems have been identified at various points in the fry-production process. Some of these problems have their origin in the natural behaviour of the fish concerned and can potentially be solved by accommodating or manipulating such behaviour. Understanding how wild fish behave, the selection pressures that act on them, the complex behavioural and physiological mechanisms that are the result of such selection and the developmental processes that mould the behaviour of adult fish can play a part in improving the efficiency of fry production in established cultured species and in 'closing the circle' in new culture species.

The question of the potential environmental impacts of fish culture arises particularly acutely in the context of reproduction, concern focusing on the impact of cultured fish, whether escapees or released deliberately in supplementation programmes, on native populations of fish. The way in which cultured fish are bred dictates the extent to which sexual and natural selection are relaxed or distorted during fry production, the strength of domestication selection and hence the extent to which farmed fish differ genetically from their wild counterparts. In addition, whether or not introgression of the farmed into the wild genome occurs depends critically on the behaviour of farmed fish at natural spawning sites. Through dialogue between aquaculture, fish population ecology and conservation it is becoming increasingly clear that careful thought and planning is needed to ensure that the aims of fish culture are not in conflict with those of environmental protection and conservation of wild fish populations. Similar considerations apply when endangered species are being reared in captivity with a view to eventual reintroduction. In both cases, an understanding of the fundamental behavioural biology of fishes can help towards achieving the aims of fish culture.

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# 11
# Conclusions: Aquaculture and Behaviour

*Felicity Huntingford, Malcolm Jobling and Sunil Kadri*

**Abstract:** This chapter draws together the information presented earlier in the book. Firstly, the criteria that must be met if aquaculture is to be effective and sustainable are discussed and summarised. Second, the reader is reminded that cultured fish show a broadly similar repertoire of behaviour to that of their wild counterparts, in spite of striking differences between the conditions prevailing in fish farms and in nature. A general account is then given of the problems that can arise from the expression of natural behaviour by fish in production systems. Such problems may come from the mechanisms that control behaviour, from the way in which it develops and from the fact that behaviour is the product of natural selection favouring traits that promote Darwinian fitness. By the same token, solutions can be found to such problems based on an understanding of these different aspects of fish behaviour and these are exemplified with reference to examples given in Chapters 4–10. Up to this point, attention has been focused on aquaculture as currently practised, but the final section looks to the future, attempting to anticipate how fish culture might change. Likely developments include diversification of culture species, increased intensification of aquaculture systems, greater use of genetic technologies for stock improvement, increased emphasis on environmental protection and fish welfare and increasing overlap with commercial fisheries, through capture-based aquaculture, and with conservation, through recruitment enhancement. In each case, the part that behavioural biology might play in influencing such developments is discussed.

**Keywords:** captive rearing; commercial fisheries; conservation; diversification; domestication; environmental protection; intensification; molecular technology; selective breeding; sustainable aquaculture; welfare.

## 11.1 THE RELEVANCE OF BEHAVIOUR IN CURRENT AQUACULTURE SYSTEMS

### 11.1.1 Aquaculture and its aims

The culture of fish is important economically and socially; for example, nearly 50% of the fish produced for food is farmed rather than caught in the wild, providing direct employment for 16.7 million people worldwide, with a further 6.8 million indirectly employed (Food & Agriculture Organisation, FAO 2011). The ornamental fish industry overall is worth 15 billion dollars; over 90% of ornamental freshwater fish are captive bred and captive breeding programmes are being developed for an increasing number of marine species (FAO 2011). The use of fish in science is also increasing; for example, in the last 5 years the number of published studies on zebrafish (*Danio rerio*), sticklebacks (*Gasterosteus aculeatus*) and medaka (*Oryzias latipes*) has

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increased by 55%, 38% and 36% respectively (Web of Knowledge, http://www.isiwebofknowledge.com/); most of these studies have used fish cultured in the laboratory.

As discussed in Chapter 1, if aquaculture is to be sustainable, a number of criteria need to be met. Some of these criteria relate to efficient production; for example, cultured fish must survive, grow well and be in sufficiently good condition to fulfil the aims for which they were reared, whether this be for food, for release, for the ornamental trade or for science. Other criteria concern the impact of fish culture on the environment; considerations here include avoiding destruction of environmentally valuable habitats, reducing the release of waste into nearby waters, providing adequate feed without depleting the natural food supply of wild fish and avoiding adverse effects on wild populations through release of cultured fish, whether intentional or inadvertent. An additional criterion for sustainable fish culture concerns welfare, primarily of the fish being cultured, but also of the wild fish with which they may interact. Considerations for welfare of the cultured fish include avoiding the development of physical abnormalities, injury and disease, ensuring effective functioning of the physiological and behavioural systems that allow fish to respond to challenges and providing conditions in which fish can behave naturally. As explained in the introductory chapter, this book is predicated on the belief that achievement of all these criteria can be influenced by the ways in which fish behave when held in production systems.

### 11.1.2 The behaviour of fish in nature and in culture

The preceding chapters give an account of several aspects of fish behaviour, including how they move around their natural habitat, how they acquire and process food and how they interact with potential predators, rivals and mates. The behaviour of fish is rich and varied, based on a complex interplay between the stimuli that impinge on an individual and its internal state, modified through interaction between genetic and environmental influences and moulded by natural (and sexual) selection to promote individual Darwinian fitness. In all aspects of their behaviour, wild fish are variable, depending on species, on population, on life history stage and gender and on individual temperament or coping strategy.

Cultured fish often experience very unnatural environments, usually being held at high densities within a limited space, being protected from predators and being provided with food. The culture environment can influence how the fish behave within a single generation, through effects of captive rearing, and over successive generations, through the effects of domestication. Even so, farmed fish bring with them broad suites of behavioural traits that are similar to those seen in their wild counterparts. For example, cultured fish swim as wild fish do and respond in the same way to spatially differentiated cues, as when salmon in sea cages show diurnal vertical migration in response to changing light levels (Chapter 4). Farmed fish also feed in similar ways to wild conspecifics, using the same stimuli to detect food (Chapter 5), showing the same preferences for food with particular sensory and nutritional properties (Chapter 6) and showing the same patterns of appetite variation over time (Chapter 7). When threatened by a predator (real or perceived), cultured fish show species-typical evasive and protective behaviours, with associated physiological stress responses (Chapter 8). Additionally, since cage or tank-mates are rivals for potentially-limiting resources, cultured fish may fight, threatening and attacking each other using species typical behaviour patterns and sometimes injuring each other (Chapter 9). Also, the size and number of eggs produced by cultured fish and the mechanisms that control sex differentiation are broadly the same as those seen in their wild counterparts. The same is the case for patterns of behaviour shown during courtship and mating and the extent and nature of care given to the fertilised eggs and young (Chapter 10).

### 11.1.3 Problems in fish culture arising from the natural behaviour of fish

The behavioural traits that cultured fish bring with them from their wild ancestors can cause a variety of problems that compromise the aims of sustainable aquaculture; some examples of such problems are summarised here. The examples have been chosen to show how production, environmental protection and fish welfare can be compromised as a result of the mechanisms that control behaviour, the way in which behaviour develops and the fact that behaviour is the product of selective processes acting over evolutionary time.

#### *Effects of the external stimuli that control behaviour*

In some cases, problems may arise because cultured fish are exposed to relevant stimuli and show natural responses to them, but in an inappropriate context or in a way that has adverse effects. For example, the natural responses of Atlantic salmon (*Salmo salar*) to gradients of temperature and light can create a conflict when fish are held in sea cages and food is provided at the water surface. Such conditions can result in aggregations of fish that are sufficiently high to cause collisions and seriously deplete

oxygen concentrations (Johansson *et al*. 2006; Chapter 4). In other cases, problems arise because natural stimuli that are important in guiding fish behaviour are absent in culture systems, as when juvenile bluefin tuna (*Thunnus thynnus*), which do not see well in dim light, collide with tank or cage walls and injure themselves at the low light intensities that occur around dawn (Ishibashi *et al*. 2009; Masuma *et al*. 2001; Chapter 4). An additional example is seen in young guppies (*Poecilia reticulata*), which fail to forage efficiently on zooplankton when the light to which they are exposed lacks long wavelengths (White *et al*. 2005; Chapter 5). In situations where responses to stimuli produce inappropriate behaviour, or where appropriate stimuli are absent, production and welfare may be impaired through stress and injury. Such conditions may also result in increased release of waste material into the environment due to reduced efficiency of feeding and digestion.

### *Effects of the internal systems that control behaviour*

Some problems in aquaculture arise as a result of the activation of the systems that control behaviour in a context that is inappropriate for the farmer. For example, when fish are underfed, either accidentally or by design, this can result in increased aggression, with resulting fin damage (Dåmsgard *et al*. 1997; Chapters 7 and 9). Such effects have an impact on production and welfare. Other problems come about for the opposite reason, through the failure of fish to activate specific behaviours at times when this would be desirable for the farmer. For example, if feed is delivered at times when fish are not motivated to feed, or when they have been disturbed, the feed may not be eaten, reducing feed conversion efficiency and increasing the release of waste into the environment (Chapter 7). In a different context, if adult Nile tilapia (*Oreochromis niloticus*) are held without visual contact with conspecifics, the mechanisms by which social interactions stimulate gonad development are not activated, the fish display little courtship behaviour and there are few spawning events (Castro *et al*. 2009; Chapter 10).

### *Effects of ontogenetic changes in behaviour*

Many aspects of behaviour change as fish develop and grow. This can be seen clearly in the case of feeding, in which the kinds of food that fish eat often changes (for example, many species that are omnivorous or herbivorous as adults eat zooplankton when young), as does the size of food items and the amounts eaten (Chapters 5–7). Such changes in diet and in aspects of feeding behaviour are particularly dramatic when young fish move from one habitat to another with accompanying metamorphic changes in body structure. This is the case when planktonic larvae of marine species settle out of the water column onto the substratum or become associated with particular structured habitats and less dramatically when salmonid species undergo parr–smolt transformation (Chapters 4 and 10). Such times of rapid behavioural and morphological change place heavy demands on culture systems and often act as bottlenecks in the development of effective aquaculture systems for new species. Failure to provide young fish with the environment and food that they need during critical periods may, in addition to resulting in poor growth, ill health and mortality at the time, also have longer term adverse consequences through effects on the development of abnormal morphology and behaviour (Chapters 1 and 2).

### *Effects of genes on behaviour*

Natural inherited variability in behaviour exists within species, populations and families. For example, in Arctic charr (*Salvelinus alpinus*; Chapter 1) and Atlantic salmon (Chapters 3 and 9) poor competitors become subordinate, use space differently to dominant conspecifics and may fail to feed and grow. Such variation means that appropriate conditions for one sub-set of a cultured population may be different from those appropriate for others. This further complicates the job of providing fish with what is required for efficient production, good welfare and environmental protection. Acting over several generations, differential growth and survival of fish with different inherited phenotypes, including behavioural traits, can result in a process of domestication. One consequence is that the inherited behaviour of fish that have been cultured for several generations may be different from that of wild fish from the original founder population. This can be seen most clearly in the case of antipredator behaviour, which tends to be less well developed in farmed fish than in fish of wild origin (Chapter 8). For example, domesticated zebrafish (*Danio rerio*) show reduced shoaling, weaker startle responses and weaker suppression of feeding response under predation risk than do laboratory-reared undomesticated fish (Wright *et al*. 2006; Oswald & Robison 2008). As a second example, domesticated brown trout (*Salmo trutta*) are slower to react to a simulated predatory attack than are hatchery-reared wild fish (Petersson & Jarvi 2006). Such differences may improve the production and welfare of domesticated fish in aquaculture systems, where predatory attacks are rare, but are likely to result in poor survival and welfare of any fish that escape or are released into the wild. Such behavioural differences will also affect the extent to which farm escapees and released fish interact with wild populations.

***Effects of experience on behaviour***

All aspects of fish behaviour are influenced by environmental events, starting early and continuing throughout life. Such effects can be general, as when feeding influences growth and consequently vulnerability to predators, success in competition and age of maturation. At the other end of the spectrum, experience with particular types of prey may have more specific influences on both the structures and the behaviours used to capture the prey (Chapter 6). In terms of reproduction, early encounters with adults displaying particular colour patterns may influence later sexual preferences (Chapter 10). In some cases, behavioural flexibility shown by fish can make life easier for the fish farmer, since it means that fish can adapt to and perform well under a fairly wide range of conditions. However, when fish are reared for release, for the ornamental trade or for scientific purposes, behavioural deficits caused by captive rearing can compromise the effectiveness of the culture process. Thus deficits in foraging ability (Chapters 5 and 6) and in antipredator responses (Chapter 8) induced by captive rearing probably contribute to the poor survival of cultured fish when released into the wild. In addition to compromising the aims of aquaculture when fish are reared for release, starvation due to inefficient feeding and attack and injury by predators raise concerns for the welfare of released fish.

***Effects of the selective forces that have shaped fish behaviour***

In some senses, the adaptive adjustments that fish make to the costs and benefits of showing particular behaviour patterns contribute to their flexibility and hence potentially to the ease with which they can adapt to culture conditions. However, where the selective advantage of showing particular behaviour patterns is very strong, this can cause problems. For example, success in competition for resources such as food and mates is a major determinant of fitness for many kinds of animal. One consequence is that cultured fish will often fight over food, for example, even when plenty is available (Chapter 9). This can cause stress and injury, compromise production and welfare and increase the release of wastes into the environment through inefficient feeding and digestion. Other aspects of fish behaviour that have been subject to strong natural selection relate to reproduction. For example, natural courtship offers the opportunity for animals to choose mates with traits that are beneficial either for the courting animal or for its offspring. The preferences shown in this context have therefore been strongly moulded by selection. Sometimes fish will fail to breed if they do not encounter potential mates with attractive traits (Chapter 10) and even if they do breed, the relaxation of natural and sexual selection that occurs in cultured fish makes a major contribution to domestication selection.

### 11.1.4 Behavioural solutions to behavioural problems

The down side of the fact that cultured fish show behaviour that is broadly similar to that of wild fish is that expression of their natural behaviour in an aquaculture system can create problems for farmers, compromising production, welfare and/or environmental protection. On the other hand, understanding why fish behave as they do can often suggest solutions to problems encountered when holding fish in captivity. These may come through focusing efforts on fish whose behavioural traits suit them for culture, through developing suitable management and husbandry systems and through finding ways to mitigate the effects of domestication and captive rearing.

***Selecting behaviourally appropriate fish for culture***

The natural variability in behaviour that exists at the level of species, strains and individuals offers the potential for reducing problems in fish culture by rearing only fish whose behaviour makes them suitable for existence in production systems. For example, some species (whitefish, *Coregonus lavaretus*, as opposed to salmon and trout; Chapter 9) and some strains (pelagic feeding as opposed to benthic feeding Arctic charr; Chapters 5 and 9) are markedly less aggressive than others, so concentrating intensive food production on less aggressive species and strains might help to reduce the adverse consequences of aggression among farmed fish. At the individual level, fish with a proactive stress coping style (Chapters 8 and 9) seem to flourish better in intensive production than do those with a reactive coping style. Selective breeding for low stress responsiveness has been successfully applied in several fish species, although the fact that fish with weak stress responses tend to be more aggressive as well as less easily disturbed raises a new set of problems. An alternative to selective breeding is to develop indicators of stress-coping style that can be easily applied to large numbers of fish at an early stage in development; age at first feeding, which is earlier in aggressive, proactive fish (Höglund personal communication and Chapters 8 and 9), and number of melanophores in the skin (which is lower in proactive fish; Kittilsen *et al*. 2009; Chapter 3) are possible candidates.

***Developing behaviourally appropriate culture systems and husbandry practices***

Solutions to some problems in fish culture can come from having knowledge about the stimuli that elicit particular

behaviour patterns. Thus, visual and chemical stimulation have been used to make formulated feed attractive to cultured fish (Chapters 5 and 6). For example, larval gilthead seabream (*Sparus aurata*) eat artificial feed more readily when also exposed to visual and chemical cues from *Artemia*, and glass eels (*Anguilla anguilla*) eat more when amino acids that act as feeding stimulants are added to formulated feeds (Koven *et al*. 2001). As a second example, husbandry practices that result in fish taking on a darker colour, for example keeping them on a dark background, can reduce levels of aggression in some species (Höglund *et al*. 2002). Solutions can also come from knowing about and accommodating the internal processes that control behaviour. This is well illustrated by feeding systems that match feed delivery to fish appetite, taking fluctuations in motivation to feed into account, rather than feeding the fish according to a preset regime. Properly deployed, such feeders can increase growth and improve feed conversion efficiency, while reducing levels of aggression and variability in growth rates (Chapter 7).

Understanding how behaviour develops can also be put to use; for example, cannibalism is common among fish and poses a considerable problem in the culture of some species (Chapters 5 and 6). In the case of the summer flounder (*Paralichthys dentatus*), fish that metamorphose and settle out of the water column early gain a size advantage and feed on smaller conspecifics. Reduced salinity is one important cue determining the timing of metamorphosis; exposure to low-salinity water during late larval development synchronises settlement, reduces variability in developmental stage at settlement and cuts down on cannibalism in newly-settled and metamorphosed flounder (Gavlik & Specker 2004). Finally, knowledge of the way in which natural selection has shaped fish behaviour can contribute to the finding of solutions to behaviourally generated problems. For example, it is known that fish become less aggressive when the benefits of winning a contest are reduced. This is one reason why fish are less aggressive when fed on demand; feed is delivered as long as the fish are hungry, thereby removing the advantage of fighting for access to food (Chapter 9). Fish also become less aggressive when the costs of fighting are increased; for example, holding fish in flowing water increases the costs of fighting and makes them less aggressive (Chapters 1 and 9). It is known that fish will invest more in reproduction when the chances of gaining successful fertilisations are increased, which may be why offspring production in Mozambique tilapia (*Oreochromis mossambicus*) is increased by the provision of artificial nests (Bhujel 2000; Chapter 10).

***Mitigating the effects of domestication and captive rearing***

The success of operations aimed at culturing fish for the purpose of supplementing exploited or endangered wild populations depends, among other things, on released fish showing an appropriate range of behaviour for survival, growth and reproduction. Whether or not this is the case will depend both on the effects of captive rearing in any given generation and on the extent to which the fish concerned have been domesticated over successive generations. In general, domestication selection should be avoided in order to prevent disruption of the genetic structure of wild populations. Knowledge of how selection has moulded the reproductive behaviour of wild fish can help in this context. Thus, in hatchery programmes designed to enhance or rehabilitate populations, it may be appropriate to increase the fitness of individual fish by exposing the parental generation to sexual selection. This would include allowing the fish to express their natural behaviour with respect to competition for and choice of mates (Neff & Pitcher 2005; Chapter 10).

The effects of captive rearing on the development of specific behaviours can be mitigated by understanding how experience shapes behaviour both during early development and in later life. Based on knowledge of the general effects of stimulation in early life on development of a range of behavioural functions, young cod (*Gadus morhua*) were reared in hatchery tanks furnished with variable spatial cues and variable food; this made them flexible in their behaviour in a variety of contexts (Braithwaite & Salvanes 2005; Chapter 4). Knowledge of the specific effects of learning has formed the basis of programmes of 'life skills training' for cultured fish of various species. For example, predator-naive Arctic charr exposed to the odour of a piscivorous fish followed by an encounter with a predator become more responsive to the odour alone, especially if they have observed a trained conspecific respond to predator odour (Vilhunen *et al*. 2005; Chapter 8).

### 11.1.5 Behavioural solutions to non-behavioural problems

Besides offering solutions to problems in fish culture that are behavioural in origin, understanding how fish behave can also help to make general husbandry more efficient and welfare friendly in other ways. For example, the depth at which Atlantic salmon swim within a sea cage is related to appetite and so can be used in the control of demand feeding systems (Ferno *et al*. 1995; Chapters 4 and 7), while their natural response to light can be used to induce them to move away from areas where the risk of infection

by larval sea-lice is high (Hevrøy *et al*. 2003; Chapter 4). Olfactory stimuli such as amino acids or sex pheromones can be used to attract fish and induce them to move from one area to another without the need for handling (Lines & Frost 1999), conditioned responses to light cues can be used to move fish through sub-surface size grading grids (Fjæra & Skogesal 1993) and the tendency of rainbow trout (*Oncorhynchus mykiss*) to avoid water that is rich in carbon dioxide can be used to 'herd' fish to specific areas for harvest (Summerfelt *et al*. 2009; Chapter 4). As a final example, fish that escape from culture systems represent lost production and it may be possible to 'recall' such fish by training them to approach an acoustic signal for food (Tlusty *et al*. 2008; Chapters 4 and 5).

### 11.1.6 A disclaimer

Understanding the causes and consequences of fish behaviour can suggest ways of solving a number of the problems encountered in fish culture and in some cases these have been effectively deployed under working production conditions. However, behavioural approaches alone will not lead to solutions of all of the problems faced by aquaculture; behavioural science is just one of many disciplines that must be used in this context. In addition, even when behavioural solutions have proven successful in small-scale experiments or in pilot studies, scaling up to the level of working productions systems, often in harsh environments, presents additional challenges that may be extremely difficult to surmount. For example, the demand feeding technology produced by AQ1 Systems for use in commercial cages (Blyth *et al*. 1993) was initially conceived in 1989, but it took a further 6 years of research and development to deliver a working prototype for testing in commercial cages. Even when behavioural solutions can be applied effectively on working fish farms it may not be possible to get the economics right. For example, a simpler version of the AQ1 demand feeding system (the AQ2) was developed for use on Japanese Red sea bream (*Pagrus* sp.) farms. The feeding systems worked well in principle, but rapid rates of bio-fouling of the sensors in Japanese waters gave increased labour and maintenance costs, making the feeders uneconomical; this system has now been withdrawn from the market (Kadri, personal communication).

## 11.2 THE RELEVANCE OF BEHAVIOUR IN FUTURE AQUACULTURE SYSTEMS

### 11.2.1 Likely developments in aquaculture

There is little doubt that the cultivation of fish for various purposes will continue and probably expand in the future, but several aspects of aquaculture are likely to change (Le Francois *et al*. 2010). There is certain to be a diversification of cultured species. In addition, depending on purpose of culture and the species concerned, developing aquaculture systems will include increased use of technological solutions, including stock enhancement based on modern genetic technology and increased use of offshore and recirculation systems. There is also likely to be increased emphasis on environmental protection and fish welfare and a blurring of the distinction between aquaculture on the one hand and commercial fisheries and conservation on the other.

### 11.2.2 Diversification of cultured species

***Development***

There is likely to be increasing diversification of culture species, as a wider range of species are farmed for food, as more species are used as models in scientific research, as the need for conservation leads to increased captive rearing of ornamental species and as more species become candidates for restoration and captive rearing programmes.

***Role of behaviour***

The previous sections have discussed how knowing about the natural behaviour of fish can help in both understanding and solving some of the problems that arise when they are cultured. Fish are so variable that one cannot simply extrapolate what is known about one species to another, but what is already known can guide and facilitate the process of finding out about the behaviours of new species that may be being considered for cultivation. Further, having information about the behaviour of related species may help to guide rational choices between candidate species for culture. Ultimately, however, there is no substitute for direct study of the species concerned.

### 11.2.3 Intensification of technology-based aquaculture

***Developments***

In the context of rearing fish directly for human consumption, for some species there is likely to be a move towards more intensive, technology-dependent methods of culture, including land-based recirculating systems. These have the advantages of lower water demands and better control over wastes than open systems (Chapter 1). To the extent that stressors such as predatory attacks and poor water quality are avoided, they are also good for fish welfare. Land-based systems are currently used for holding brood stock and for the on-growing of some high value species such as sturgeon, turbot and halibut, as well as for the rearing of several species of ornamental fish. To be economically

viable for a wider range of species, it will be necessary to hold fish at increased densities and to maximise the use of the systems, both of which could potentially have a negative effect on welfare (Le Francois *et al*. 2010). In the future, there is also likely to be greater use of large offshore units. Use of such systems poses problems for effective husbandry and for monitoring fish status. Offshore systems of various types have been used for rearing Atlantic salmon, European seabass, sea bream, bluefin tuna, Atlantic cod, haddock, halibut, Pacific threadfin and cobia (Le Francois *et al*. 2010). In both recirculating and offshore systems, there are likely to be challenges related to the combating of disease outbreaks.

***Role of behaviour***

Intensive farming often requires handling of fish and may induce greater stresses than less intensive systems. For land-based recirculating systems, behavioural challenges include knowing how fish respond to lack of environmental variability and high densities, how they swim when held in such systems and the effects of swimming on water movements. Since frequent grading is needed for high through-put of fish cultured in recirculating systems, development and deployment of behaviourally based, hands-free grading systems would be advantageous. In the case of large offshore units, behavioural knowledge can help to solve operational difficulties related to feeding, monitoring and harvesting. For example, as described above, behaviour can be used as an indicator to operate automated feeding systems. Since altered behaviour is often an early indictor of adverse conditions, such as poor water quality and the onset of disease (Chapter 3), behavioural monitoring might provide useful indicators of fish condition and health status. This might include 'inspection stations'; areas in which cameras and other recording devices are located and to which fish are attracted on the basis of their responses to localised stimuli (Jeff Lines, Silsoe Research, personal communication).

### 11.2.4 Molecular technology and selective breeding

***Developments***

As more species are cultured, as the culture of fish for food becomes more intensive and technology-based and as the culture of fish becomes more important in conservation, there is likely to be increasing emphasis on stock improvement through selective breeding. Effective, targeted breeding requires a full understanding of quantitative genetics of desirable traits and selective breeding programmes are likely to be enhanced by the use of modern molecular technologies to identify genetic markers for such traits. This approach has already been used in aquaculture (Le Francois *et al*. 2010), especially in the context of disease resistance. For example, cross breeding studies, followed by quantitative trait analysis have been used to find gene loci associated with resistance to infectious pancreatic necrosis and this knowledge has then been used in broodstock selection (Houston *et al*. 2008, 2010). Molecular technologies may also be used eventually for genetic modification. To date, research has been concentrated on fish with growth hormone transgenes, but knowledge of the molecular genetics of the biochemical traits involved in nutrient biotransformations might eventually be used to engineer fish that can either process nutrients more efficiently or have changed nutritional requirements. Molecular technologies may also have reproductive applications, in the production of sterile fish and possibly for the generation of surrogate brood stock for endangered or particularly valuable species. Genome sequencing is underway for several farmed species, including channel catfish, Atlantic salmon, rainbow trout and Nile tilapia.

***Role of behaviour***

The use of genetic technologies in aquaculture to date has concentrated on morphological, physiological and life history traits, but in principle there is no reason why they should not be applied to morphological and physiological traits closely related to behaviour (stress responsiveness, for example; Massault *et al*. 2010) and for behavioural traits of importance (aggression, for example).

### 11.2.5 Increased emphasis on environmental protection and fish welfare

***Developments***

In the future, there is likely to be more emphasis on environmental protection; this will probably include increased focus on the immediate impact of fish culture systems on the environment, as well as pressure for use of sustainable feed resources and for mitigating the effects of farming operations and farm escapees on wild fish populations. Public anxiety about the welfare of cultured fish is unlikely to abate. In both cases, new regulations and legislation will probably be introduced and it is also expected that there will be an increase in the use of eco-labels and welfare-labels for cultured fish.

***Role of behaviour***

There is more to be learned about how the behaviour of cultured fish influences the amount of waste released from culture systems, whether this is the result of swimming patterns dispersing food and waste or stress responses

compromising food intake and feed conversion efficiency. Intensification of fish culture could raise problems in the form of increased risk of disease and here too fish behaviour will be important, since behaviour can influence the probability of disease transmission. This is especially the case because diseased animals may behave differently from healthy ones, sometimes in ways that promote disease transmission. Thus in the face of increasing disease risk, there will be greater need for information on movement patterns in healthy and diseased fish; such information can be included in epidemiological models and used to determine, for example, the placement of cages. There is likely to be increasing need for knowledge about how and why the behaviour of cultured fish may differ from the behaviour of their wild conspecifics, in order to understand and predict possible impacts of cultured fish on wild populations. In addition, behaviour can play a role in developing environmentally-friendly diets, through the use of food attractants to induce fish to eat feed formulated from novel ingredients that do not form part of the natural diet.

Given the uncertainty about the cognitive abilities of fish and the implications of these capacities for welfare, there is clearly a need for more fundamental behavioural research as part of an interdisciplinary programme aimed at a better understanding of what fish welfare is. There is also a need for both fundamental and applied information about what aspects of fish culture potentially compromise fish welfare. A behavioural component will be important here and is likely to include collection of information about how fish in production systems distribute themselves in relation to environmental conditions (using the technologies described in Chapter 3) and on the choices and compromises that they make in a spatially variable environment. Chapter 6 provided an example of how nutritional ecology can be used to explore dietary impacts on the environment and fish welfare (Ruohonen *et al*. 2007), showing that fish chose a diet that optimised their welfare with no regard to loss of wastes to the environment. This is a powerful approach that is likely to prove increasingly useful in the future.

On commercial farms, there is a need for simple but accurate methods for monitoring the welfare of the fish in culture systems (operational welfare indicators) and observations of behaviour have a special role to play here. It will be important to gather information about individual fish as well as the population as a whole, since decisions might have to be made about the extent to which a few individuals can be allowed to suffer poor welfare if the majority of fish are healthy and are performing well. When it comes to developing husbandry systems that mitigate the adverse effects of fish culture on welfare, there are already a number of behaviourally based techniques available or in the pipeline and more are likely to appear. For example, it has recently been shown that an initial negative response to an imposed stimulus (a flashing light) in farmed Atlantic salmon can be transformed into a positive response by paired association of the stimulus with food, switching the fish 'from fright to anticipation' (Bratland *et al*. 2010). Since ensuring good welfare is a key criterion for welfare-labelling, behavioural studies will be important in the establishment of such labels for new species.

### 11.2.6 Blurring distinction between aquaculture and commercial fisheries

***Developments***

Increasing interactions between aquaculture and commercial fisheries are likely in the future, as wild fish stocks continue to decline. In some areas and for some species, there may be a move towards less intensive culture systems, including various forms of ranching, partly in response to the need for diversification and environmental protection. These operations may include the increased use of fish aggregation devices, artificial reef structures and limited provisioning of wild stocks with food. Ranching and food provisioning may grade into various degrees of capture-based aquaculture, as in the case with tuna and some codfishes, which may be held alive after capture to allow gradual harvesting.

***Role of behaviour***

Actions that might be taken to improve welfare of cultured fish based on knowledge about their natural behaviour could potentially also be applied to commercial fisheries and related operations (Kaiser & Huntingford 2009; Huntingford & Kadri 2009; Metcalfe 2009). In the case of capture-based aquaculture, as when wild-caught cod are held in cages prior to slaughter without being fed, understanding of natural appetite patterns of the species concerned could help to predict adverse effects on welfare. Likewise, supplementary feeding of wild stocks could be made more efficient by using knowledge of the feeding behaviour of the fish concerned. In the case of ranching of fish, issues relating to the ownership of stock and of harvesting rights are likely to be (perhaps terminally) problematic, but knowing about the behaviour of the particular species concerned might help to solve some of the problems. For example, olfactory imprinting has been used to induce some salmonid species to return to release sites.

### 11.2.7 Increased emphasis on aquaculture in conservation programmes

***Developments***

We can also expect to see an increased interface between aquaculture and conservation, in the context of both supplementation and restoration programmes. At one extreme, depleted fish populations may be enhanced by temporary interventions at times of high natural mortality. For example, holding the larvae of coral reef fish in tanks for a week around the time of settlement, when they are very vulnerable to predation, improves survivorship by up to 36% (Heenan *et al*. 2009). At the other extreme, wild populations may be supplemented using programmes that involve combinations of captive rearing and targeted management. As described in Chapter 1, such programmes are controversial, not least because of effects on the fitness of wild fish (Araki *et al*. 2007), but they are widespread. For example, the State of Alaska began a programme of captive rearing and targeted management in about 1960 and from the late 1970s onwards, commercial catches increased and included significant numbers of cultured fish. For the year 2008, the Alaska Department of Fish and Game reported 146 million salmon to have been commercially harvested, of which 60 million, or 41%, were identified as ocean ranched (Alaska Department of Fish & Game 2011).

***Role of behaviour***

In the future, where captive breeding for release is deemed appropriate, avoiding the adverse effects of domestication on natural populations will be dependent on breeding programmes driven by knowledge of evolutionary biology, including quantitative and population genetics, and of conservation biology. An understanding of how sexual selection interacts with reproductive behaviour and mate choice, based on behavioural ecology, will also be useful in this context. Understanding how selection acts on behavioural variants as fish develop and grow is likely to be important, since this could be used to develop culture systems that allow fish with different inherited behavioural phenotypes to flourish. In addition, knowledge of how behaviour develops can help to mitigate the within-generation effects of captive rearing at high densities in impoverished environments. The previous chapters have given examples in which potential benefits of environmental enrichment and life skills training have been demonstrated under laboratory conditions. What is needed now is the development of methodologies that can be scaled-up to be effective, readily applicable and economically viable under commercial conditions.

We end this book with three examples offering hope that such methodologies could be established. The first concerns a seminatural incubation system for salmonid eggs in which eggs are buried in a layer of gravel with water flowing over its surface, each unit holding around 1000 eggs. Atlantic salmon fry emerging from such units are larger and heavier than those reared in conventional troughs, have considerably fewer deformities and survive better. They show similar temporal emergence patterns to those seen in wild fish and, on emergence, are better able to hold station against a current. Low initial costs of establishing the seminatural systems and lower labour costs compared to traditional systems, together with better egg survival and fry quality, mean that the new system is economically viable (Bamberger 2009). The second example shows that 'less is more' for cultured brown trout (*Salmo trutta*). Fish reared in standard tanks but at one third the standard culture density show less fin damage and undergo smoltification more successfully than those reared at standard densities. They also grow faster after release into the wild (Brockmark *et al*. 2007; Brockmark & Johnsson 2010).

The final example is provided by a study of the effects of environmental enrichment on the behaviour of cultured Atlantic salmon parr held at production densities (Rodewald *et al*. 2011). Experimental fish were the offspring of either wild salmon or hatchery-bred fish, raised either in standard or in enriched tanks; enriched tanks contained submerged shelters (black PVC plates placed on top of bricks) of two sizes and the water current varied in speed, depth and direction. All fish were fed standard pellets using automatic feeders, but in the enriched tanks the variable flow regimes produced unpredictable feed distribution patterns that may have mimicked the situation in the natural habitat of the fish. After about 30 weeks, the fish were transferred to a seminatural stream with a gravel substratum and natural prey. During the first 24 h, parr reared in the enriched tanks ate more natural prey (larval and adult insects) than did those reared in standard tanks, a trend that persisted to some extent over successive days. Interestingly, the effects were stronger for the offspring of wild fish compared to hatchery-reared fish from the same river system, indicating the potential impact of a few generations of captive rearing on fish behaviour. To the extent that the poor performance of cultured salmon on release is due to a reduced ability to feed effectively on natural prey (Olla *et al*. 1998), this study suggests that relatively simple, easily applied and cheap manipulations could potentially produce an improvement in the foraging efficiency, growth and hence survival, of newly released fish.

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