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# Fish Behavior 2

## *Ethophysiology*

**Jacques Bruslé**
**Jean-Pierre Quignard**



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# Contents

**Preface** . . . . . ix

**Introduction** . . . . . xi

**Chapter 1. Reproductive Behavior: Spawners** . . . . . 1

1.1. The preparatory phase of pre-spawning: the preliminaries . . . . . 5
1.1.1. Selection of sexual partners . . . . . 5
1.1.2. Seducers . . . . . 5
1.1.3. Courtiers . . . . . 18
1.1.4. Reversal of roles . . . . . 22
1.1.5. Forbidden love . . . . . 24
1.1.6. Spawning aggregations . . . . . 28
1.1.7. Practicing polygamy* . . . . . 31
1.1.8. Homosexuals . . . . . 33
1.1.9. Sexual disabilities . . . . . 34
1.1.10. More or less aberrant sexuality . . . . . 37
1.2. The phase of realization: couplings and spawning . . . . . 39
1.2.1. Alternative mating strategies . . . . . 39
1.2.2. Freely consensual couplings . . . . . 45
1.2.3. Harassers . . . . . 47
1.2.4. Violent couplings . . . . . 49
1.2.5. Hybrids . . . . . 53
1.2.6. Fleeting loves . . . . . 56
1.2.7. Discreet love . . . . . 57
1.2.8. Cuckolds and cuckolders . . . . . 58
1.2.9. Hermaphrodites . . . . . 59
1.2.10. Transsexuals . . . . . 61
1.2.11. Unisex populations . . . . . 67

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1.2.12. Fatherless fish by parthenogenesis . . . . . 68
1.2.13. Posthumous paternity . . . . . 70

**Chapter 2. Reproductive Behavior: Parents** . . . . . 73

2.1. The post-spawning phase: the future of the offspring . . . . . 73
2.1.1. Nest builders . . . . . 73
2.1.2. Incubating clutches in the mouth . . . . . 85
2.1.3. Deserters . . . . . 88
2.1.4. Gestation . . . . . 90
2.2. Parental care . . . . . 96
2.2.1. Providing parental care . . . . . 96
2.2.2. Having good parents . . . . . 107
2.2.3. Larval recruitment . . . . . 113
2.2.4. Metamorphoses . . . . . 116
2.2.5. Miniaturized fish . . . . . 118

**Chapter 3. Remarkable Capabilities** . . . . . 119

3.1. Aces of ballistics . . . . . 119
3.1.1. Stronger than William Tell? . . . . . 119
3.1.2. Using a stream of water to hunt . . . . . 120
3.2. Possession of a black box . . . . . 120
3.2.1. An inviolable personal identity card . . . . . 120
3.2.2. Traveling leaves traces, like a real passport . . . . . 121
3.2.3. A birth certificate . . . . . 122
3.2.4. Proof of diet . . . . . 122
3.2.5. Belonging to a stock . . . . . 123
3.2.6. Parasites used as biological markers . . . . . 124
3.3. Using tools . . . . . 124
3.3.1. A form of intelligence from which fish are not excluded . . . . . 124
3.3.2. Using an anvil . . . . . 125
3.3.3. Capabilities related to the size of their brains? . . . . . 125
3.4. Capacity to play . . . . . 126
3.4.1. Expression of a certain well-being . . . . . 126
3.4.2. A toy in an aquarium . . . . . 126
3.5. Artists . . . . . 127
3.6. Counting . . . . . 128
3.6.1. Quantitative knowledge of their environment . . . . . 128
3.6.2. Innate quantitative knowledge which is perfected . . . . . 130
3.6.3. Clever fish . . . . . 130
3.6.4. Inter-individual variability . . . . . 131
3.7. Having a personality . . . . . 132

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3.7.1. Not all fish are identical . . . 132
3.7.2. Individual and inter-sexual differences . . . 132
3.7.3. Customized food preferences . . . 134
3.7.4. Differences in risk-taking . . . 134
3.7.5. Personality changes related to age and parental life . . . 136
3.7.6. Personality traits varying according to environmental factors . . . 136
3.7.7. Differences in migratory behavior . . . 137
3.7.8. Personalized mutual relations . . . 137
3.7.9. Complex motivations . . . 138
3.7.10. Different brain potential . . . 138
3.7.11. Higher metabolic potential . . . 139
3.7.12. Influence of the genome . . . 140
3.7.13. Early expression of personality . . . 140
3.7.14. Social influence . . . 141
3.8. Disguise . . . 142
3.8.1. Offensive mimicry for feeding . . . 142
3.8.2. Offensive mimicry for reproductive purposes . . . 143
3.8.3. Defensive mimicry . . . 145
3.8.4. A dual strategy, both offensive and defensive . . . 146
3.8.5. Deceiving one's sex partner: the height of dishonesty? . . . 146
3.8.6. Fooling rivals . . . 148
3.8.7. Counter-adaptation to flush out cheaters . . . 148
3.8.8. Fooling customers . . . 149
3.9. Having a very precise biological clock . . . 150
3.9.1. The day–night "circadian" cycle . . . 150
3.9.2. The lunar or semi-lunar cycle of tides or tidal rhythm* . . . 152
3.9.3. Fish showing original qualities . . . 155
3.9.4. Additional role of melatonin in health and fitness . . . 155

**Chapter 4. Neurological and Neuroendocrine Conditioning Requirements** 157

4.1. Experience of stress and suffering . . . 157
4.1.1. Sensitivity to stress . . . 157
4.1.2. Actual suffering? . . . 159
4.1.3. Neuropsychological data compared and a mental construct of pain in fish 160
4.1.4. Safeguarding well-being . . . 161
4.2. A question asked about their period of inactivity: are they able to sleep? . . . 163
4.2.1. Do fish really sleep? . . . 163
4.2.2. Experimental sleep deprivation generating anomalies in cognitive performance . . . 164
4.2.3. Insomniac populations . . . 164
4.3. The complexity of their brains: their cognitive abilities . . . 165

Downloaded From Vet-eBooks.com

4.3.2. Physiological basis of stress common to all vertebrates . . . . . 168
4.3.3. Memorization skills . . . . . 169
4.3.4. Brain differences between the two sexes . . . . . 169
4.3.5. Brain differences related to the physical and social environment . . . . . 171
4.3.6. Brain activity stimulated during the reproductive period . . . . . 173
4.3.7. Morpho-anatomo-physiological lateralization . . . . . 174
4.3.8. Lateralization of the brain . . . . . 176
4.3.9. Differences between selachians and teleosts . . . . . 179
4.3.10. Cerebral sexual dimorphism . . . . . 180
4.3.11. Forms of training . . . . . 180
4.3.12. Really intelligent fish? . . . . . 181
4.3.13. Remarkable cognitive skills in sharks . . . . . 183
4.3.14. Fish as victims of optical illusions . . . . . 184
4.3.15. Recognition of human faces . . . . . 184
4.3.16. Sensitivity to music . . . . . 186
4.3.17. Active embryonic and/or larval ontogenesis* or neurogenesis . . . . . 187
4.3.18. The certain existence of collective intelligence . . . . . 187

**Conclusion** . . . . . 189

**Glossary** . . . . . 193

**Species Index** . . . . . 217

**Summary of Volume 1** . . . . . 223

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# Preface

Fish, our distant cousins, are able to perform a considerable number of daily tasks to survive, having conquered all aquatic environments, in all climates and at all latitudes and depths.

They are the vertebrates most widely used by humans: fisheries exploit stocks of wild fish populations and carry out intensive fish farming, making fish, in number and mass, the most consumed of all vertebrates. They also occupy an important place in aquariology and are used as experimental models in scientific research (second only to mice). However, the general public's perception remains limited, particularly with regard to their sensitivity, "well-being" and cognitive abilities. Contemporary ichthyologists have a fairly high level of scientific information that can shed new light on the actual behavioral potential of fish.

Observations of animal behavior have long focused on species that are familiar to us and considered worthy of interest, such as birds (parrots, titmice, swallows or wild geese) and, in particular, mammals, especially those to whom we are most closely related (gorillas, chimpanzees, bonobos, etc.) or who live near us (horses) or in our homes (cats and dogs). The enthusiasm they inspire justifies the success of circuses and zoos. Fish, although they arouse a certain curiosity, especially among anglers and aquarists, rarely receive the attention they deserve, being reduced to the unflattering status of "inferior vertebrates", beings who seem devoid of language, memory and apparent sensitivity. It is an unflattering and erroneous public perception, linked to the fact that we communicate little with them, separated as we are by such distinct natural environments.

Scientists, through observations and experiments published in credible international journals and from whom the authors of this book take their inspiration, bear witness to the surprising abilities of fish. Abilities that are not so far removed

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from those of other vertebrates, and even humans with similar characteristics because they are derived and inherited from these "fish ancestors".

This book consists of two volumes that provide data of 630 species cited, originating from more than 1,500 bibliographical references. It provides new information on recent achievements in the field of ichthyology. These data reveal that our distant cousins are well endowed with cognitive abilities and a potential for memorization and innovation that explains their remarkable capacity to adapt to often difficult environments.

"Ordinary" fish are capable of doing extraordinary things. Some of them are not only great travelers able to orient themselves using the sun and navigate through terrestrial geomagnetism, but are also capable of adopting sophisticated behaviors. Some are subtle hunters or breeders who call upon collective strategies, clever architects and builders of complex nests designed to protect their eggs, courageous fighters willing to sacrifice their lives to defend their offspring and cooperative beings united with a shared goal or producing descendants. Some are even talented imitators anxious to perhaps deceive their partners or predators, Machiavellian strategists, clever courtiers, flamboyant seducers and great lovers. They also demonstrate memory and calculation skills, and the ability to play, use tools and even indulge in artistic creation. Finally, they can sometimes even be good models that can inspire advances in technology and human health.

Jacques BRUSLÉ
Jean-Pierre QUIGNARD
January 2020

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# Introduction

Those of you who are interested in the natural world and are curious to better understand animal behavior, in all its capacity to surprise and be misunderstood, will probably be satisfied to be able, thanks to this book, to learn what fish really are. They deserve much better than their current, hardly flattering, status as "inferior vertebrates".

Advancing knowledge in the field of fish ethology requires abundant scientific literature consisting of numerous publications in international journals that constantly provide new data to contribute to enriching our view of the behavior of these "conquerors of the aquatic world", who are rich in their biodiversity and never cease to amaze us.

The authors of this book, academics who have devoted their careers to icthyological studies, have made extensive use of the most recent data in order to present a broad overview of the knowledge acquired in the field of behavior related to fish feeding, protection, social interrelationships and reproduction. This is based on the most representative and original examples cited among the 30,000 species currently listed, but only a few of them have given rise to field observations and laboratory experiments. Recent technological advances in human penetration of the underwater world (submarines, bathyscaphes, etc.) and *in situ* observation of fish (video cameras, acoustic markers, satellite telemetry, etc.), as well as laboratory data (samples, video images, etc.), have led to the development of new technologies. Those acquired through the use of advanced technologies applied to fish (radioactive isotopes, magnetic resonance, genetic sequencing, etc.) have greatly contributed to providing a modern perspective on their remarkable strategies and surprising behaviors.

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The considerable progress made in the field of neurophysiology, as regards their sensory perception, communication, memory, innovation and so on, suggests that they are so sensitive to stress and pain that they deserve to be treated with more care than they usually are. Their need for "well-being" is as important as ours or that of our cats and dogs.

## Acknowledgments

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# 1

# Reproductive Behavior: Spawners

Fish respond to their "reproductive duty" and their reproductive needs by adopting a large diversity of adaptive behaviors in relation to constraints exerted by environmental conditions. In fact, acts of reproduction are highly variable in time: in terms of duration and position in the annual cycle, they spread over a whole year in hot regions or thermally stable regions such as the abysses, reduce to a single season in temperate and cold regions, and are more often limited to a few months or sometimes even reduced to a few days. They also vary greatly in space: in the same area as their habitats or in more or less distant habitats, which require reproductive migration. These behaviors differ from one family to another and from one species to another. Fish have shown remarkable inventiveness in succeeding in what constitutes an essential part of their existence: to mate and produce quality offspring with an optimum survival.

It should be noted that, among the initial phases of fish reproduction, those of emission, control and management of gametes show a great diversity of original behaviors. Potential fertility rates are strongly variable: there are 300 million oocytes in the female of the ocean sunfish *Mola mola*, while there are only 3,000–4,000 oocytes in the common goby *Pomatoschistus microps*. Knowing that their respective masses are 1 tonne and 2 g, the reproductive effort is thus 1,500–2,000 oocytes per unit of mass (gram) in the former and 2,000 oocytes/g in the latter. In comparison, males are generally very productive in gametes: 27 billion sperm per milliliter of semen in the pike *Esox lucius*. Such gametic production is justified by the fact that the aquatic environment is a great "devourer" of sexual cells, and subsequently eggs, due to the rapid dilution of sexual cells which reduces their chances of being fertilized, their high mortality due to osmotic shock, in both fresh and salt water, as well as predation by various species of oophagous predators. As a result, very few of these gametes (approximately 0.001–0.01%) will give birth to a new generation.

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Two major strategies of bisexual reproduction are often seen: one is based on a "numbers effect" and anonymity of spawners, which is at the mercy of chance for the meeting of gametes and the survival of clutches, and the other is a "quality effect" and personalization of gametes based on sexual selection, which is supposed to operate for the benefit of the "best", in order to ensure optimal reproductive success.

It is the "populational" strategy based on the vagaries of the encounter of gametes within an anonymous "spermato–oocyte cloud" that is practiced by the sardine *Sardina pilchardus* and the Atlantic bluefin tuna *Thunnus thynnus*, among which the concept of "filiation" does not apply (fish born to an unknown father and mother). However, despite the fact that this "spawning in open water" results in a considerable waste of gametes, and then of eggs, it shows itself to be rather successful if we are to judge by the number of the species concerned and the density of the schools of pelagic fish ("blue fish") that successfully practice this.

In contrast, the strategy of forming couples tends to aim at a certain "personalization" of spawners who "select" each other based on their own supposed qualities of "best partners" who are able to offer "the best genes", conditions for the best perspectives for reproductive success. However, such a "safe" management of gametes, although ideal in principle, is subject to various vagaries linked to the intervention of sneakers* who practice "parasite fertilization" (Volume 2, section 1.2.1), to the cases of coercive couplings (Volume 2, sections 1.2.3 and 1.2.4) or to the errors of judgment by partners whose couplings are harmful at the level of genetics and/or immune systems (consanguineous matings and hybridizations which are considered to be "genetic pollution" (Volume 2, section 1.1.5)).

Original variants of sexuality involve hermaphroditic species* (Volume 2, section 1.2.9): either synchronous hermaphrodism as in the painted comber *Serranus* or successive hermaphrodism, protandrous* as in the gilthead bream *Sparus aurata*, protogynous* as in the Nassau grouper *Epinephelus striatus*, and species whose sex change is reversible as in the dwarf hawkfish *Cirrhiticthys falco* (Volume 2, section 1.2.10) and species which practice parthenogenesis* (Volume 2, section 1.2.12), gynogenesis* as in the Prussian carp *Carassius gibelio* (Volume 2, section 1.2.12) and exceptionally androgenesis* as in the spiny dogfish *Squalius acanthias* (Volume 2, section 1.2.12). All these, often very subtle, variations of gametic production and fertilization reveal a certain "inventiveness", which is not only anatomical but also physiological and behavioral.

One form of "progress" for reducing gametic waste concerns the tactics of oocyte immobilization: for females, this consists of setting their oocytes on a rocky substrate rather than dispersing them in open water (such as the ruffe

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(such as the brown trout *Salmo trutta*) and fastening them onto vegetal supports (such as the big-scale sand smelt *Atherina boyeri*). For the males of these different species, this consists of "spreading at random" their semen in the immediate vicinity of clutches, where the waste of sperm is less costly in energy than oocyte production. In all these cases, the spawners abandon their eggs and then their larvae.

An additional step in securing gametes and then eggs and larvae consists of the building of nests by males (Volume 2, section 2.1.1), which leads to a cavitary containment of gametes and the provision of parental care by both partners of the couple or by the males only (Volume 2, section 2.2.1). The "ultimate" search for gametic and embryonic protection is reached with incubation in the mouth such as that practiced by the cardinal fish *Apogon* sp. (Volume 2, section 2.1.2) and especially with gestation in incubator pouches, as in male seahorses *Hippocampus* sp. (Volume 2, section 2.1.4) and in the genital tracts of females, as among elasmobranchs and various teleosts (Volume 2, section 2.1.4). Hydroclimatic vagaries and threats of predation are reduced to the extent that parental investment is increased. If females are more invested in these "conservational" concerns and if "maternal effects" are often considered significant (Volume 2, section 2.2.1), males are often effectively involved in the achievement of optimal conditions of survival of gametes, eggs and subsequently larvae, and "paternal effects" are far from negligible (Volume 2, section 2.2.1).

Thus, if many species adopt populational strategies, reproductive strategies of fish may also reach a high level of "personalization" associated with a common concern for reducing gametic waste and sometimes larvae (viviparity), which reflects the fact that nature has explored, at all times and in all places, the various "pathways" which have been available to ensure the diverse reproductive successes of fish.

Bibliography: *Acad.Sci.Lett.Montpellier*, 2018, **49**: 12 pp, *J.Fish Biol.*, 2006, **69**: 1-27.

This "mating" period includes a number of successive steps under neuroendocrine control that are correlated with environmental factors: the lunar cycle, the solar cycle, water levels, tidal movements, thermal and haline variations.

The reproductive act may be unique in the life of the fish (semelparity*[1]), as in short-lived fish such as the sand goby *Pomatoschistus minutus*, and also among long-lived species such as the eels *Anguilla anguilla* and *A. rostrata.* In contrast, among long-lived species such as the carp *Cyprinus carpio*, the act of egg-laying

1 Terms with an asterisk are defined in the Glossary at the end of the book.

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may be repeated several times during the course of their life (iteroparity*), such as for most species, whether they are freshwater or marine.

The reproductive scenario can be broadly divided into four major phases:

1) an anticipatory phase during which, in reproductive migration, the population of mature age moves from its feeding habitat to spawning grounds. These zones are hydrologically favorable: in terms of temperature, salinity, quality of substrates, quantity of potential food. Other factors may also intervene, so the list is indefinite: for example, the protection and development of clutches, and then of larvae, to ensure greater reproductive success. In contrast, some particularly far-sighted species build spawning nests to host their offspring before even going in search of mating partners;

2) a preparatory or *pre-spawning* phase which features the end of gonadal maturation and selection of sexual partners, appealing to seduction and/or force;

3) a phase of realization or *spawning* and fertilization during a more or less intimate encounter of the two sexes and which gives rise to a coupling, with or without copulation, and a mixture of their respective gametes, followed by fertilization with the ejaculation of males and ovulation of females. Fertilization may be extracorporeal in open water or intracorporeal in the genital tract of the female (oviparity*, viviparity) or in the marsupium* of the male (paraviviparity);

4) a terminal or *postspawning* phase which relates to the fate of fertilized oocytes, then the eggs and then the larvae that may develop in open water, in the genital tracts of females and in other body cavities (mouth, gill chamber, marsupium of male syngnathids, etc.), or in nests that are sometimes subject to parental care intended to promote the survival of the offspring. They may also entrust custody to other animals (mollusks, crustaceans, ascidians, etc.). Most spawners abandon their offspring and return to their feeding habitats, and sometimes even die. Others remain at the spawning site and provide parental care to their offspring.

The search for sexual partners, the success of couplings, the production of eggs and larvae and subsequently their protection thus constitute the major tasks. These tasks depend on the development of behaviors, often elaborate and generally complex, intended to enable the greatest reproductive success, both qualitative and quantitative.

Reproductive migrations (Volume 1, section 2.2) involve movements of spawners of varied magnitude and variable duration according to the species. They are particularly large among amphihaline* fish such as the Atlantic salmon of the *Salmo* and the Pacific salmon of the genus *Oncorhynchus*, the brown trout *Salmo trutta*, the lamprey of the genus *Petromyzon*, the sturgeon *Acipenser* sp., the

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time and determined in space, have not ceased to impress observers. They also concern marine species such as tuna, sharks, etc. whose holobiotic* movements, although apparently less spectacular, are no less important. After spawning, the migration of spawners on an outbound journey is followed or not by return migration.

The foresighted behaviors of spawners concerned with the survival of their offspring have led some species, especially freshwater species such as sticklebacks *Gasterosteus* sp. as well as marine species such as the wrasses, to build laying nests (Volume 1, section 2.2.2.1) before even mating and proceeding to the act. Such nests are often a determining factor in the behavior of females who are led to choose a partner (Volume 1, section 3.7; Volume 2, section 1.1.1).

## 1.1. The preparatory phase of pre-spawning: the preliminaries

### *Selection of sexual partners*

The behaviors conditioned by the exchanges of communication signals (visual, olfactory, auditory, tasting and/or electric) have been discussed in Chapter 3 of Volume 1.

### *Seducers*

#### 1.1.2.1. *The requirements of sexual selection*

The choice of sexual partners by females, in the framework of strict sexual selection (Volume 1, section 3.7), forces males to adopt forms, display colors and practice behaviors which are as ostentatious and spectacular as possible in order to attract their attention and earn their favors. They must often "make themselves beautiful" for a chance to please the females. Thus, these males adopt colorful patterns, which is considered as secondary sexual characteristics controlled by the *androgenic hormone 11-KT*, in contrast to females who, in general, only display drab grayish or brownish color patterns which make them less detectable by predators. Various ornamentations are thus exhibited by males under the gaze of females whose visual acuity is such that they are able to recognize the best among

Bibliography: *J.Fish Biol.*, 2006, 68: 1636-1661, *Mar.Ecol.Prog.Ser.*, 2014, **514**: 207-215 & DOI:10.3354./meps11032

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### 1.1.2.2. *A wide range of colorful patterns*

During reproductive periods, the vivid and even flamboyant colors of males are an ornamentation with the value of a sexual signal of recognition. They reflect a quality that is required by females who tend to choose the more colorful of their suitors judged to be, *a priori*, the best bearers of good genes which their descendants will inherit.

Teleosts have several types of pigment cells: chromatophores* (melanophores*, erythrophores, xanthophores, cyanophores, leucophores, iridophores, etc.) present in their skin (epidermis, dermis) and containing a variety of colored pigments (*melanin*, *carotenoids** such as *astaxanthin*, *canthaxanthin*, *zeaxanthine* and *β-carotene*), *pteridines* (*pterins* or *flavins*) or reflective crystals of *purine*. The carotenoid pigments* involved in red, orange and yellow colorations, pigments which are not synthesized *de novo* but derived from their algal diet, possess antioxidant and immunostimulatory properties which play a protective role in cells and tissues. The other pigments – the *melanins* responsible for black, brown and gray colorations, *pterins* inducing red, orange and yellow colorations – also have antioxidant functions and contribute to the fish's immune defenses.

*Carotenoids** and *melanins* are the most commonly found pigments in the coloration of fish, the former acting as indicators of the physical condition of their owner in direct relation to its feeding activity, while the latter has an indicator value for the dominant–subordinate social status. These chromatophores* have the ability to alter the concentration or the spread of their intracellular colored pigments in cells possessing contractile dendrites*, in order to modify the intensity of certain colors under hormonal control: *adreno-adrenocorticotropic hormone* (*ACTH*) and *-melanocyte-stimulating hormone* (*α-MSH*).

Bibliography: *Anim.Behav.*, 2005, **69**: 757-764 & OI:10.1016/j.anbehav.2004.06.022

#### 1.1.2.2.1. Red

The males of the minnow *Phoxinus phoxinus* present vivid and spectacular abdominal red colors, corresponding to a concentration of carotenoid pigments* which constitute honest signals of high quality: best fitness*, greater vigor and better swimming performance. Reproductive success is achieved by the most strongly colorful individuals that are free of parasitic infestations by the nematod *Philometra* , which cause fading of the color pattern due to a decrease in the level of carotenoids*. It is also achieved by those who are bearers of reproductive tubercles which diffuse encouraging olfactory cues for females who have previously acquired a certain olfactory experience.

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The males of the threespine stickleback *Gasterosteus aculeatus* also exhibit, under the gaze of the females, a nuptial color pattern in the form of flamboyant red colors linked to carotenoid pigments* (*astaxanthin*, *β-carotene*) originating in their food (gammarids). *β-Carotene* accumulates in the skin of the chin and the sides during the spring, in order to reach its maximum concentration at the beginning of the reproductive period, in April–May. This is precisely the time where the retinas of females, the opsin of their retinal* cones*, are the most sensitive to red radiation, which enables them to select the most richly colored males. A phenotypic plasticity in the expression of retinal opsin* enables a remarkable visual adaptation to different conditions of brightness: the clear or colored waters of lakes constitute a visual background. These males, which are rich in carotenoids* with antioxidant properties, have strong capabilities for fertilizing oocytes and thus show high rates of reproduction. This color shows seasonal variations, which is highest at the beginning of the breeding season (spring–summer) and then reduces quickly as soon as the mating ends when males become guardians of nests (Volume 2, section 2.2.1) and are no longer concerned with pleasing. In Alaska, guardianship of nests and protection of clutches against groups of cannibals have such a high energy cost that the intensity of coloration decreases over time. It should be noted that these males may "fade" if they are parasitized by the cestode *Schistocephalus solidus*, with the color of their eyes then becoming the object for determining the choice of females.

The males of the guppy *Poecilia reticulata* use the same type of color signals to temporarily display themselves before the eyes of females. The orange-red color is the most common feature used by the males of a large number of species, associated with black areas of *melanin* and iridescent reflections. Present in most of the world populations of this small poeciliid, it has been judged universal. Such carotenoid pigments* (*β-carotene*) find their origin in microalgae such as *Dunaliella* sp., in which they represent more than 10% of dry mass and are consumed by these males. Those who have the largest feeding activity show the most intense color patterns. These pigments that have antioxidant properties that are capable of reducing oxidative stress by neutralizing *free radicals** confer on these spawners a health value which is very much appreciated by females. The latter thus give to the world a progeny made of a greater number of males than females (85♂ vs. 45♀); these dominant males are therefore as beautiful and as seductive as their fathers.

Red ornamentation, by far the most widespread, not only provides males with chances of success in love, but also increases their risk of predation, because predators do not fail to recognize the sign of a good meal in the good health of these males. Hence, when predators are present in their habitat, these males reduce the intensity of their coloring.

Females of the guppy are more sensitive to the size of the orange-colored area

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spot produce abundant and high quality sperm (in terms of swim speed and longevity), indicating a fine progeny. The quality of the sperm is determined by the richness of the food in *polyunsaturated fatty acids* (*PUFAs*) and *carotenoids**. Some male guppies experience high reproductive success that can be measured by the number of genetically identifiable descendants. Various characteristics other than color and size, for example, explain the multiple paternities of these beautiful males. The colors of male guppies can give rise to a wide polychromatism ranging from drab color patterns comparable to those of females to brilliant red, blue, yellow, etc., often accompanied by transverse black bands which accentuate the contrasts and mark out shapes of original colors among *Poecilia immaculata* and *P. parae* in Guiana. These colors, which play an important role in sexual selection, enable increases in the biodiversity of various progenies. More common colors are less valued and new chromatic combinations resulting from mutations and crossings provide greater reproductive success. Various predation pressures exerted by sympatric* predators select survivors who are likely to be all the rarer, the more strongly colored, and therefore optically identifiable, they are. Thus guppies, originating in Trinidad in Central America and widely introduced to natural waters around the world, have given rise to diversified populations, characterized by a large polymorphism of colors in males: red, orange and yellow color patterns due to carotenoids*, with black spots of melanin and reflections which are more or less iridescent under UV light, which explains their considerable success in aquaria.

The red nuptial color pattern of male bitterlings *Rhodeus amarus* is a signal of quality for the benefit of females, since the intensity of this coloration relates to large testes and the production of a large number of sperm. Such spermatic potential is an important criterion which is very useful for females who fear seeing their oocytes poorly fertilized by a partner subject to a limitation of sperm or, worse, possible infertility. A fertile male is a strong guarantee of greater reproductive success for a female who is always anxious to produce beautiful descendants. The male of the dwarf gourami *Trichogaster lalius* (formerly *Colisa lalia*), an osphronemid, is distinguished by an ornamentation of bright red color based on a diet rich in astaxanthin, a synthetic carotenoid* pigment used in aquaria.

Note that the color red is considered to be sexually very attractive in very many animal species as well as among the human species (see *The Woman in Red*, Gene Wilder, 1984).

Bibliography: *Anim.Behav.,* 2008, **75**: 1041-1051 & DOI:10.1016/j.anbehav. 2007.08.014, 2009, **77**: 1187-1194 & DOI:10.1016/j.anbehav.2008.12.032, *Behav.,* 2007, **144**: 101-113, 2011, **148**: 909-925 & DOI:10.1163/000579511X584104, *Biol.Lett.,* 2007, **3**: 353-356 & DOI:10.1098/rsbl.2007.0072, 2010, **6**: 191-193 & DOI:10.1098/rsbl.2009.0815, *Ecol.Freshwat.Fish*, 2008, **17**: 292-302 & DOI:10.1111/j.16000-0633.2007.00279.x, *Env.Biol.Fish,* 2014, **97**: 209-215, *Ethol.,*

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& DOI:10.1111/eth.12102, *Evol.Ecol.,* 2007, **21**: 601-611 & DOI:10.1007/s10682-006-9138-4, *J.Compilation Eur.Soc.Evol.Biol.,* 2006, **19**: 1595-1602 & DOI:10.1111/j.1420-9101.2006.01117.x, *J.Exp.Biol*., 2013, **216**: 656-667 & DOI:10.1042/jeb.078840, *J.Fish Biol*., 2007, **70**: 165-177 & DOI:10.1111/j.1095-8649.2006.01292.x, 2015, **86**: 1638-1642 & DOI:10.1111/jfb.12661, *Zool.Sci*., 2007, **24**: 571-576 & DOI:10.2108/zsj.24.571

#### 1.1.2.2.2. Blue

During the 1980s in Japan, as a result of mutations, males of the guppy *Poecilia reticulata* with blue coloring were discovered. The evolution of this original color affects the size, shape and intensity of the areas colored in blue to which females are visually very sensitive, to the point of having made a decisive criterion of choice of sexual partners. Blue has become attractive to the detriment of the red and orange colors of all the other populations in the world. Females are attracted by the bluest individuals, who also find great success with aquarium keepers. These blue frequencies of short wavelengths are easily transmitted in clear and transparent waters, enabling these guppies to colonize new waters and not be limited to turbid aquatic environments which favor the transmission of red radiation with longer wavelengths. It is necessary that females of these populations show new preferences for this color pattern for it to establish itself as the reference color for their romances and become, thanks to generalized natural selection, the single color of natural populations.

The males of the ornate rainbow fish or Australian dwarf perch *Rhadinocentrus ornatus*, a freshwater melanotaeniid, display two color patterns: one is blue, which is shown by the majority (more than 80% of the population), and the other is red, which is rarer (18%). A female preference for mating with males of blue phenotype* should lead to the gradual disappearance of those of red phenotype* and the establishment of generalized monochromatism*. This has not occurred, and non-rigorous sexual selection enables females to not comply with the preference model, thus ensuring the persistence of a dichromatism* that affects one-fifth of the population.

Bibliography: *Proc.Roy.Soc.B,* 2018, **285** & DOI.org/10.1098/rspb.1335, *Anim.Behav*., 2010, **80**: 845-851 & DOI:10.1016/j.anbehav.2010.08.004

#### 1.1.2.2.3. Black

The black nuptial coloration of *melanin* in the males of the brook stickleback *Culaea inconstans* in North America apparently plays no role in sexual selection, although it exercises a function of strengthening contrasts in the tea-colored waters which it often encounters in this geographical area. The synthesis of this pigment, *melanin*, is under genetic control. It does not reflect a physiological state as

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constituting a signal of expression of behavioral dominance. It is also a signal of aggression, especially when these males guard their nests (Volume 2, section 2.2.1).

Bibliography: *Anim.Behav*., 2006, **71**: 749-763 & DOI:10.1016/j.anbehav.2005.07.016, *Behav.,* 2006, **143**: 483-510, *Funct.Ecol.,* 2010, DOI:10.1111/j.1365.2010.01781.x

#### 1.1.2.2.4. Blue-green

The male of the blue-throated wrasse *Notolabrus tetricus* displays a brilliant blue-green coloration of the most beautiful effect due to the presence of *biliverdin*, a pigment derived from the degradation of bile pigments. In fact, it has inherited this metabolic pigment originally accumulated by the female at its sex change. This species is protogynous* (Volume 2, section 1.2.9) and the female is brown in color.

Bibliography: *J.Fish Biol*., 2006, **68**: 1879-1882 & DOI:10.1111/j.1095-8649.2006.01033.x

#### 1.1.2.2.5. Iridescence

The cheeks of the males of the bluegill *Lepomis macrochirus* and stickleback *Gasterosteus aculeatus* strongly influence their attractiveness, determining the choice of females measured by the number of females who visit their nests, the number of eggs laid and the time they spend in the nest.

Bibliography: *Ethol*., 2010, **116**: 416-428 & DOI:10.1111/j.1439-0310.2010.01755.x, *J.Exp.Biol.,* 2013, **216**: 2806-2812 & DOI:10.1242/jeb.0874889

### 1.1.2.3. *…and also seductresses*

The red color of seduction is not a nuptial exclusivity of males. Females of the pink-belly wrasse *Halichoeres margaritaceus* also show nuptial color in the form of a red belly which, associated with body-swaying behavior, is intended to alert males to their availability for spawning. The largest, with the largest colored spots, benefit from the greatest reproductive success.

Among the Arctic char *Salvelinus alpinus*, the two sexes are bearers of a red abdominal color pattern rich in *carotenoid*s*, which is more intensely colorful and more brilliant in males than in females. The females invest their pigment potential for the benefit of their eggs, which are thus assured of a better quality of survival and hatching, related to a greater antioxidative potential. They thus gift their carotenoids* to their offspring, while males prefer to selfishly allocate them to their personal adornment. Studies of human ethology have shown that red color has the value of a sexual signal for women, who use this color to increase their

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attractiveness. In this respect, they copy the females of primates, whose red genitals play a comparable role.

A yellow spot on the belly of the females of the Adriatic dwarf goby *Knipowitschia panizzae* constitutes a signal that is very attractive to males, regardless of the size of the female, but especially if it is large in size.

A reversal of roles (Volume 2, section 1.1.4) is seen among syngnathids, among whom there are females who make a charm offensive to seduce the males. Among Gulf pipefish *Syngnathus scovelli*, sexual selection takes place among settled populations within marine coastal eelgrass beds, in which males, generally less numerous than females, observe the seductive behaviors of potential partners who, equipped with attractive colorful patterns, move by swimming above the seagrass beds. These "dancers of the sea" seek to attract the attention of males in order to choose among them the most beautiful and also the strongest, *a priori* the best spawners. Therefore, these secondary sexual and behavioral characteristics assume, among these pipefish as well as among seahorses who are their near relatives, a greater energy investment by females, while the males save their energy to better cope with their subsequent constraints, which consist of ensuring the internal brooding of eggs in their incubation pouch; such an effort is equivalent to actual gestation (Volume 2, section 2.1.4).

Bibliography: *Behav.,* 2015, **152**: 705-725 & DOI:10.1163/1568539X-00003250, *Behav.Ecol.Sociobiol*, 2008, **62**: 521-528 & DOI:10.1007/s00265-007-0476-1, *Ecol.Freshxat.Fish*, 2008, **17**: 328-339 & DOI:10.1111/j.1600-0633.2007.00286.x, *Ethol*., 2013, **119**: 692-701 & DOI:10.1111/eth.12110

### 1.1.2.4. *Seasonal sexual dichromatism*

The adoption of nuptial colors described in the previous examples is only seen among one gender: either the male or the female. In contrast, among the kelp* bass *Paralabrax clathratus*, both males and females who are monochromatic* for a large part of the year change their colors during the breeding season (from April to October); they adopt colors which are distinct from their adult color pattern during sexually dormant times and which differ from one another. Males acquire black color patterns with white dots and a bright orange snout, while females acquire black color patterns without white dots, which facilitates intersexual recognition during courting and spawning behaviors, at sunset (6–10 p.m.), in low-light conditions and in groups of 3–20 individuals.

Bibliography: *Bull.South.Calif.Acad.Sci,* 2005, **104**: 45-62*, J.Fish Biol.,* 2006, **68**: 157-184 & DOI:10.1111/j.1095-8649.2005.00886.x

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### 1.1.2.5. *Instant seductive power*

Most nuptial color patterns require long metabolic preparation over several months to reach their maximum expression at the time of the mating season and to be maintained during the entire period of reproduction that lasts from several days to several weeks and/or several months. However, certain chromatic modifications are much more ephemeral, which are only expressed during intersexual meetings, with a one-time role of attraction during the few minutes or hours of courtship behavior, as zebrafish *Danio rerio* among whom the dark transverse bars appear briefly, then disappear by fading, in relation to the behavioral variations of males. Rapid changes of color also occur in response to changes in the color of habitats in order to escape the gaze of predators, becoming more or less light and/or dark based on the environmental color, as well as when forming schools in order to avoid attracting attention by adopting the same color as all its species-mates to dilute the risk of predation (Volume 2, section 2.3), as in the guppy *Poecilia reticulata*. Regardless of the energy cost of this change in color, it is always advantageous, for these "chameleon fish", to adopt inconspicuous behavior.

Bibliography: *Anim.Behav.,* 2005, **70**: 1063-1066 & DOI:10.1016/j.anbehav.2005.02.005, *Ethol.,* 2012, **118:** 1208-1218 & DOI:10.1111/eth.12027/pdf, *Fish Fish*., 2010, **11**:159-193 & DOI:10.1111/j.1467-2979.2009.00346.x

### 1.1.2.6. *Other sexual ornamentation*

#### 1.1.2.6.1. Eye color

Females of the stickleback *Gasterosteus aculeatus* are sensitive to the color patterns (red-colored throats) of males and are also strongly attracted by their eyes, which become blue and iridescent at the time of reproduction, which constitutes an important signal in courtship behavior; the red color of their throat reinforces the contrast of their eyes. The diameter of the iris, of red coloration in male bitterlings *Rhodeus amarus*, the development of which is among their greatest criteria of dominance, plays an attractive role in females and participates in sexual selection.

Bibliography: *Anim.Behav.*, 2006, 71: 307-313, *J.Exp.Biol.,* 2013, **216**: 2806-2812 & DOI:10.1242/jeb.084889

#### 1.1.2.6.2. The size of the gonopod

Among other characteristics attractive to females of the guppy *Poecilia reticulata* are the size of the gonopod, the organ of mating and the intromission of semen, in the form of spermatozeugmas*, into the genital tract of females. Its length of about one third of that of the body is a selective trait that explains a large part of reproductive success, as shown in a study of the progeny of males.

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**Figure 1.1.** *The copulatory organ or gonopod of the male guppy* Poecilia reticulate. *For a color version of the figures in this book, see www.iste.co.uk/bruslé/fish2.zip*

Bibliography: *Biol.Lett.,* 2013, **9** & DOI:10.1016/rsbl.2013.0267

### 1.1.2.6.3. A sword

Male swordtails of the genus *Xiphophorus*, such as *X. helleri*, possess a "sword" resulting from the association or grouping of the lower rays of their caudal fin. This constitutes a signal of good physical condition and masculine aptitudes, as well as a criterion of deterrence in inter-male rivalry and of selection by females who attentively choose a mating partner with the longest sword. This characteristic, associated with a vivid red color in a localized band on its flanks, constitutes for them a sign of virility. A rapid change, in less than 2 min, of color (from black to red) of this colored strip shows the status of the dominant male, which is quite distinct from that of subordinates* who are males with a black band.



**Figure 1.2.** *The caudal sword of the swordtail* Xiphophorus sp

In addition, this signal of dominance towards rivals offers the advantage of imposing submission on the latter, thus avoiding energy-costing conflicts such as physical assaults. This secondary sexual characteristic, if it provides advantages in terms of reproductive success, also presents a cost, in the form of a handicap to locomotion. It decreases the swimming speed because of an unfavorable

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of the swimming performance of *X. montezumae* shows that if the sword is excised, the propulsion speed increases by 21%. However, other research on the supposed handicap on the swimming behavior of swordtails tends to show that this exaggerated adornment has only a minor impact on the fish's swimming system, and does not impose a locomotive penalty as previously assumed. The removal of the organ induces a change in the amplitude of beats of the tail, but not their frequency, and physiological mechanisms are presumed to compensate for the possession of this cumbersome structure.

Surprisingly, the natural preference of females for males carrying long swords can be manipulated by the social environment, which shows its lability. In fact, females of *X. helleri* who are exposed from their youth only to the presence of males with short swords retain an attraction for this phenotype* and mate with them without problem Only experienced females, having a certain familiarity with males with long swords, are able to make the right choices. Sexual requirements relating to male ornamentation are not confined to the size of their sword. The selection of partners is more complicated when attractiveness is based on multiple visually detectable components, as the presence of three colored bands on the sword of *X. helleri*, which is shiny and contrasting – two black bands and one band of green or orange –, serves as amplifiers of visual signals and strengthens their attractiveness. The loss of a black band renders the male inferior.

The color patterns of the males of the delicate swordtail *X. cortezi* serve as a signal of attractiveness for females, particularly the presence of dark bands which are symmetrical or asymmetrical according to the individual as a result of a lateralization phenomenon. The oldest females show a clear preference for males showing asymmetric bands, while young females are less discriminating. These males show off this characteristic during their courtship behavior by performing a figure-eight swim, in order to be better appreciated. A preference for this type of male means that this genetic characteristic is selected for in the population, so that the number of asymmetric males therein becomes increasingly large. Young females *X. malinche* can also be distinguished by their preference for symmetric males (6 bars to the right and 6 bars to the left), while large females choose asymmetric ones (6 right and 8 left). Virgin females, regardless of their age, are indifferent to the size of the swords of males. This results in an advantage for them, that of being able to mate with all the types of males present. The preferences of older females do not manifest until later, with a certain degree of experience.

The development of the sword among the swordtails is genetically determined, under the control of several genes, principally *MSX*, which is common to all poeciliids and associated with the secretion of the *androgenic hormone testosterone*. In fact, juveniles do not possess swords; the expression of the gene is under-

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male swordtails are distinguished by their caudal sword, a Mexican species, *X. continens*, presents the originality of not possessing such an organ, due to a relaxation of sexual selection. Females are neither attracted by the size of males nor by the designs on their color patterns, while in turn these males give up on courtship and refuse to attack other male rivals, with no competition taking place.

Bibliography: *Anim.Behav*., 2005, **69**: 1415-1424 & DOI:10.1016/j.anbehav. 2004.08.013, 2006, **71**: 129-134 & DOI:10.1016/j.anbehav.2005.05.004, 135-140 & DOI:10.1016/j.anbehav.2005.04.007, 2008, **75**: 1981-1987 & DOI:10.1016/ j.anbehav.2007.12.008, **76**: 271-276 & DOI:10.1016/j.anbehav.2008.03.008, 2014, **87**: 39-44 & DOI:10.1016/j.anbehav.2013.10.001, *Behav.* 2005, **142:** 283-303, 2009, **146**: 727-740 & DOI:10.1163/156853909X446172, *Biol.Lett.,* 2006, **2**: 8-11 & DOI:10.1098/rsbl.2005.0387, 2007, **3**:144-146 & DOI:10.1098/rsbl.2006.0608, *Ethol*., 2009, **115**: 812-822 & DOI:10.1111/j.1439-0310.2009.01676.x, *Evol.Dev.,* 2003, **5**: 466-477, *Funct.Ecol*., 2014, **28**: 924-932 & DOI:10.1111/1365-2435.12222, *J.Fish Biol*., 2007, **70**: 1161-1170 & DOI:10.1111/j.1095-8649.2007.01379.x, 2012, **80**: 722-727 & DOI:10.1111.1095-8649.2011.03212.x

### 1.1.2.6.4. Lower jaw and adipose fin

Male salmonids have these sexual characteristics which express their dominant status in social interactions: a hooked lower jaw or hooknose* and a developed adipose fin, such as among the Arctic char *Salvelinus alpinus*. These characteristics feature at the same time in inter-male competition and in the sexual selection made by females.



**Figure 1.3.** *Adipose fin of a salmonid* Salmo trutta *fario*

Bibliography: *J.Fish Biol.,* 2011, **79**: 107 & DOI:10.1111/j.1095-8649.2011.0387.x

### 1.1.2.6.5. A badge

Males of all species are constantly trying to please females during the mating

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females' choice towards them, among all the contenders. Males of the long ear sunfish *Lepomis megalotis* are equipped with an opercular expansion which they wave, like a flag, in front of females who, being curious and interested, show interest in this ornament. Males whose flags are the largest thus enjoy the greatest reproductive success. The swordtail characin *Corynopoma riisei* also uses an opercular expansion, imitating a terrestrial insect, that he displays to the gaze of females and which operates as a lure. Hungry females are attracted and become victims of this subterfuge (Volume 2, section 3.9).



**Figure 1.4.** *Opercular expansion imitating the form of an insect (ant) and intended to attract females who consume this prey in the male of the swordtail characin* Corynopoma risei

Bibliography: *Curr.Biol.,* 2012, **22**: 1440-1443 & DOI:10.1016/j.cub.2012.05.050, *Env.Biol.Fish*, 2011, **92**: 159-166 & DOI:10.1007/s.10641-011-9825-z, *Ethol.Ecol.Evol*., 1997, **9**: 223-231 & DOI:10.1080/08927014.1887.9522882, *J.Evol.Biol*., 2010, **22**: 1907-1918 & DOI:10.1111/j.1420-9101.2010.02055.x, *J.Fish Biol.,* 2013, **83**: 343-354 & DOI:10.1111/jfb.12175

### 1.1.2.6.6. Other characteristics

A large caudal fin in the guppy *Poecilia reticulata*, a large dorsal fin in the Yucatan molly *Poecilia velifera*, the Amur goby *Rhinogobius brunneus* or again the swordtail *Xiphophorus helleri*, cephalic ridges among blennies *Blennius ocellaris*, *Salaria pavo*, etc. constitute sexual characteristics which are generally attractive, although they are costly in energy and generally handicap their owners whose movements are limited. Females, seduced by male guppies with long tails, experience high reproductive success, superior to that from their matings with short-tailed males. Males of the Pacific blue-eye *Pseudomugil signifer* are more attractive to females due to their highly developed dorsal fin that testifies to their high

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fins by males of the threadfin rainbow fish *Iriatherina werneri* constitutes a quite extravagant sexual ornament. Such an exaggerated desire to please results in a serious handicap to locomotion and an inordinate cost of energy expenditure in swimming.

The possession of long and symmetrical ventral spines by the males of the threespine stickleback *Gasterosteus aculeatus* contributes to their reproductive success. The presence of skin growths or reproductive tubercles on the head and fins of male cyprinids has a positive effect on the choices made by females, as evidenced by their reproductive success.

Bibliography: *Anim.Behav*., 2005, **70**:1339-1348, 2009, **77**: 823-829 & DOI:101016/j.anbehav.2008.12.006, *Behav.,* 2005, **142**: 191-202, 2006, **143**: 183-195, 2008, **145**: 897-913, *Ethol*., 2006, **112**: 678-690 & DOI:10.1111/j.1439-0310.2006.01213.x, 1050-1055 & DOI:10.1111/j.1439-0310.2006.01261.x, 2007, **113**: 802-812 & DOI:10.1111/j.1439-0310.2007.01388.x, *Funct.Ecol*., 2013, **27**: 1034-1041 & DOI:10.1111/1365-2435.12097, *J.Fish Biol.,* 2002, **60** & DOI:10.1006/jfbi.2002.2096, **61**: 899-914, 2007, **71**: 77-89, *Zool.Sci.,* 2006, **23**: 255-260 & DOI:10.2108/zsj.23.255

### 1.1.2.7. *Dual function of certain visual signals*

These multiple ornamentations in the form of cumulative multi-signals presented by males generally play a dual role and are intended, as in the minnow *Phoxinus phoxinus*, not only to trigger an attractive response on the part of interested females practicing sexual selection, but also to indicate to other males, who are potential rivals, their good health and aggressive potential. Males of the sheepshead swordtail *Xiphophorus birchmanni* court females by straightening their dorsal fin. This behavior not only ensures success in mating, but also has the complementary effect of scaring their rivals.

Bibliography: *Biol.Lett*., 2007, **3**: 5-7 & DOI:10.1098/rsbl.2006.0556

### 1.1.2.8. *Permanent sexual dichromatism*

In other species, the two sexes can be distinguished by their color patterns during all seasons, for example the male of the yellowfin grouper *Mycteroperca venenosa*, in the Gulf of Mexico, has yellow spots on the two sides of its lower jaw and the female has red jaws. The male of the tiger grouper *M. tigris* is characterized by black pectoral fins, while the females have bright orange pectoral fins. These colors are particularly well visible as far as –35 m of depth where matings take place and are very useful for sexual partners to recognize each other in the areas of mating, with each male finding a female among the crowds of spawners grouped around the tropical spawning grounds (Volume 2, section 2.1.1).

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Bibliography: *J.Fish Biol*., 2006, **69**: 1744-1755 & DOI:10.1111/j.1095-8649.2006.01241.x

#### 1.1.2.9. *Female signals*

Females of the guppy *Poecilia reticulata* and the mosquitofish *Gambusia* sp. sometimes exhibit original sexual characteristics, such as a black-pigmented gravidity spot in close proximity to their cloacal sexual orifice.

### *Courtiers*

#### 1.1.3.1. *Knowing the ways of courtship…*

There is a general rule in the animal world that it is males that court females and that the latter are sensitive to the courtship behavior of their partner, which determines their assent to coupling. The intensity of courtship conducted by a male who displays his sexual preferences is classically measured, as in the guppy *Poecilia reticulata*, by the time he spends in the company of a female and by the number of sexual parades made up of sigmoidal* movements that he performs in the presence of one who might become the lucky chosen. Such ritual dance movements reflect a body language often used with success by the males of various fish species. The success of this courtship behavior assumes perfect environmental visibility. The presence of visual barriers, such as obstruction by the physical structures of the habitat by dense vegetation which disrupts courtship signals, induces a certain disinterest in females towards their courtiers. The presence of predators usually increases their rates of *cortisol*, the stress hormone, to the detriment of that of their *androgenic hormones*, which reduces their courtship behavior.

Among the Mexican swordtail *Xiphophorus multilineatus*, larger males court females, whereas small males behave as *sneakers** who seek to steal fertilizations (Volume 2, section 1.2.1). Large females appreciate being courted and choose these courting males as partners, whereas small females only show a low preference for them, leaving the field open to small males. Mating preferences of the females of *X. nigrensis* are based on multiple signals: the criterion of size functions alone when a large male is accompanied by small members of the same species; a great difference in size is sufficient to induce the choice of females. However, at a constant size, their preference is for those who show the most vigorous courtship; the criterion of the intensity of courtship behavior becomes crucial as a result of a strengthening of the second signal over the first. Males of the sheepshead swordtail *X. birchmanni* court females by swimming near them and parallel to them, which straighten their dorsal fin in the shape of a sail with their body trembling. They raise this sail particularly in the presence of rivals in order to intimidate them. The recipients of this signal are therefore other males and not females, who are not

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sensitive to this unattractive characteristic and also fear males with large sails who are judged as highly aggressive. In addition, the length of the caudal sword does not constitute, in some female swordtails, an attractive characteristic as if this sexual stimulus had been lost during the course of evolution. Females of the Mexican swordtail or mountain swordtail *X. nezahualcoyotl* are sensitive to the courtship behavior of large males who adopt a characteristic posture, i.e. head downwards and body tilted to 45–90° above the substrate. This signal, also used by the delicate swordtail *X. cortezi*, has the value of expressing dominance and aggressive potential towards male rivals in a situation of competitive interactions. The winners of inter-male competitions adopt more of a head-down body tilt than the vanquished. Such postures are an effective means of sexual selection.

Male courtship behavior in the goby *Pomatoschistus canestrinii*, in the lagoon of Venice, like that of many other gobies, is multimodal, based on a synchronized double signal: visual by rapid movements of the head and audible by staccato booms, 3–16 brief sounds lasting 200 ms* at a frequency of less than 200 Hz*. It may also be olfactory and tactile; all these additional signals are intended to attract females to its nest.

In the Mediterranean, on the spawning grounds where they meet in large numbers, males of the dusky grouper *Epinephelus marginatus*, a territorial fish, court females in the twilight, from 6 to 10 p.m., producing low frequency sounds that have been interpreted as signals for the beginning of courtship. The black grouper *Mycteroperca bonaci* also produces sounds below 100 Hz at sunset in the western Atlantic.

The acoustic courtship signals issued by the males of the Mozambique tilapia *Oreochromis mossambicus* reflect their social status. They differ between the dominant winners of inter-male conflicts (longer duration and lower frequency) and subordinates* defeated in these clashes. These behaviors relate to their respective of the stress *hormone cortisol* and *androgenic hormones* such as *11-KT*. Acoustic courtship signals are frequent among cichlids of the genus *Pseudotropheus* endemic* to Lake Malawi whose vocal repertoires among males differ in a specific way: the same duration of issuance of 700 ms, but *pulses* of variable number and frequency, enabling interspecific recognition between the many (450–600) and various sympatric species*. Females of the round goby *Neogobius melanostomus* are equipped with hearing organs which feature a high density of *hair cells* in their otolithic* pouch. Under the control of their *sexual hormones estrogen -estradiol*, this device is particularly sensitive, during reproduction, to vocalizations at 100–600 Hz* from their partners.

Among the threespined stickleback *Gasterosteus aculeatus*, the very ritualized

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females only mate with males of their own species and neglect those of the sympatric* neighboring species, the blackspotted stickleback *G. wheatlandi*, whose dance ritual is substantially different from that of *G. aculeatus*. One courtship behavior in *G. aculeatus*, a zigzag dance, differs, on the coasts of Japan, between populations of the Pacific coast to the west and those of the Sea of Japan to the east where it is more a wheeling or rolling dance; the females only mate with males who respect their geographical particularism, similar to regional folk dances. This behavior is also different between populations of Canadian open water or limnetic* and benthic* populations, with the zigzag being more open among the latter. These behavioral variants are critical in maintaining differentiation of the ecotypes*.

Bibliography: *Anim.Behav.,* 2005, **69**: 595-601 & DOI:10.1016/j.anbehav.2004.06.016, 2007, **73**: 415-422 & DOI:10.1016/j.anbehav.2006.09.002, **74**: 633-640 & DOI:10.1016/j.anbehav.2007.01.002, 2011, **82**: 1313-1318 & DOI:10.1016/j.anbehav.2011.09.014, 2017, **129**: 237-247 & DOI:10.1016/j.anbehav.2017.05.017, *Behav.,* 2004, **141**: 1371-1387, 2008, **145**: 443-461, 485-508, 2015, **152**: 963-993 & DOI:10.1163/1568539X-00003264, *Ethol.,* 2008, **114**: 977-988 & DOI:10.1111/j.1439-0310.2008.01541.x, 1122-1134 & DOI:10.1111/j.1439-0310.2008.01564.x, 2013, DOI:10.1111/eth.12087, *J.Exp.Biol*., 2013, **216**: 1075-1084 & DOI:10.1242/jeb.076935, *J.Fish Biol*., 2006, **69**: 938-944 & DOI:10.1111/j.1095-8649.2006.01135.x, 2008, **72**: 1355-1368 & DOI:10.1111/j.1095-8649.2008.01802.x, 2698-2694 & DOI:10.1111/j.1095-8649.2008.01828.x, 2009, **75**: 1883-1887 & DOI:10.1111/j.1095-8649.2009.02430.x, 2015, **87**: 400-421 & DOI:10.1111/jfb12733, *Mar.Biol*., 2014, **161**: 141-147 & DOI:10.1007/00227-013-2324-3, *TREE*, 2002, **17**: 480-488.

### 1.1.3.2. *… but nevertheless remain prudent…*

Males of the bicolor damselfish *Stegastes partitus*, a pomacentrid of the Gulf of Mexico, usually court females through a very ritualized series of movements and postures, especially those who are large in size and are therefore highly sought after. This behavior to which females are very sensitive, however, depends on the environment. The presence of a predator such as a grouper or an eater of eggs such as a wrasse has a significant lessening effect, as if this male were making a choice between its own security and spawning activity: between a cost to be paid, the risk of predation and a reward to obtain, the glories of love!

Dominant male guppies *Poecilia reticulata* are strongly colored and do not modify their active courtship behavior towards females, even in the presence of a rival, whether they are highly colored or not. In this respect, they differ from fellow males with less brilliant color patterns and of lower social status who abandon their courtship in the presence of a rival of a superior colorful phenotype, and are then content to mate with females who had originally not been the object of their preference. Such resignation is imposed by social domination.

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Bibliography: *Anim.Behav*., 2007, **74**: 329-336 & DOI:10.1016/j.anbehav.2006.12.010, 2016, **118**: 33-37 & DOI:10.1016/j.anbehav.2016.05.022

#### 1.1.3.3. … *and know how to save effort*

Among the neighboring species of beau-gregory damselfish *Stegastes leucostictus*, females are naturally fond of large males that give them hope of the best reproductive success and a high quality of defense and parental care. The latter, confident in the preference shown to them, reduce their courtship behavior in contrast to males who are non-preferred and rejected by females, who are forced to increase their efforts of seduction to try to get some meager success. A high intensity of courtship behavior thus indicates males of low quality who dance too much to be considered honest.

#### 1.1.3.4. *Need for self-improvement*

Females of the monogamous convict cichlid *Amatitlania nigrofasciata* (formerly *Archocentrus nigrofasciatus*) select their partners based on a series of criteria which are seldom in favor of large males. The latter, being rejected the first time, devote themselves to strengthening their courtship behavior, in contrast to the males already *a priori* selected who tend to relax their efforts. Faced with hard-to-convince females, males often seek to manipulate their final decision.

Males of the sailfin molly *Poecilia latipinna* increase their production of sperm in the presence of many females. Small males are more sexually boosted by the presence of large females. Those of the stickleback *Gasterosteus aculeatus* are stimulated by the presence of many rivals and, wishing to win the sperm competition, increase the volume of their ejaculations.

Bibliography: *Anim.Behav.,* 2005, **69**:143-149 & DOI:10.1016/j.anbehav.2004.02.020, *Behav.Ecol.Sociobiol*., 2003, **54**: 205-209 & DOI:10.1007/s00265-003-0612-5, *Ethol*., 2004, **110**: 193-203.

#### 1.1.3.5. *Need for encouragement and concentration*

The male stickleback *Gasterosteus aculeatus* practices courtship behavior by swimming in a zigzag manner before a female, and the posture of the latter helps stimulate continuation or desistance of this courtship: before a female who holds herself in a horizontal position, he stops the courtship and even becomes aggressive towards her, whereas if she holds herself in a “head-up” position, which stimulates, he strengthens his courtship demonstrations.

In addition, the courtship behavior of males is disturbed by the presence of rivals of the same species; therefore, the “audience effect” has negative consequences on

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Bibliography: *Anim.Behav.,* 2000, **60**: 63-68 & DOI:10.1006/anbe.2000.1462, 2004, **68**: 465-471.

#### 1.1.3.6. *Incentive to spawning*

Males of the sea lamprey *Petromyzon marinus* build nests into which they seek to attract females by emitting attractive chemical messages – pheromones*. Once a female is well installed in the nest, the male courts her with cuddling and caresses, in particular by rubbing her belly with his so-called cephalic hump located in front of the dorsal fin which develops at sexual maturation, encouraging his partner to emit her oocytes. This hump is made up of fat cells or adipocytes* and has thermogenic capabilities such that, during mating, the ambient temperature rises by 0.3°C.

Bibliography: *J.Exp.Biol.*, 2013, **216**: 2702-2712 & DOI:10.1242/jeb.085746 & DOI:101242/jeb.089771

### *Reversal of roles*

In most animal species, it is the males who are the more enterprising and court females (Volume 2, section 4.1.3), thus behaving as the main actors in reproductive behavior, while females are content, more often than not, to be observers. Some species do not respect this conventional, "macho" strategy of traditional sexual selection and adopt contrary behavior corresponding to a reversal of roles, with females becoming active in courtship and males being reduced to suffering the domination of their partners and being relegated to the exclusive function of distribution of paternal care (Volume 2, section 2.2.1).

#### 1.1.4.1. *Courtesans with attractive sexual ornamentations*

Female pipefish of *Syngnathus* sp. and *Nerophis* sp., female seahorses *Hippocampus* sp. and leafy seadragons *Phycodurus* sp. develop sexual ornamentations and, finding themselves in competition with other females, adopt attractive behaviors of postures of ritualized dance in order to display themselves to males and be chosen by the best of them. These males choose as their partners the bigger, most decorated and most colorful among them, but their reproductive potential is limited by the volume of their incubation pouch that enables them to only host a limited number of eggs, then of embryos deposited by their single or multiple partners. The number of female pipefish *Syngnathus typhle* and *S. abaster* sometimes exceeds that of their male partners. They must then, in a situation of strong inter-female competition, make the effort to seek to seduce them. Females who are larger and more active than males, after engaging in a ritual dance which acts as courtship behavior, have a potential production of oocytes – a fertility rate – which often exceed the capacity for accommodation of eggs by the incubator

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pouches of males, especially in the case of a large female coupling with a smaller male. They are therefore led to seek out multiple couplings with multiple partners in order to accommodate many eggs.

Among the peacock blenny *Salaria pavo*, an aggregation of nests built and occupied by less number of males forces females to make an effort in courtship behavior. These courtesan females display nuptial colors consisting of alternating dark and light vertical bands and adopt a very stereotyped courtship behavior of fast beats of the pectoral fins, opening and closing of the mouth, trembling of the body, etc., which is under the control of their *estrogen hormones estradiol* $E_2$; an interruption of this courtship occurs after ovariectomy. In addition, *prostaglandins* $_2\alpha$) act on their brain, which enables them to show their partner that their mature oocytes are ready to be ovipositioned. The first hormone controls the behavior of seeking male partners in their nests which they visit with a view to coupling, and the second controls the effective spawning behavior.

Among the blue-banded goby *Lythripnus dalli*, a reef fish, females practice assiduous courtship of males, and their reproductive success, as estimated by the number of eggs laid and deposited in nests, directly depends on the intensity of this activity. Females of higher rank α, in intrasexual competition, interrupt the courtship solicitations of females of lower rank β. As for males, they restrict themselves to the accomplishment of their domestic task, namely parental care (Volume 2, section

Bibliography: *Anim.Behav*., 2010, **79**:885-893 & DOI:10.1016/j.anbehav.2010.01.001 , *Behav*., 2014, **151**: 1367-1387 & DOI:10.1163/1568539X-00003188, 2015, **152**: 917-940 & DOI:10.1163/1568539X-00003262, *J.Fish Biol*., 2006, **69**: 66-74 & DOI:10.1111/j.1095-8649.2006.01064.x, 1837-1844 & DOI:10.1111/j.1095-8649.2006.01254.x, 1860-1869 & DOI:10.1111/j.1095-8649.2006.01229.x, 2009, **74**: 754-762 & DOI:10.1111/j.1095-8649.2008.02153.x, 2011, **76**: 1647-1661 & DOI:10.1111/j.1095-8649.2011.02972.x, *Proc.Roy.Soc.B*, 2010, DOI:10.1098/rspb.2009.2290, 2014, **281**: 20133070 & DOI:10.1098/rspb.2013.3070

### 1.1.4.2. *Seasonal behavioral alternations*

Courtship activity varies during the breeding season as a function of the imperatives of activity for each of the sexes. Among the sabre-tooth blenny *Petroscirtes breviceps*, males are the usual courtiers in accordance with the conventional scenario, which takes place at the beginning and end of the breeding season (April and September–October), while females become the courtesans in the middle of this mating season (from May to August). This plasticity is a function of the availability of males and females on the sexual market. The operational sex ratio* may vary as a function of two divergent requirements: first of all, the males are in competition for availability of nests that are rare, and the females compete for

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access to mating with males who, as guardians of nests at mid-season, are then no longer available.

Bibliography: *J.Fish Biol*., 2006, **69**: 203-213 & DOI:10.11111095-8649.2006 .01086.x

## *Forbidden love*

### 1.1.5.1. *Avoiding bad relationships between different species*

The males of most species are only concerned with a desire to mate with the largest possible number of females and, by sowing their sperm "without limits", to produce the largest possible descent. The number of their progeny appears, in their eyes, more important than their quality. Females, however, are much more anxious to preserve the genetic characteristics of their own population which they have inherited from their ancestors, avoiding, through adventurous crosses in uncontrolled hybridization with males of other species, the production of bastards. They thus look preferentially as sexual partners upon good male bearers of a "good genome" of their species. This constant concern to maintain the genetic purity of the species, population and even the family makes females conservative and attentive guardians of a genetic heritage. Maintaining this purity requires that reproductive crosses occur between individuals of both sexes belonging to the same species, as opposed to heterospecific crosses which produce hybrid progeny (Volume 2, section 1.2.5), characterized by a mixture of the genes of the two species and which often has the value of "genetic pollution" by introduction of allochthonous* alleles into the genome of natural populations. Therefore, spawners of all species learn, from visual, olfactory, auditory and/or electrical criteria, to recognize members of the same species well and to favor homospecific couplings in order to avoid inbreeding.

Reproductive success of the stickleback *Gasterosteus aculeatus* is diminished in some populations due to genetic depression linked to consanguineous matings responsible for low rates of embryonic survival and hatching. Some experiments have shown that females may choose not to become incestuous by mating only with males of the same species and non-family members. Consanguineous matings are all the more difficult to prevent in that these fish have a strong natural tendency to form family groups (Volume 1, section 3.11). The temptation is then great, for females, to mate with their parents, brothers and sisters.

Bibliography: *Behav.,* 2008, **145**: 425-441, *Biol.Lett*, 2006, **2**: 232-235 & DOI:10.1098/rsbl.2005.0432, *Ethol*., 2007, **113**:276-282 & DOI:10.1111/j.1439-0310.2006.01316.x

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### 1.1.5.2. *Other bad encounters between individuals of different populations*

Whatever may be the merits and the zeal of these females, guardians of the "genomic temple", results do not always meet their expectations. In addition to the fact that they are often mistaken about the alleged quality of the partner whom they have chosen or who is imposed on them, opportunities for "bad encounters" do not cease to multiply, in natural environments, by voluntary introduction (Volume 1, section 2.3.1), by humans, of foreign spawners – of aliens! – bearers of a genome different from that of the indigenous populations and who contribute, by interpopulational hybridizations*, to seriously impairing the original genetic purity of the population. These phenomena occur particularly in populations of the brown *Salmo trutta* in European rivers. In effect, due to a numerical decline in wild trout, victims of the degradation of their living environment, various kinds of pollution and overfishing*, the natural populations have been gradually replaced by those of trout produced in hatcheries, which are discharged into water courses in the context of repopulation campaigns organized by fishing companies under the pressure of the growing demand of anglers. Only rarely are wild populations spared by this genetic pollution, which has become traditional and is quasi-generalized, in Western Europe and particularly in France. Rare examples of trout that are still "pure" are known in Corsica where pure Corso-Sardinian trout are still present in the headwaters of basins, in very small mountainous streams isolated from the downstream by waterfalls which are impassable, either by trout in upstream migration or by fishermen who demand artificial rearing. These lucky Corsican trout, isolated from other populations since the last glaciation, are well adapted to the characteristics of their habitats and have retained their morphotype.

Crosses between the threespine stickleback *Gasterosteus aculeatus* of different ecotypes* – of lakes or rivers – sometimes prove to be infertile, as a result of sperm incompatibility which has the value of postcopulatory genetic isolation.

Crossings occur between populations of the same species which, geographically separated for millions of years, have evolved differently to the point of showing divergent phenotypes and genotypes which may lead to the differentiation of different species. If they accidentally meet, the crosses that take place generate a mixture of genes likely to harm the morpho-physiological qualities and behavioral characteristics inherited from their parents. A decrease in the quality of offspring occurs in the guppy *Poecilia reticulata*, as a result of consanguineous matings between members of the same family, something that females tend to avoid.

Non-native populations of these small poeciliids, when they have been transferred by humans to new habitats containing native populations, have cross-bred with the latter, producing offspring that have lost the genetic originality of each of the parental populations. Adverse effects may result, affecting, for example, the

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anti-predator defensive behavior of grouping in schools (Volume 1, section 3.3). The latter is found to be significantly weakened in the native population at the time of the arrival of a invasive* population, which, not having suffered the same selection pressures due to lower risk of predation in its original environment, possesses a genome that is less defensive and finally less protective for their descendants who are now faced with a risky environment.

Female guppies *Poecilia reticulata* should, for the sake of genetic purity, seek to avoid inbreeding by refusing to mate with males of their own family; such crosses are negative because of genetic depression due to the presence of homozygous* alleles* in the family progeny which are responsible for problems of inbreeding. Although they are capable, based on olfactory criteria such as pheromones*, in particular those linked to the system of the major histocompatibility complex (MHC) (Volume 2, section 1.1.1), of recognizing males of their family, and their brothers and sisters in particular, and of distinguishing them from non-male family, they mate, most often interchangeably, in a river in Trinidad, with all males present. Moreover, no precopulatory* mechanism for the prevention of risks of inbreeding has been identified. In contrast, males of the bishop livebearer *Brachyraphis episcopi* show clear preferences for unfamiliar females, which precludes the risk of interfamilial mating.

Bibliography: *Anim.Behav.,* 2005, **70**:1429-1437 & DOI:10.1016/j.anbehav.2005.04.003, *Behav*., 2014, **151**: 1479-1490 & DOI:10.1163/1568539X-00003196, *Ethol.* 2006, **112**: 716-726 & DOI:10.1111/j1439-0310.2006.01225.x, 807-814 & DOI:10.1111/j.1439-0310.2006.01236.x010, **116**: 448-457 & DOI:10.1111/j.1439-0310.2010.01763.x

### 1.1.5.3. *The risk of couplings with foreign partners*

Male guppies *Poecilia reticulata* of Mexico, in waters where they live in sympatry* with neighboring species, recognize, among females, those of their own species and learn to distinguish them from females of the neighboring species *P. picta* and completely foreign females, those of the invasive goodeid *Skiffia bilineata*. This recognition, both innate and learned (6–14 days being necessary to learn to identify *P. picta*), should condition the choice of courting behavior and couplings. However, males of *P. reticulata* very often prefer the females of the introduced goodeid. As for females of the sheepshead swordtail *Xiphophorus birchmanni*, they manifest a clear preference for the males of their own species and are sensitive to their olfactory signals which are very attractive when homospecific males are numerous in their environment. In contrast, when the latter are rare and heterospecific males are numerous, their preferences weaken and they do not shy from accepting mating with males of neighboring sympatric* species such as *X. variatus* and *X. malinche.* Deficient olfactory signaling between sister species is

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deadly diseases (melanomas*). Similarly, females of *X. continens* are strongly attracted by the smell of the males of the neighboring species *X. montezumae* and mate with them rather than those of their own species. This heterospecific attraction is asymmetric, since females of *X. montezumae* are not sensitive to the smell of the males of *X. continens* who court them. The usual olfactory signal of the male destined for the female of his species is to indicate his presence at a distance, before visual signals can take effect, which enables him to be recognized as such and to foster homospecific couplings. Pheromonal* olfactory stimuli such as *metabolites**, *steroid hormones* and *prostaglandins* emitted by the males of the second species exercise here an attractiveness so strong that the choice of the females of the first species is invariably drawn to them. Signaling error can also occur as a result of confusion between olfactory messages differentiating the dominant males and courting females from small males, sneakers*, who are to be avoided. The male–female message outweighs that which indicates a heterospecificity.

Bibliography: *Anim.Behav*., 2008, **75**: 1731-1737 & DOI:10.1016/j.anbehav.2007.10.030, 2009, **78**: 265-269 & DOI:10.1016/j.anbehav.2009.02.029, 441-445 & DOI:10.1016/j.anbehav.2009.05.018, *Ethol.,* 2009, **115**: 1-7 & DOI:10.1111/j.1439-0310.2009.01710.x

Crosses between members of the same family, between brothers and sisters, between parents and children, are generally responsible for homozygosity*, generating a genetic depression which is accompanied inexorably by a decline of the genetic quality of descendants. Spawners avoid such a danger by putting in place behavioral corrections intended to reduce the harmful effects of these crosses within families and to promote crosses between individuals without a family relationship, generating the heterozygosity* required for the health and survival of their population. Among guppies, after several generations of consanguineous matings, males exhibit a weakening of their sexual motivation (decrease in the frequency and intensity of courtship behaviors) and a decrease in their reproductive success (lower number of progeny), lose the liveliness of their carotenoid*-based red color which was part of their attractiveness (Volume 2, section 1.1.2) and become much less attractive to females, this color being an indicator of their genetic quality. Females, thus informed of their lesser value, seek good males, owners of a better genome, at least if they are able to find them.

A behavioral adaptation to the risks of a deficit of fitness* linked to such consanguineous matings consists, for females, of eliminating the semen received during these incestuous crosses; such postcopulational avoidance can be frequently observed in the aquarium. However, there is counter-adaptive behavior on the part of males who, when mating with females of their own family, reduce their courtship behavior, but increase the quality and quantity of their ejaculations.

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Bibliography: *Biol.Lett.,* 2014, DOI:10.1098/rsbl.2014.0166

#### 1.1.5.4. *Insufficient behavioral barriers and successful consanguinities*

Although certain behavioral barriers exist, which tend to reduce their number, hybridizations* occur frequently in natural environments, between sympatric* species (Volume 2, section 1.1.5). On the Great Barrier Reef in Australia, spawning aggregations of groupers (Volume 2, section 1.1.6) bring together a large number of spawners of various species. Two of them, *Plectropomus leopardus* and *P. maculatus*, whose timing of reproduction and mating and fertilization behaviors are identical, sometimes court each other and release, at the same time, their gametes into the water column, giving rise to cross-fertilization which produces hybrid descendants who are perfectly viable and recognizable by their color patterns which are intermediate between those of their parents. The absence of reproductive isolation therefore makes these heterospecific crosses easy. Such hybridization has been easily reproduced in the laboratory, confirming the compatibility of the gametes of the two species.

Bibliography: *Aquacult.Res.*, 2007, **38**: 215-218 & DOI:10.1111/j.1365-2109.2007.01659.x, *J.Fish Biol.*, 2006, **68**: 1013-1025 & DOI:10.1111/j.1095-8649.2006.00977.x, *Mar.Ecol.Prog.Ser,* 2015, **518**: 239-254 & DOI:335 meps.11060

### *Spawning aggregations*

The grouping of members of the same species, in bands, groups, schools, aggregates, masses, leks*, etc. (Volume 1, section 1.1.1), obeys various imperatives: protection, locomotion, migration, feeding and reproduction. Truly solitary species are ultimately rare.

#### 1.1.6.1. *Temporary sexual segregation*

It is not uncommon for the two sexes to adopt different geographical areas and distinct habitats during their growth and during the period of sexual dormancy, but to find themselves gathered together in the reproductive period. Thus, the small-spotted catshark *Scyliorhinus canicula* practices sexual segregation in the Cantabrian Sea, to the south of the Bay of Biscay, with temporal and spatial differences of distribution. Adult males prefer shallow, warmer water habitats and adult females choose areas rich in euphausiacean prey (krill) in order to satisfy their large energy needs. Their sperm reserves, following a storage of semen, are such that they can dispense with the need for seeking a meeting with males every year.

Bibliography: *J.Fish Biol*., 2007, **70**: 1568-1586 & DOI:10.1111/j.1095-8649.2007.01444.x

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### 1.1.6.2. *Assured reproductive success*

The concept of aggregates particularly concerns spawners of a large number of species who tend to group together during reproduction and to form more or less dense groups which promote couplings between partners of both sexes and ensure greater fertilization success. For spawners dispersed in multiple habitats distant from each other, it often involves meeting in large numbers at the chosen sites, at a specific time in the seasonal calendar, in order to exchange their gametes and genes so as to grow the genetic diversity of their population.

Ephemeral spawning aggregations of pelagic species such as sardines *Sardina pilchardus* are observable in the Eastern Mediterranean, as also observed in the Aegean Sea, which promotes crosses between different stocks occupying a wide geographical area.

The mutton snapper *Lutjanus analis* of the Caribbean, which remain solitary on coral reefs, experience (from May to July of each year, with a peak in June) collective mating at well-identified traditional sites, as their ancestors have always done. Long migrations to such spawning areas are also of interest to spawners of neighboring species such as *L. cyanopterus* which, in Belize, are found in large numbers (4,000–10,000 spawners of both sexes), from June to August, on a reef promontory with a surface area of less than 1,000 $m^2$, upon which synchronization of spawning with the lunar phases ensures maximum breeding success. The stimuli inducing these behaviors are both thermal and photoperiodic, so as to ensure the best environmental conditions for survival of the eggs and then the larvae. However, many oophagic predators also attend the meetings at these spawning grounds where the density of the clouds of eggs can reach 1,500 eggs/$m^3$. Professional fishers also know very well the timetable of these immense sexual bacchanals.

The brown-marbled grouper *Epinephelus fuscoguttatus* forms spawning groups from November to January: a large number of spawners meet each year at specific sites in the Seychelles, respecting a lunar periodicity of 1–7 days before the new moon and 8–14 days after the full moon, during which period these spawners are particularly vulnerable to fishing, whether it is professional or recreational. The tropical groupers *Ep. guttatus*, *Ep. tigris* and *Mycteroperca venenosa* assemble similarly, during 1 or 2 months of each year, at –5 to –20 m depth, on the reefs of the Gulf of Mexico, when oceanographic conditions – temperature and speed of the currents at the level of upwellings* rich in nutrients* which enable a high concentration of chlorophyll a, leading to the development of a rich zooplankton – are favorable to the survival and dispersal of planktonic larvae who enable themselves to drift passively towards the reefs where they are assured of recruitment* (Volume 2, section 2.2.3). Those of *Ep. striatus* concentrate on the reef promontories of Belize, as these sites are geomorphologically determined as points

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for the annual rendezvous of spawners. Males of the white-streaked grouper *Ep. ongus* who are fatter – richer in *lipids* – remain longer than others at the breeding areas; their sexual activity is linked to their quantity of energy reserves.

The humphead wrasse *Cheilinus undulatus* meet in numbers (250) on the reefs of Palau. Females are more numerous than males, with ratios ranging from 6♀/1♂ to ♂. Courtship behaviors (Volume 2, section 1.1.3) before spawning are synchronized to the high tides so as to promote the dispersion of eggs. The Australian snapper *Pagrus auratus* of the western coasts of Australia meet in large numbers from September to January, and spawning occurs at the time of the full moon and new moon of each of these months, when low tides facilitate a weak hydrological circulation of eggs and their retention in these bays.

Tagging* spawners of the Atlantic cod *Gadus morhua* in Icelandic waters shows the existence of spawning aggregations of males who remain close to the substrate, at depths of -20 to -400 m, the level at which they form the leks* that females visit in search of spawning partners. They remain on these areas twice as long as the females who successively visit several of these places; the larger individuals of both sexes tend to remain faithful to a single aggregation.

Aggregations of nests in rock cavities of the peacock blenny *Salaria pavo* in Portuguese coastal areas favor their monopolization by a small number of males. As these owners of nests are rare, the females who are in a situation of intrasexual competition find themselves obliged to make courtship efforts for access to couplings, and demonstrate a high level of aggressiveness towards other females of the same species who are seeking to make the conquest of a rare male owner of a

Concentrations of spawners in nesting areas attract masses of consumers of eggs who seek to benefit from this manna of high nutritional value because of a wealth of fatty acids*, as shown by examination of the liver of the Indo-Pacific sergeant *Abudefduf vaigiensis*, an egg feeder that stores these lipids.

Bibliography: *Bull.Mar.Sci.,* 2008, **83**: 531-551, *Env.Biol.Fish*, 2015, DOI:10.1007/s10641-015-0362-8, *Fish.,* 2005, **103**: 404-410*, J.Fish Biol*., 2005, **67**: 83-101 & DOI:10.1111/j.10195-8649.2005.00714.x, 2007, **71**: 795-817 & DOI:10.1111/j.1095-8649. 2007.01545.x, 2010, **76**: 987-1007 & DOI:10.1111/j.1095-8649.2010.02553.x, **77**: 822-840 & DOI:10.1111/j.1095-8649.2010.02704.x, 1359-1378 & DOI:10.1111/j.1095.8649.2010.02756.x, *Mar.Biol*., 2008, **155**: 293-301 & DOI:101007/s00227-008-1027-7, 2014, **161**: 669-680 & DOI:10.1007/s00227-013-2369-3, *Mar.Ecol.Prog.Ser*., 2004, **517**: 265-270 & DOI:10.3354/meps11031, 2010, **405**: 243-254 & DOI:10.3354/meps08512, 2014, **506**: 279-290 & DOI:10.3354/meps10787, 2014, **517**: 209-216 & DOI:10.3354/meps11021, 2015,

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#### 1.1.6.3. *An attraction for predators*

On an atoll in French Polynesia, at the level of the pass connecting the lagoon to the open sea, a concentration of 600 grey reef shark *Carcharhinus amblyrhynchos* was observed over 17.5 ha. This corresponds to a biomass two to three times higher than any other concentration described for the aggregations of sharks, and requires a biomass of prey of 90 t/year, whereas the production of fish on this site is only about 17 t/year. Satisfaction of the energy needs of these resident sharks is offered, during the months of June and July, by the spawning aggregations of camouflage groupers *Epinephelus polyphekadion*, which include up to 17,000 individuals, with 971 individuals/hectare. These provide the sharks with a sufficient biomass of prey and even a surplus. This "windfall" tends to dry up when the surviving groupers leave their spawning grounds. The energy reserves accumulated by the sharks are then sufficient to enable them to await the arrival of successive new spawning aggregations of surgeonfish, parrotfish and various others during the lunar cycles of the following full moon and new moon. In their seasonal absence, sharks are forced to search for food outside of their usual habitat. Thus, the spawners of various species gathered on the reefs and which form traditional spawning aggregations in no way constitute occasional prey and "booster" energy resources, but are actually the basis of nutrition and even one of the conditions for the survival of shark populations. The overexploitation of spawning aggregations by local fisheries is likely to put at risk not only the targeted populations, but also those of their predators.

Bibliography: *Fish.Bull.*, 2005, **103**: 404-410, *J.Fish Biol.*, **86**: 162-185 & DOI:10.1111/jfb.2015, DOI:10.3354-1449, 2009, **74**: 754-762, *Mar Ecol.Prog, Ser.,* 2000, **534**: 149-161 & DOI:20.3354/meps11031

### *Practicing polygamy**

#### 1.1.7.1. *Fairly rare monogamy*

Some fish are known for their fidelity in love. The couples they form are sometimes sustainable, for the duration of a reproductive cycle or in exceptional cases for their whole life, as with some syngnathids. Thus, the dragon-head pipefish *Corythoichthys haematopterus* is strictly monogamous over a long duration. Males may complete a series of 10 consecutive cycles of reproduction with the same partner and are unable to improve their performance in the presence of a substitute female which is imposed on them, even though she is of greater size and more fertile. The short-snouted and long-snouted seahorses *Hippocampus hippocampus* *H. guttulatus* of the Atlantic and Mediterranean are thought to be faithful and live in couples throughout their lives, which is difficult to prove. More surprising is the fact that females of the tiger shark *Galeocerdo cuvier* of the north-eastern coasts

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of Australia appear to be monogamous based on the genetic examination of embryos collected from gravid females. Is this the result of a single copulation or of a "cryptic" selection of sperm of one of their multiple partners?

Bibliography: *Biol.Lett.,* 2008, **4**: 362-365 & DOI:10.1098/rsbl.2008.0157, *Ethol.,* 2007, **113**: 764-771 & DOI:10.1111/j.1439-0310.2007.01370.x, *Roy.Soc.Open Sci*, 2018, **5**, 1 & DOI: 10.1098/rsos.171385

### 1.1.7.2. *Wide sexual freedom*

Most species practice large sexual freedom with frequent changes of partners, which offers the advantage of a large mixing of genes inducing a large genetic diversity that is beneficial to the population. Males are adept at multiple couplings with a great diversity of females (polygyny*) and most often achieve greater reproductive success, but females are not passive and some practice polyandry*. Polygynandry is therefore common among fish.

Reproductive success of the Chinook salmon *O. tshawytscha* is higher in the case of polyandrous females when compared with monandrous* females. The presence of *hooknose** males and small *jacks** significantly improves the rates of fertilization and hatching. The development of practices favoring alternative couplings is recommended in breeding, given its populational benefits.

Male guppies *Poecilia reticulata*, very sexually active, have considerable reproductive potential, as evidenced by their multiple fatherhoods. Females who are able to choose as a partner firstly an ornate male, then a more shiny than the first, perform sequences of copulations based on the quality of the males encountered. These are stimulated by the presence of females and then produce ready-to-use sperm of good quality (36 spermatozeugmas containing 750,000 sperm per day). When females conduct multiple copulations with different males, it leads them to bring a series of genetically diverse newborns into the world.

Polygyny* is found, for example, among the daffodil cichlid *Neolamprologus pulcher*, a Lamprologini cichlid of Lake Tanganyika in which polygamous males are larger than monogamous* males and have larger testes in relation to their respective body size, in correlation with higher rates of the *androgenic hormone 11-KT*. In contrast, as owners of multiple territories and several spawning nests, they practice parental care (Volume 2, section 2.2) of lesser quality due to a lower energy investment. Among another cichlid of the same lake, the masked julie *Julidochromis transcriptus*, females benefit largely from the joint presence of large α males and β males in order to ensure their reproductive success thanks to their propensity to deposit their clutches on the edge of the territories of large males, where they are assured of a greater number of likely matings in areas frequented by various males.

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In general, all the mbuna cichlids, more than 295 species of Lake Malawi and other African Great Lakes, have been used as models of rapid speciation* and adaptive radiation; the extreme diversity of the morphs* and the remarkable polymorphism of colors are linked to the practice of broad polygamy*: polyandry* and polygyny*.

Bibliography: *Anim.Behav.,* 2003, **65**: 53-58 & DOI:10.1006/anbe.2002.2024, 2008, **75**: 1771-1779 & DOI:10.1016/j.anbehav.2007.09.037*, Behav.,* 2015, **152**: 231-245 & DOI:10.1163/1568539X-00003242, *Biol.Lett*., 2008, **4**: 623-626 & DOI:101098/rsbl.2008.0423, *Ecol.Freshwat.Fish*, 2012, **21**: 109-118& DOI:10.1111/j.1600-0633.2011.00528.x, *Ethol*., 2005, **111**: 1-23, *Fish Fish*., 2005, **6**: 1-34, *J.Fish Biol*., 2005, **67**: 1184-1188, 2017, **90**: 1244-1256 & DOI:10.1111/jfb.13223, **91**: 409-428 & DOI:10.1111/jfb.13377, *Proc.Roy.Soc.B*, 2003, **270**: 1623-1629 & DOI:10.1098/rspb.2002.2280

#### 1.1.7.3. *Viviparous females who store the semen of their multiple partners*

Among the viviparous shiner perch *Cymatogaster aggregata*, semen deposited by the various males (from 1 to 8) who have mated with the same female and inseminated her is retained for more than 6 months in the ovaries, in the form of packets called spermatozeugmas*. This storage ensures a rich descent with diverse genomes, as attested by microsatellite* genetic monitoring during successive parturitions*: 30 newborns every 2 months. A comparable storage of sperm is frequent in many viviparous teleosts and among elasmobranchs. A microsatellite* examination of embryos of the gray shark *Carcharhinus plumbeus* (3–8 per litter) confirms the existence of multiple fatherhoods.

Bibliography: *Can.J.Fish.Aquat.Sci*, 2007, **64**: 198-204, *Mar.Biol.,* 2011, **158**: 893-901 & DOI:10.1007/s00227-010-1616-0

### *Homosexuals*

#### 1.1.8.1. *The influence of early encounters*

The social environment influences the sexual orientation of fish, and their sexual behaviors are the consequence of their early encounters with members of the same species of one or the other sex. In the guppy *Poecilia reticulata*, early sexual orientation depends on the social environment. An absence of females and promiscuity with groups consisting only of males do not predispose to heterosexual behavior. Individuals reared for 15 weeks in all-male groups engaged in attempts at copulation, by thrusting gonopods*, with other males. This homosexuality, as a result of sustainably consolidated imprinting, continues even when females are presented to them and are accessible. They are then frightened by these females who

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behavior requires education in a mixed environment and early contact with females. The males then learn, during a critical period, how to behave with females in courtship (Volume 2, section 1.1.3) by observing other males in a copying process. Similarly, juvenile guppies *Poecilia wingei* raised in all-male communities for 30 days are then attracted by waters containing male olfactory messages – *pheromones* – and are not attracted to the odors of females. Such sexual odors influence their sexual performance and guide their courtship behaviors which remain exclusively inter-male. Evidence shows that the early social environment exerts a decisive influence on the later sexual behavior of fish whose sexual orientation becomes irreversible for the rest of their existence.

Bibliography: *Anim.Behav.,* 2004, **68**: 1381-1389 & DOI:10.1016/j.anbehav.2003.12.022, *Behav.,* 2016, **153**: 1419-1434 & DOI:10.1163/1568539X-00003387

#### 1.1.8.2. *An attractive effect on females*

Large males of the Atlantic molly *Poecilia mexicana*, whether belonging to surface populations or cave-dwelling, seek couplings with females, whereas small males of these populations prefer to associate with large males. Those of the cave-dwelling populations of Mexico who show no inter-male aggressiveness enable them to freely interact with them. Such homosexuality in males may appear, at first sight, to mean a waste of gametes and a loss of energy. On the contrary, this ejaculation is used to attract females, by rendering attractive some of these males that the females consider to be of quality. The buccal contacts that these males practice with the genital orifices of other males seem to constitute proof of virility, which induces attractive behavior in females. A small drab-colored male behaving in this way may then be preferred to a large colorful male.

Bibliography: *J.Exp.Biol*., 2013, **216**: vi & DOI:10.1242/jeb.081646, *Zeitschr.für Fischkunde*, 2005, **7**: 95-99.

### *Sexual disabilities*

#### 1.1.9.1. *Males who lose their attractiveness*

Even while males strive to use ornamental sexual characteristics (Volume 2, sections 1.1.1 and 1.1.2) in order to appeal to females and use stratagems to promote themselves by appearing, in the eyes of the latter, as attractive as possible (Volume 2, section 1.1.2), they sometimes fall victim to parasitic infestations that strongly affect their “look”. Females, who are often very demanding as to the quality of males with whom they agree to mate, often refuse those who suffer from any deficit compared to the standards which are usually required. Small size is a frequent reason for rejection, especially on the part of larger females, but being affected by a

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worm infection constitutes a criterion for refusal of mating and rejection. Thus, males of the sailfin molly *Poecilia latipinna* who are affected by black spot disease, morphologically recognizable by the presence of black spots on their skin caused by encystment of metacercariae* of the trematode *Uvulifer* sp., are inevitably excluded by females from sexual selection, to the benefit of other males in good health.

Males of the American rainbow darter *Etheostoma caeruleum* adopt brilliant nuptial color patterns consisting of orange and blue colored bands which attest to their quality. A parasitic load responsible for black spots of the *black spot disease* affects the orange pigmentation of λ* = 550–625 nm, regarded as an honest signal of the state of health of these males and which is used by females in the practice of sexual selection. Similarly, males of the minnow *Phoxinus phoxinus* parasitized by the worm *Philometra ovata* experience a lower rate of reproductive success. Females use both visual (coloring) and olfactory signals at the same time to detect suspect individuals. The sticklebacks *Gasterosteus aculeatus*, at the juvenile stage, are frequently infested, via an ingestion of copepods which act as vectors, by the cestode *Schistocephalus solidus*, an endoparasite which disrupts their breeding capacity in England, Scotland and Canada where the parasite is endemic*. A deficit of their gonadal development and a weakening of their physical condition are notable. When the red coloration of the males is blurred, they show less attractiveness. A reduction of secretion of spiggin* by the kidney (Volume 2, section 2.1.1) that accompanies the parasitic infestations is responsible for a deficit in nest construction. However, in Alaska, such parasitic castration has not been seen. Infested males and females are still able to produce gametes and reproduce in spite of high parasitic loads and lower energy investment. If the red pattern of the males' throats has lost all meaning, females estimate their sexual value by the color of their

Females of the Siamese fighting fish *Betta splendens* reject males contaminated by chemicals such as *17α-ethinyl estradiol* (*EE2*, *endocrine disruptive chemical*). These chemical pollutants disrupt sexual selection.

Bibliography: *Behav.,* 2008, **145**: 625-645, *J.Fish Biol.,* 2009, **75**: 2095-2107 & DOI:10.1111/j.1095-8649.2009.02411.x, 2014, **84**: 1590-1598 & DOI:10.1111/jfb.12361

### 1.1.9.2. *Spermatic handicap*

The worst sexual handicap that a male may experience is a depletion of its intratesticular sperm reserves. It is therefore appropriate for him to be able to manage his potential of available semen in order to allocate it properly to the females with which he mates, without the risk of being a victim of running dry. The males of the European bitterlings *Rhodeus amarus* who practice multiple repeated

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decline after the fifth ejaculation, especially if they are forced to increase the amount of their ejaculations in the presence of male rivals who sometimes form groups of 60 and above, in order to be the victors of the sperm competition. The size of ejaculates is higher in the morning than in the afternoon (90,000 and 40,000 sperm respectively). The difficulty is all the greater for males in that, if the sperm concentration is at its maximum within the mussel which hosts the oocytes freshly deposited by females (Volume 1, section 3.4), during the first 30 s after ejaculation, the semen is then removed from the branchial cavity via the excurrent siphon of the mollusk. "Bourgeois" males of the lamprologue *Lamprologus callipterus* who practice a high rate of polygyny* during a long breeding season have a limited sperm potential, imposing upon them a reduced reproductive effort. In the presence of rivals superior in number, dwarf males have the advantage of being able to penetrate into the empty shell of the gastropod where the female is located. Males whose size prohibits them such access must ejaculate in the vicinity of the opening of the shell. They are, however, able to reduce their output of sperm by approximately 50%. It is useful to be able to save sperm with the perspective of future successes in the absence of rival competitors.

The tactic of spermatic retention is commonly practiced by nesting males subjected to the pressure of the ejaculates of sneakers*, fertilization thieves.

In addition to these problems, the male may be the victim of simulated spawning on the part of the female. It thus ejaculates for nothing. The fertility of male Japanese rice fish *Oryzias latipes* decreases over successive ejaculations, with fertilization success being 83.7% during the first mating and 40% during the 17th mating. The duration of courtship reduces in parallel, 1.5 min against 3.4 min, constituting an indicator of their reproductive potential. Females adapt the dimensions of their clutches and the number of eggs laid to the gradual decrease in their partner's virile capacities.

Bibliography: *Anim.Behav.*, 2009, **77**: 1-7 & DOI:10.1016/j.anbehav.2009.01.027, 1227-1233 & DOI:10.1016/j.anbehav.2009.01.027, 2017, **125**: 3-12 & DOI:10.1016/j.anbehav.2016.12.06, *Biol.Lett*., 2010, **6**: 727-731 & DOI:10.1098/rsbl.2010.0139

### 1.1.9.3. *Immunological disability*

Among the peacock blenny *Salaria pavo*, the dominant males called bourgeois, owners of nests who generally encounter greater success in mating and fertilization, suffer from a certain immune deficit, an immunological disability not suffered by the small male *sneakers** (Volume 2, section 1.2.1), who, although weaker, possess a certain health benefit.

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Bibliography: *Behav.*, 2005, **142**: 979-996, 2008, 2011, **148**: 909-925, 2013, **150**: 1709-1730, *Behav.Ecol.Sociobiol.*, 2006, **60**: 159-165, *J.Fish Biol.*, 2007, **71**: 298-303, 2009, **75**: 2095-2107, 2014

## 1.1.10. *More or less aberrant sexuality*

### 1.1.10.1. *Behavioral abnormalities*

Reproductive behaviors are usually the result of learning and copying by young adults who take advantage of the experience of older adults who are their demonstrators. A social environment is thus useful for the completion of successful reproduction. Deprivation of such a social environment, following experimental isolation, is reflected in the cichlid *Pelvicachromis taeniatus* by clumsy behavior, a deficit of courtship activity performed by males, an absence of intrasexual aggressive behavior in a situation of competition and even of a certain disinterest in couplings.

Bibliography: *Anim.Behav.,* 2016, **111**: 85-92 & DOI:10.1016/j.anbehav.2015.10.004

### 1.1.10.2. *Hybrid crossings*

A capacity for self-perpetuation, in the absence of regular sexuality, is found in an original and exceptional way among the American minnow *Phoxinus eos-neogaeus*. This is a hybrid resulting from the crossing between a female of *P. neogaeus* sp. and a male of *P. eos* sp. which has no preference for coupling between females of its species and those of *P. neogaeus* sp. Having spread widely in North America, this sterile hybrid maintains its populations thanks to the regular parental activities of two species which intersect continuously. It has several advantages of *fitness**, in relation to its parental species: more rapid growth during the first 60 days and greater vigor – the heterosis* effect. The species is maintained and resists attrition over time thanks to unceasing sexual activity of the two mother spawner species.

Bibliography: *Can.J.Fish.Aquat.Sci*, 2012, **90**: 577-584 & DOI:10.1139/z.2012-023, *Env.Biol.Fish*., 2013, **96**: 1111-1121 & DOI:10.1007/s.10641-012-0107-1

### 1.1.10.3. *Precocious and simplified sexuality*

Rare species, in particular of gobies, are distinguished by their small size and conservation of larval characters at the adult stage, with a simplified anatomy – of juvenile characteristics such as a transparent body devoid of scales – and reproduction at a very early stage or paedomorphosis*. The Indo-Pacific Schindler's *Schindleria praematura* of the Red Sea is among the smallest vertebrates, where

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females reproduce at a size of 7.5 mm to a mass of 2–6 mg. Their life is a brief 3 months, which is an interesting case of neoteny*.

Among the transparent goby *Aphia minuta*, these infantile characteristics are considered to be an adaptation to pelagic* life and a short lifespan of less than 1 year, with the achievement of two clutches of eggs during this brief period which precedes their death in the autumn.

Bibliography: *J.Fish Biol*., 2000, **58**: 656-669 & DOI:10.1016/jfbi.2000.1478, 2008, **72**: 1539-1543 & DOI:10.1111.j.1095-8649.2008.01811.x

### 1.1.10.4. *Gynogenesis, a form of aberrant sexuality*

The gynogenesis* of the Prussian carp or Gibel carp *Carassius gibelio* is included in the category of aberrant sexuality (Volume 2, section 1.1.10).

### 1.1.10.5. *Natural androgenesis*, very exceptional*

Reproducing in the absence of the genome of the female gamete seems like something extraordinary, even impossible. And yet…

No natural androgenesis had ever been described up to the recent discovery, in Portugal, of the case of a cyprinid *Squalius alburnoides* endemic to the Iberian peninsula, whose genome is of exclusively paternal origin, with any maternal nuclear *DNA* being totally absent. Examples of males capable of generating descendants who are solely theirs, giving birth to individuals who are thus clones* of their paternal spawners, were only known, up until then, among some insects (bees, wasps, ants, etc.), following neutralization or natural elimination of the maternal chromosomes. This would therefore be the first proven cases of natural androgenesis described in a vertebrate species. In effect, only artificial cases of androgenesis making use of techniques of artificial fertilization have been described in carp. It is evidence of the remarkable capabilities of genetic substitution.

Note that the genetic peculiarity of this fish is that it is aneuploid*, i.e. it possesses an abnormal number of chromosomes with a triple set of chromosomes – integral trisomy – due to an ancient mutation which would be fatal in a mammal, but which is viable in this fish, the expression of one of the sets of chromosomes is being inhibited by a process that is still poorly understood.

Bibliography: *Roy.Soc.Open Sci*, 2017, **4** & DOI:10.1098/rsos.170200

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## 1.2. The phase of realization: couplings and spawning

The partners of both sexes, having made the effort – and sometimes, especially the males, large efforts! – to promote themselves and to display their qualities, owe it to themselves to reap the benefits and to carry out couplings which promise beautiful reproductive success as quickly as possible. These operations are not always simple to conduct, in view of intrasexual competition linked to the presence of rivals everywhere, the variable mood of their partners who must be permanently convinced and the risk of predation during a lapse in their vigilance.

### *Alternative mating strategies*

#### 1.2.1.1. *Males with optional and/or alternative behavior*

Sexual behaviors are not as stereotyped as we might believe. In various species, males have several strategies for access to females and reproductive success, either consequently to courtship behavior inducing consensual couplings (Volume 2, section 1.2.2), or in a less courteous manner, by the imposition of force during forced couplings (Volume 2, section 1.2.4) or by cunning: sneakers* performing stolen fertilizations.

The choice of behavior adopted by males is generally not premeditated, but depends both on the potential of the spawner – its genome, size, age, know-how, previous experience and social history – and on the environmental conditions at the present time with the respective number of rival males and females, as well as that of predators.

Male guppies *Poecilia reticulata* adopt the most favorable tactic, which corresponds to a compromise between the benefits and costs of each available alternative strategy in the existing environmental conditions, depending on the sex ratio* of spawners where there is frequently an imbalance in favor of males and/or females, as well as the presence or absence of predators in the neighborhood. When females are numerous, males choose long courtships (Volume 2, section 1.1.3) by using sigmoidal* swimming movements in order to obtain the favors of the best of them, the most fertile, within the framework of natural sexual selection. On the contrary, if the number of males is high, the latter, faced with strong intrasexual competition, abandon their gallant and polished manners in favor of stolen fertilizations, behaving as thieves or sneakers*: approaching the females from behind and taking advantage of their high swimming maneuverability, they try to insert their gonopod* in the female's genital orifice, being capable of reoffending at a rate of one attempt per minute and thereby achieving the insemination, against their will, of 15% of non-receptive females. These sneakers* are generally males of

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compensate by seeking to impose themselves by cunning. Such behavior corresponds to a real intersexual conflict; this form of parasite fertilization runs contrary to the natural choice exerted by females in the framework of sexual selection which tends to favor the best males (Volume 2, section 1.1.1), with such undesired descendants rarely being genetically compatible and prosperous.

Courtship and *sneaker** behaviors may alternate depending on the number of females present. When these are many, the male guppy ceases to expend a large amount of semen which is costly in energy and, ceasing to play a courtship role, contents itself with forced copulation followed by ejaculations of lesser volume, which are therefore more economic. Males of the Endler's guppy *P. wingei* maximize their reproductive success by alternating their behavior in approaching females between courtship and *sneaking** based on the nearby competition, opting for courtship behavior in a population where the sex ratio is biased towards females and, on the contrary, practicing stealth couplings if the sex ratio is biased towards males. The largest, most colorful and most courageous males of this species court females, in contrast to those who are small, drab-colored and of fearful disposition who behave as *sneakers**.

The modalities of mating affect the behavior of female guppies *Poecilia reticulata* who prefer copulation which is desired and freely made with males that they have chosen, because these are superior to forced copulation, imposed by small males towards whom they feel no attraction. The modalities of cooperation outweigh those of coercion – thrusting of gonopods* – in terms of reproductive success, because chosen couplings with males of large size who have color patterns rich in *carotenoids**and perform courtship behaviors produce progeny in greater numbers and of better quality than those produced with less desirable partners. Females retain the ability to eject a part of the semen with which they are inseminated by sudden movements, for example by shaking themselves.

However, it does occur that females are satisfied with these imposed fertilizations which assure them a high reproductive potential and guarantee them a wide genetic diversity. The best of a bad job. In addition, they have the ability to manipulate the sex of their offspring according to the attractiveness of the males with which they mate. When they mate with males whom they like in cooperative copulations, the number of males is higher in their progeny; these males are of high genetic quality, which corresponds to an increase of the fitness* of the couple. As for the males, they tend to manage their large spermatic stock which is costly in energy so as to proceed to a well-measured allocation of sperm depending on the circumstances of the couplings. The quality of the semen is also a function of environmental conditions: males who court females in a peaceful environment tend to produce sperm whose swimming performance is superior to that when males are

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response to visual stimuli which reflect opportunities for immediate couplings and adjust their insemination, emitting up to 92% of their stock of sperm to ensure for the lucky female an optimal rate of successful fertilizations.

Males of the sailfin molly *Poecilia latipinna* also have high behavioral plasticity with respect to their mode of mating, being capable of either courting females or stealing fertilizations in the manner of sneakers*. If large males preferentially practice courtship behaviors, fins erect and body curved, and small ones the theft of fertilizations by thrusting gonopods*, intermediate-sized males show a plasticity in alternating between the two types of behaviors. These behavioral differences are expressed in genetic terms, on the molecular basis of neurological function: at the level of expression of certain genes in the brain, sneaking* is associated with an over-regulation of genes involved in learning and memory, as if this plasticity of behavior required a cognitive effort higher than that of simple courtship. Males of Yucatan molly *P. velifera* present a large variability of the size of their dorsal fin compared to their body size, which has the consequence of inducing a large range of choice for females to the advantage of large males with large dorsal sails, and fostering a high degree of expression of alternative behaviors between dominant courting males and sneakers* in search of stealth couplings.

Among the grass goby *Zosterisessor cephalus*, the males' coupling strategy, courtship or sneaking*, during their first breeding season, depends essentially on their acquired size at the time of reproduction, which is a direct consequence of their age. The black goby *Gobius niger* of the lagoon of Venice also chooses its alternative coupling tactic based on its own capabilities (size, age, amount of reserves of energy and sperm, richness in mucins* of its seminal vesicles*) and especially on the surrounding social context (number of male competitors) in order to avoid wasting its energy needlessly. Male sneakers*, free riders and pirates, compete with bourgeois males of the common goby *Pomatoschistus microps*. Such "liberalism" of sexual practices promotes broad genetic intermixing which generates gene diversity.

Bibliography: *Anim.Behav.,* 2007, **74**: 679-688 & DOI:10.1016/j.anbehav.2007, 03.005, 2014, **88**: 195-202, 2016, **112**: 105-110 & DOI:10.1016/j.anbehav.2015.11.024, *Ethol*., 2016, **122**: 456-467 & DOI:10.1111/eth.12491, *J.Exp.Zool.,* 2004, **301**A: 177-185 & DOI:10.1002/jez.a.20019, *J.Fish.Biol*., 2000, **56**: 1381-1368, 2007, **71**: 1864-1872, *J.Evol.Biol.*, 2006, **19**: 1641-1650J.*Mar.Biol.Ass.UK*, 2002, **82**: 333-337, *Proc.Roy.Soc.B*, 2013, **277**: 3195-2001 & DOI:10.1098/rspb.2010.0826, 2014, **281**: 20132310 & DOI:10.1098/rspb.2013.2310, *Zool.Sci.,* 2011, **28**: 98-104 & DOI:10.2108/zsj.28.9811

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### 1.2.1.2. *Variable reproductive success*

In the zebrafish *Danio rerio*, large dominant individuals coexist with small *sneakers**. If large size is an advantage in terms of dominance and attractiveness to females, small size does not necessarily constitute a disability if we are to judge by the number compared to reproductive success. In effect, a low size is associated with high maneuverability that enables these small subordinates* to quickly gain close proximity to females.

The populations of the pumpkinseed *Lepomis gibbosus* of American origin (today widespread in Western Europe) comprise two categories of males: the larger and older build nests and attract females to them while the smaller, taking advantage of their body shape which gives them maneuverability and speed, behave as parasites who perform lightning raids on parental nests to furtively approach females and attempt to fertilize a part of their oocytes. Endowed with high endurance, they are able to frequently repeat their mating attempts. These sneakers*, who constitute 40% of males in the population, often achieve 15% of the fatherhoods of the progeny, evidence that large males, in spite of their efforts for the hunt, are cuckolded quite regularly (Volume 2, section 1.2.10).

It is not always so. Social factors also determine the chances of reproductive success. Thus, among the three-spot wrasse *Halichoeres trimaculatus*, the secondary males called terminals, who are the result of the masculinization of females (Volume 2, section 1.2.10), are dominant and owners of territories, monopolizing females and ensuring almost all the couplings, in contrast to the primary males who are males from birth and who, being too small, are deprived of such opportunities.

The reproductive success of the two categories of males of the blenny *Enneapterygius* sp. depends on the vigilance of the territorial males who hunt small sneakers* and seek to prohibit them from approaching the females. Video tracking* in nature shows that small male "thieves" are forced to ejaculate later than territorial males and at a greater distance from the females, leading to many failures and low rates of fertilization. However, some sneakers*, who hide in shelters and then "rush" upon females, taking advantage of the absence of the territorial male busy pursuing other small males, enjoy fertilization success.

The fertilization success and performance of their progeny, in females of the Arctic char *Salvelinus alpinus*, in the case of fertilization of oocytes with the semen of dominant males, are not higher than those obtained in crosses with the semen of subordinate males.

The competitive situation of subordinate males is sometimes like that among the cichlid *Astatotilapia burtoni* which leads to, among them, social suppression of

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their spermatogenetic activity is not interrupted and, after a weakening of the dominance exerted by large males, they can, after a few days, produce powerful semen and participate in reproduction. As sexual opportunities can always occur, it is good to be constantly ready.

Hydrological environmental conditions sometimes prove unfavorable to the practice of *sneaking**. Thus, during the phenomena of eutrophication* which occur in the Baltic Sea, small males of the stickleback *Gasterosteus aculeatus* show less activity, hampered as they are by a lack of visibility for detecting mating opportunities which are likely to arise.

Bibliography: *Anim.Behav.,* 2015, **108**: 129-136 & DOI:10.1016/j.anbehav. 2015.07.029, *Environ.Biol.Fish*, 2010, **89**: 71-77 & DOI:10.1007/s10641-010-9691-0, *Ethol*., 2011, **117**: 1003-1008 & DOI:10.1111/j.1439-0310.2011.01953.x, *J.Fish Biol*., 2007, **71**: 284-289 & DOI:10.1111/j.1095-8649.2007.01477.x, 2009, **75**: 2163-2174 & DOI:10.1111/j.1095-8649.2009.02403.x, *Mol.Ecol*., 2008, **17**: 2310-2320 & DOI:10.1111/j.1365-294X.2008.03746.x, *Proc.Roy.Soc.B*, 2012, **279**: 434-443 & DOI:10.1098/rspb.2011, 0997

### 1.2.1.3. *Three categories of males*

The social status of males of the dwarf gourami *Trichogaster lalius* (formerly *Colisa lalia*) is established around three categories of individuals: dominant territorial males who defend their territory and the nest that it contains, secondary males who are found in the vicinity of the nest and who sometimes dispute the authority of the first, and males who remain distant from the nest and do not display aggression. The size of the testes is correlated with the status of each category, with their gonadosomatic index (GSI)* being respectively 1.20, 0.80 and 0.60. The dominant males are the best producers of semen; their activity of territorial defense increases their reproductive success, because females are sensitive to this behavior.

Among the ocellated wrasse *Symphodus ocellatus*, three male phenotypes coexist: owners of nests, the sneakers* and the satellites who are all in competition for access to females. Their respective behaviors depend on their concentrations of *androgenic hormones 11 KT–testosterone* and the expression of their neural cerebral genes (Volume 2, section 4.3) which determine the plasticity of their tactics of reproduction that alternate between competition and cooperation.

Alternative strategies of reproduction are frequent in salmonids, among whom three categories of males seek the favors of females: large hooknose* males, and small jack* males who are either sneakers* or satellites*. The success of fertilization of oocytes spawned by the females in the spawning nests (Volume 2, section 2.1.1) varies depending on the situations imposed: by force for some or by cunning for others. Alternations of phases of cooperation and coercion, with large aggressive and

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combative males and small *sneaker** males, characterize the reproductive behavior Coho salmon *O. kisutch* on their spawning grounds in California. Females tend to prefer to mate with small males who are less agitated.

An alternative spawning strategy occurs in the sockeye salmon *O. nerka*, among whom coexist two categories of females: the "classics" with red nuptial coloration, but also silver females with later sexual maturation, reducing the risk of inter-female competition, whose clutches avoid the risks of overuse of resources (Volume 2, section 2.1.1.3).

Among the endemic* cichlids of Lake Tanganyika such as *Neolamprologus callipterus*, large bourgeois males and males of medium size are in competition with small dwarf males of 28–47 mm, whose weight is about 2.5% of the large ones and who seek, according to a parasitic tactic, to steal fertilizations by penetrating furtively into the gastropod shells where the females are located. Although possessing well-developed testes, these sneakers* contribute only weakly to the rates of paternity of offspring. Similarly, among the cichlid *Telmatochromis temporalis* of the same lake, small males of 20–40 mm are able to penetrate into the shells of gastropods where the females are located, while large males of 10 cm cannot enter into these shells and are forced to ejaculate outside. The competition is such that the young are faced with a choice: to remain small, invest their energy in precocious testicular development and finally adopt sneaker* behavior, or else concentrate on growth with the hope of becoming dominant males. Among the cichlid *Ophthalmotilapia ventralis*, large bourgeois males tirelessly pursue the small sneakers* to prohibit their access to females, benefiting a third category of males, the floaters, sexually mature and whose size and physical condition are such that the females are interested in their courtship behavior and willing to succumb to reproductive parasitism.

Bibliography: *Anim.Behav*., 2005, **70**: 1055-1062 & DOI:10.1016/j.anbehav.2005.01.025, 2009, **77:** 1409-1413 & DOI:10.1016/j.anbehav.2009.01.039*, Ethol.,* 2004**, 110**: 49-62*,* 2014, **121**: 152-167 & DOI:10.1111/eth.12324, *Funct.Ecol.,* 2010, **24**: 131-140 & DOI:10.1111/j.1365-2435.2009.01605.x*,, J.Fish Biol*., 2006, **69**: 1731-1743, 2009, **75**: 1846-1856 & DOI:10.1111/j.1095-8649.2009.02442.x, *Zool.Sci*., 2005, **22**: 555-561, 2012, **29**: 141-146.

### 1.2.1.4. *Knowing how to make choices*

A status of dominance related to large size is not always an assurance of greater reproductive success, because the energy consumed in the growth of the body is sometimes lacking for gonadal development. Unlike the case of gouramis previously mentioned, large males of the sand goby *Pomatoschistus minutus*, strongly colored and territorial, show a testicular mass three to four times lower than that of small

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activity*. Disadvantaged by their small size and not popular with females, these sneakers* compensate for their disability with a better ability to win the sperm competition, by using a large number of sperm which are very mobile during a longer period, approximately 2 h as opposed to a few minutes, which gives them a greater power of fertilization.

Among the peacock blenny *Salaria pavo*, competition between males for access to nests dug into the rocks is severe and not all males can claim possession of one of them, as cavities conducive to nesting are often scarce. It is the large dominant males, richest in the secretion of the *androgen hormone 11-KT*, who monopolize them. Younger, smaller males become sneakers* who must be satisfied with seeking to steal fertilizations and who are in competition, not only with dominant nest-makers who are known as bourgeois, but also with satellite* individuals with ornamented color patterns imitating those of females and with a high hormonal rate, but who are not the owners of nests. The bourgeois males, however, pay a price for their hormonal valor in displaying an immune deficit due to a lesser immunocompetence of their lymphocytes*, the reverse of that of *sneakers** who, on the contrary, display better potential health. Dominance has a cost in health.

Part of the population of the Atlantic cod *Gadus morhua* in the North Atlantic (up to 35% of the biomass of potential spawners) do not participate in spawning. These are young females whose "past nutritional deficit" has not allowed them to accumulate sufficient energy reserves to ensure normal vitellogenesis. Rather than produce deficient oocytes, they prefer to practice temporary abstinence and wait for the following year to reproduce. Do they not still have a "reproductive future" of a dozen years?

Bibliography: *Can.J.Fish Aquat.Sci*, 2006, **63**: 186-189, 200-211, *Ethol.,* 2009, **115**: 555-565 & DOI: 10.1111/j.1439-0310.2009.01636.x, *J.Fish Biol*., 2010, **76**: 1609-1625 & DOI:10.1111/j.1095-8649.2010.02587.x

### *Freely consensual couplings*

Fish reproduction puts into play various behavioral tactics which promote the meeting of the gametes of the two sexes.

The various modalities of mating range from simple contact between spawners, with the formation or not of a coupling followed by "external fertilization", to a very intimate encounter with the meeting of gametes in the genital tract of the female followed by "internal fertilization". In the latter case, several behavioral modalities are found: genital coitus by touching together the male and female genital pores, as in the case of the oviparous and ovoviviparous scorpaenids, cloacal coitus (in the

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elasmobranchs) and the "kiss" or buccogenital coitus among drinkers of semen and among some cichlids.

Complex reproductive equipment has been described in the males of South American catfish (genera *Corydoras*, *Callichthys*, etc.). The modalities of intromission relate to the transfer of sperm assembled into packets of spermatozeugmas thanks to the combination of seminal vesicles which secrete mucins (*mucopolysaccharides*, *mucoproteins*). Due to a low dilution of male gametes in a space formed by the meeting of the pelvic fins of females during couplings followed by external fertilizations, males produce only a small amount of semen and invest only little energy in their spermatogenetic production.

Bibliography: *J.Fish Biol*., **70**: 243-256.

### 1.2.2.1. *Perfect love*

When the courtship behaviors of males, who perform ritual swimming movements such as zigzags, figures of 8, dances, etc., have been satisfactorily completed and the preliminaries to coupling are sufficiently advanced, with the females having been fully seduced, the two mutually chosen sexual partners often show, by agreed signals, the intention to conclude and move on to the act. Thus, females of the delicate swordtail *Xiphophorus cortezi* show their partner their imminent intention to lay their mature oocytes in order to invite him to prepare to fertilize them. For this, they lower their head (head-down) and, their body being tilted at 30–45°, they peck at the substrate in order to visually show their receptiveness and positive motivation. These events are the more numerous and spectacular, the larger their partner is in size and the more he corresponds to the desired status of the preferred male. Presentation to the gaze of the male of the black spot that indicates their gonopore* can only facilitate the latter's task.

Males of the sailfin molly *Poecilia latipinna* see their spermatogenetic activity* increase when they are in the presence of females, which has the effect of increasing their distribution of semen during a transfer of spermatozeugmas* into the gonoduct of females. Such successful insemination maximizes their reproductive success, which is all the greater when it is freely granted by the female.

The reproductive success of the female guppy *Poecilia reticulata* is greater when they mate with desirable males whom they have chosen during cooperative cooperation, as opposed to forced copulation which gives rise to descendants of low quality. The number of sperm inseminated during a copulation depends directly on the perception that the female has of the attractiveness of her partner. This is most often a richly colored partner (Volume 2, section 1.1.2) whose sperm production is precisely optimal. The duration of this copulation is decided by the female who is

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she does not like. In addition, when females mate with the most attractive males, the sex ratio* of their descendants is biased in favor of males.

However, if courtly love, accompanied by courtship behaviors (Volume 2, section 1.1.3), is often practiced between fish who desire each other, it is not always so and forced couplings are not rare, sometimes even becoming violent (Volume 2, section 1.2.4).

Bibliography: *Biol.Lett.,* 2009, **5**: 792-791 & DOI:10.1096/rsbl.2009.0413, *Ethol.,* 2009, **115**: 682-690 & DOI:10.1111/j.1439-0310.2009.01650.x, *Zool.Sci,* 2011, **28**: 98-104 & DOI:10.2108/zsj.28.98

### *Harassers*

Social relations between the two sexes depend essentially on the respective number of males and females within a population at the time of reproduction. They are peaceful when the sex ratio* is balanced, but become conflictual when one sex is in deficit in numbers – an unbalanced sex ratio* – which causes high intrasexual competition among the representatives of the sex in excess. However, such harassment is conditioned by the presence of an "active" organ of insemination: only species possessing a gonopod* or pterygopods* may have recourse to it, as is the case for small poeciliids (guppies) and elasmobranchs (skates, rays and sharks) who practice "phallic coitus".

#### 1.2.3.1. *Very numerous and very active males*

Couplings of the guppy *Poecilia reticulata* are often harmonious when the partners form well-matched and cooperative couples. On the contrary, hyperactive and/or frustrated males adopt more violent behaviors and proceed to forced copulation by performing gonopod* thrusts into the genital pore of non-consenting females. These males do not harass only the females of their own species, but are also capable of practicing sexual harassment against females of *Skiffia bilineata*, a goodeid of Mexican origin introduced into the waters of Trinidad which resembles them. They court them intensely – 25% of courtship behaviors are heterospecific – and attempt forced copulation upon them, even when females of their own species are present in excess; the rounded silhouette of these foreign females is particularly attractive to them. As no hybridization is possible between these two species, the inseminations are sterile and, in the end, only constitute a waste of time and energy. However, these defenseless females are at risk of suffering genital lesions due to the spiny gonopod* possessed by male guppies.

western mosquitofish *Gambusia affinis*, sexual intercourse is also often

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section 1.2.1), seek to mate with females in a coercive manner, leaving only a few opportunities for the latter to practice the sexual selection to which they aspire. Males of their cousin species *G. holbrooki* are distinguished, in Australia, by their ability to manifest an intense mating activity, spending the greater part of their time (90%) in pursuing females at a rate of one attempt to couple per minute in a very wide range of temperatures between 22 and 34°C. It is only at less than 18°C and more than 34°C that these males cease their harassment.

Bibliography: *Anim.Behav*., 2005, **70**: 463-471 & DOI:10.1016/j.anbehav. 2004.12.010, 1387-1394 & DOI:10.1016./j.anbehav.2004.12.024, 2006, **72**: 585-593 & DOI:10.1016/j.anbehav., 2005.11.016, *Biol.Lett.,* 2008, **4**: 149-152 & DOI:10.1098/rsbl.2007.0604

### 1.2.3.2. *Avoiding coercive couplings*

When they become victims of such sexual harassment, female guppies reduce their fertility and may even stop feeding, limit their growth and fertility, and die. They thus never cooperate with such ungallant males and resist them by brutal accelerations of swimming, so that more than 90% of mating attempts made by these males are unsuccessful. They most often seek to flee, and adopt an avoidance strategy by gathering together and excluding males, forming tight schools in order to dilute the risk of coercive couplings. They are also sometimes forced to occupy difficult habitats such as those rich in predators, thereby accepting an increased risk of being eaten for having peace. Another way for female guppies to escape small male harassers is to locate themselves in flowing waters of great speed where small males are excluded. Acts of copulation decrease with increasing speed of the currents, which prohibit mating attempts carried out by those with low swimming abilities. Only males of great size and with high energy capacities, which enable them to be the best swimmers and be sufficiently valiant to court them in a full current, will have access to these females who will then have the best chances of wide reproductive success. Some females may also find an advantage of remaining in the vicinity of a large male, who vigorously excludes the unwelcome. Some studies also tend to demonstrate that such harassment is not without negative consequences for male harassers, since their mortality rate increases.

Females of the shortfin molly *Poecilia Mexicana* often flee from the presence of males who pursue them with assiduity and disrupt their feeding. In addition the visual presence of male rivals reduces the sexual harassment to which females are victim. Males, in a situation of strong sexual competition, are then victims of a diversion effect that obliges them to prioritize dealing with their rivals and to abandon the females for a while.

When they become victims of harassment by over-ardent males, female eastern

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females in order to dilute the risks, or attach themselves to other males with a view to try to provoke inter-male competition that would generate intrasexual conflict and reduce the intensity and the frequency of their pursuit.

In contrast, cave-dwelling populations living in difficult environments – darkness, $H_2S$ (Volume 1, section 1.1.3) – do not experience this "lustful fever".

Bibliography: *Anim.Behav.,* 2006, **72**: 75-81 & DOI:10.1016/j.anbehav.2005.09.022, *Behav.,* 2007, **144**: 503-514, 2008, **145**: 73-98, 2009, **146**: 1739-1758 & DOI:10.1163/000579509X12483520922124, *Biol.Lett*., 2008, **4**: 449-451, *Ethol.,* 2006, **112**: 592-598 & DOI:10.1111/j.1439-0310.2006.01188.x, 2017, **123**: 242-250 & DOI:10.1111/eth.12593, *Proc.Roy.Soc.B*, 2012, **279**:1748-1753 & DOI:10.1098/rspb.2011.2212

#### 1.2.3.3. *Imposed preferences*

Alternative coupling tactics are frequent in salmonids and female preferences are sometimes surprising, contrary to the choices made by many other species in favor of large males (Volume 2, section 1.2.1). Females of the coho salmon *O. kisutch* prefer to mate with small males, the jacks*, rather than with the large hooknose males who are aggressive fighters. The duration of their oviposition is longer with these jacks*, as if they wanted to give the latter opportunities to succeed in their fertilizations. In nature, however, they are often brought to mate with large males whom they do not prefer, in order to avoid having to pay the cost of harassment and the risk of injury or deprivation of food.

### *Violent couplings*

The male of the priapus or penis head fish *Phallostethus cuulong* – Priapus, the Greek god of fertility – is a small Vietnamese freshwater fish in the delta of the Mekong River. Its anatomical particularity lies in possessing its testes in a very forward position, under its mouth. This oddity is accompanied by an original mode of coupling, since this male seizes its partner by harpooning her, thanks to a copulatory organ named "priapium", a clamping system consisting of appendices corresponding to its modified pectoral and pelvic fins which form a pair of claws and enable the male to better grab hold of his partner. This fish, who has a penis on its head, rises rapidly towards the female, grabs her head which he grips, and transfers his sperm into her genital orifice which is located at the cephalic level, thus ensuring high reproductive success.

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**Figure 1.5.** *Male of the priapus* Phallostethus cuulong *possessing a cephalic clamping system intended to inseminate the female*

Some male guppies *Poecilia reticulata*, like those of other poeciliids, especially if they are small and not accepted by females – sneakers* (Volume 2, section 1.2.1) – proceed, bluntly and without courtship behavior, to direct insemination of females, following an intromission of their copulatory organ, the gonopod*, into their genital tract. This organ is made up of several rays of the anal fin and is equipped at its end with a pair of claws that enable the male to better grab hold of his partner, especially when the latter, not consenting and non-receptive, resists mating attempts and seeks to escape. This system of grasping proves effective: three times more semen are transferred into the genital tract of females by a clawed gonopod* than by a gonopod experimentally deprived of its spikes.

Some couplings, although not deemed to be violent, leave traces, in the form of spawning marks on the skin of the females, as in those of the spined loach *Cobitis* . Such marks are the result of a strong embrace by the male winding his body around the abdomen of the female in order to establish close contact between their respective genital orifices, which promotes the success of fertilizations. These marks, which disappear after a few weeks, are used by biologists to assess the dates of reproduction.

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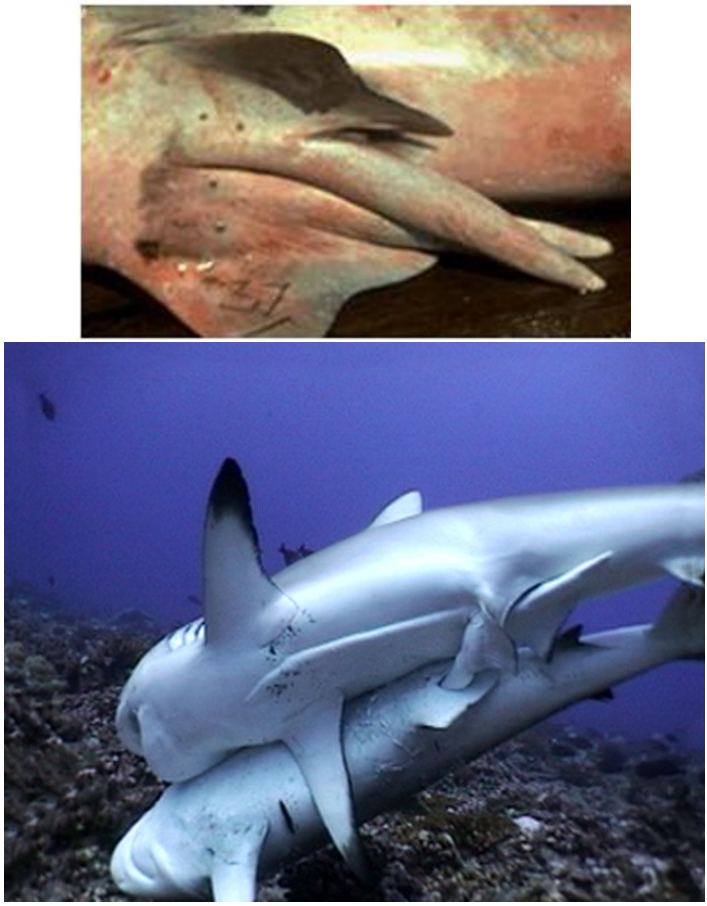


**Figure 1.6.** *The two pterygopods of a shark (top); copulation of sharks (bottom): a male pterygopod penetrates the genital tract of the female whom he holds on the bottom (source: Y. Hubert)*

The couplings of sharks are particularly ungentle, such as those of the reef shark *Triaenodon obesus* which have been filmed in Costa Rica: three or four males surround one female, then one of them seizes her with his jaws by her pectoral fin while holding her head down, firmly pushed onto the bottom. The insemination of semen is conducted by one of the two paired copulative organs, the pterygopods, which is introduced into the cloaca of the female. The male's siphon bags filled with sea water exert hydraulic pressure to expel the semen into the genital tract. The injuries caused by the bites of these violent males are long visible in the form of

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scarification on the skin of the females and constitute a useful indicator for biologists who can thus date their mating periods.

Visible scars on females of the manta *Manta alfredi* are significantly lateralized, 99% of them affecting the left pectoral fin due to bites inflicted when coupling. Males present a dental dimorphism with more developed cuspids* than those of females; their teeth are functional only for copulatory purposes. It has been deduced that this quite stereotyped precopulatory bite is intended to induce the receptivity of females.

The females of the bull shark *Carcharhinus leucas*, the blacktip reef shark *C. melanopterus*, the scalloped hammerhead *Sphyrna lewini*, the blue shark *Prionace glauca* or the mako shark *Isurus oxyrinchus* also suffer this type of coupling which generates injuries inducing lasting scars. As the smell of blood excites the surrounding males, the latter advance upon the injured female, not to mate with her, but to devour her. The rate of multiple mating is about 50% in the gray shark *Carcharhinus plumbeus* according to genetic estimates of their progeny at Hawaii. In the Northwest Atlantic, male blue sharks impose themselves on females, even though the latter are still immature; precopulatory couplings are responsible for scarification at the level located between the gill slits and the first dorsal fin, as well as on the pectoral fins. Measurement of the diameter of the semi-circular bites, which reflect the size of the oral opening of males, is used to assess their size and age. The presence of fresh semen in the genital tract of these sub-adult females reflects these couplings, and the absence of scarification on the skin of the males shows the absence of reciprocal bites. However, males are only aggressive during the period of reproduction that is generally seasonal; females may then enjoy necessary periods of sexual rest.

As the cycle of sexual development is slow for the sand devil *Squatina dumerili* in the Gulf of Mexico, entailing 2 years of vitellogenesis for 10 oocytes of a size greater than 60 mm + 1 year of gestation, the females only undergo sexual assault every 3 years.

Bibliography: *Anim.Behav.*, 2004, **68**: 1435-1442 & DOI:10.1016/j.anbehav.2004.02.018, *Biol.Lett.*, 2013, **9**: 20130267 & DOI:10.1098/rspb.2013.0267, *Can.J.Fish.Aquat.Sci*, 2007, **64**: 198-204 & DOI:101139/F07-005, *Env.Biol.Fishes*, 2017, **100**: 1603-1608 & DOI:10.1007/s10641-017-0668-0, *Fol.Zool.*, 2008, **57**: 168-171, *J.Fish Biol.*, 2007, **70**: 1350-1364, 2008, **72**: 488-1503 & DOI:10.1111/j.1095-8649.2008.01810.x, 2010, **77**: 169-190 & DOI:10.1111/j.1095-8649.2010.02669.x, 2015, **86**: 1845-1851 & DOI:10.1111/jfb.2015.86.issue-6/issuetoc

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## Hybrids

### 1.2.5.1. *Interspecific crosses considered to be genetic pollution*

Crosses between individuals of different species generate a hybrid progeny that generally shows mixed characteristics transmitted by the separate genomes of their parents. These crossings are generally adverse, considered to be “genetic pollution”, because it infringes on the genetic purity of each of the parental species.

Two species of American mosquitofish (*Gambusia affinis* and *G. nobilis* are capable of hybridizing, the barriers of reproductive isolation not being strict, because forced copulation occurs. However, their low number (less than 10%) also implies the existence of postzygotic* barriers in the form of embryonic mortalities and sterility of the offspring.

Hybridizations are frequent between salmonids, either between species of trout, or between trout and salmon. Thus, the Slovenian marbled trout *Salmo marmoratus*, endemic* to the Soca River, was threatened with extinction as a result of intensive restocking of this river by the brown trout *S. trutta*, with which they mate to produce hybrids. An attempt at the preservation of this original species was undertaken, putting an end to this genetic pollution by a policy of repopulation involving exclusively Slovenian marbled trout. Such a policy of rehabilitation of the original populations has been partially successful.

In the United States, hybridizations between rainbow trout *Oncorhynchus mykiss* introduced into water courses populated by the native cutthroat trout *O. clarkii* have caused genetic depression in native trout, whose reproductive success has fallen sometimes by 50%.

In France, repopulation operations of river trout *S. trutta fario* carried out for decades at the initiative of fisheries federations in Mediterranean watercourses have infringed on the genetic purity of the populations of Mediterranean origin, which have been introgressed* by the genomes of Atlantic trout from fish farming who served as spawners in the hatcheries. Efforts at repopulation by spawners of local origin are practiced today. Such efforts are undertaken to attempt to maintain the originality of the Mediterranean strain *S.t. macrostigma*, which are still naturally present in some Corsican and Sardinian rivers, upstream from isolated watercourses and not sullied by restocking. Two sympatric species of barbels, *Barbus carpathicus* *B. barbus*, hybridize in the Vistula, but in an asymmetrical manner; the genetic introgressions* of the first into the second are not reciprocal and are thus only dangerous for this latter.

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In Finnish lakes, the introduced vendace *Coregonus albula* hybridizes with the native whitefish *C. lavaretus*, the latter undergoing a stronger genetic introgression*, with their hybrids being viable and productive.

Marine hybridizations may be seen at the oceanic level following introductions, as in the archipelago of Hawaii where the recently arrived Indo-Pacific sergeant *Abudefduf vaigiensis* hybridizes with the native species *A. abdominalis*. Genetic data – nuclear* loci, *mtDNA** – confirm the existence of their interfertile crosses: the possession of a transitory yellow color pattern by the invasive* species during reproduction coincides with the similar permanent coloring of the endemic species*; such phenomena of genetic introgression* risk the extinction of the native species.

Bibliography: *Ethol.,* 2011, **117**: 208-216 & DOI:10.1111/j.1439-0310.2010.01861.x, *Mol.Ecol*., 2011, **20**: 3838-3855 & DOI:10.1111/j.1365-294X.2011.05209.x, 2014, **23**: 5552-5565 & DOI:10.1111/mec.2014.23.issue-22/issuetoc – *Les Poissons d'eau douce de France*, Berrebi *et al*., 2011, ed. Biotope, p. 231

### 1.2.5.2. *Crosses between individuals of different origin*

Crossings often occur, in nature, between wild individuals and members of the same species resulting from selection by aquaculturists who escape from fish farms, as occurs in the Norwegian fjords between Atlantic cod *Gadus morhua*; more than 300,000 individuals escaped in 2008 in Norway. Wild males mate interchangeably with females of both categories, while females have a preference for the wild males, which enables them to be the origin of 75% of the progeny. Hybridizations between wild fish and hatchery fish are considered to be dangerous because of introgressions* and the fact that individuals of domestic origin disrupt natural spawnings.

Crosses between populations of the same species generally induce a certain deficit of fitness* in their descendants, who are likely to suffer from incompatibility between the parental genomes. Evidence of infertility as well as non-viability of embryos, which are subject to anomalies and skeletal deformations, have been described in a variety of species of African cichlids, in relation to an incompatibility of their genomes. Viability of the descendants depends on the nuclear and mitochondrial genetic characteristics of the female. Thus, a spawning female of weak ancestry is responsible for the production of small numbers of newborn, following the existence of abortive embryos in a viviparous poeciliid in the south-west of the United States, the killifish *Heterandria formosa*, even though the father belongs to a prolific population. Such crosses are considered to be asymmetric, since a reciprocal cross between a prolific female population and a male from a population of numerically weak ancestry produces offspring consistent with the genetic characteristics of the maternal population, i.e. capable of producing a large progeny.

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Crossings occur, in Canada, between males of Chinook salmon *O. tsawytscha* escaped from fish farms and wild females. No difference was found between the fertilization success of the two categories of males in competition on the spawning grounds, but the fish originating from hatcheries show, in nature, lower survival rates of their fry compared to those of the wild strains.

Bibliography: *Biol.Lett*., 2013, **9**, DOI:10.1098/rspb.2013.0327, *Can.J.Fish.Aquat.Sci,* 2010, **67**: 1221-1231 & DOI:10.1139/F10-066, 2013, **70**: 1691-1698 & DOI:10.1139/cjfas-2013-0181, *Mar.Ecol.Prog.Ser.,* 2010, **412**: 247-258 & DOI:10.3354/meps08670

### 1.2.5.3. *Successful interspecific hybridization*

Many natural hybridizations are not accompanied by genetic defects. Identification of genetic markers – mtDNA*, microsatellites* – reveals a high rate of hybridization between the two species of shad *Alosa alosa* and *A. fallax* from Irish waters; their genomes are introgressed* without apparent disadvantage. Similarly, European sturgeon *Acipenser sturio*, *A. oxyrinchus* and *A. naccarii* are capable of hybridization that constitutes a harmless natural phenomenon.

Hybridizations are common between cyprinids of different species such as between the common nase *Chondrostoma nasus* and the south-west European nase *C. toxostoma* in the Durance River whose hybrids are viable, as well as those derived from the roach *Rutilus rutilus* and the common nase *Chondrostoma nasus* in the Danube. Reciprocal natural hybridizations are also frequent between the two species of European bream, *Abramis brama* and *Blicca bjoerkna*. Embryonic development and hatching rate are high and comparable to those of the parental species. Interactions occur, in Sweden, between males and females of several species of sympatric cyprinids* such as the common rudd *Scardinius erythrophthalmus*, the crucian carp *Carasius carassius* or bream *Blicca bjoerkna*. The production of semen by males – the volume of milt constituted sperm and secretions of seminal fluid – is identical in the presence of pre-ovulational females, conspecific as well as heterospecific, which proves an interspecific identity of endocrine signals and reveals a strong ability for cross-fertilization.

Bibliography: *Cybium,* 2004, **28** suppl: 51-61, *J.Fish Biol*, 2009, **74**:1669-1676 & DOI:10.1111/j.1095-8649.2009.02230.x, 2012, **80**: 147-165, *PLoS ONE*, 2009, **4**: e5962 & DOI:10.1371/journal.pone.0005962

### 1.2.5.4. *Hybridizations which generate biodiversity*

The populations of cichlids in the African Great Lakes (Victoria, Malawi and Tanganyika) are remarkable for their extreme biodiversity that is largely due to the existence of very many hybridizations between sympatric species* rich in

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of remarkable speciation*. Similarly, coral reefs, which cover less than 0.1% of ocean surfaces, are among the richest in marine species (approximately 5,000). The explanation advanced for such biodiversity involving the labrids, pomacentrids, serranids, gobiids and chaetodontids, as well as acanthurids focuses on the existence, in the absence of geographic barriers, very many interpopulational crosses, as well as intergeneric and interspecific hybrids. Geneticists are currently undertaking to explain these – gene flow by allopatry*, sympatry* or parapatry* – by trying to give them a chronology in relation to molecular clocks.

The diversity of modalities of hybridization is such that their genetic consequences are highly variable, from a deplorable form of genetic pollution to some cases which are quite normal and even those of vital necessity. It also constitutes an engine for the creation of new species or speciation* and an irreplaceable source of biodiversity.

Bibliography: *Biol.Lett.*, 2013, 9 & DOI:10.1098/rsbl.2013.0658, *Ethol.*, 2007, **113**: 673-685 & DOI:10.1111/j.1439-0310.2007.01372.x, *Evol.,* 2010, **64**: 617-633 & DOI:10.1111/j.1558-5646.2009.00849.x

### *Fleeting loves*

If a few species form sustainable couples, others, the most numerous, experience only brief passing romances, forming ephemeral couples. The dusky grouper *Epinephelus marginatus* experiences mating in which the only moments of intimacy for each spawning couple are reduced to the sexual act itself, which only lasts for a few seconds. Indeed, in the breeding areas of the Medes Islands in Catalonia where hundreds of candidates for love meet and form, in August, spawning aggregations (Volume 2, section 1.1.5): each male who manages to seduce a female by patrolling near the bottom springs up quickly with her, flank against flank, in the water column, towards the surface (a vertical ascent from 6 to 10 m in height). This rush culminates in the synchronous emission of their sexual products, as evidenced by the cloud of sperm and oocytes, which, like fireworks, punctuate this act of reproduction, after which the couple separates to restart its “rise to the seventh heaven” a few minutes later with a new partner.

A good number of marine species practice such rituals of spawning by proximity: couples quickly form only to separate, immediately after the act of mating, in order to find new adventures.

Bibliography: *Mar.Ecol.Prog.Ser.*, 2006, **325**: 187-194.

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### *Discreet love*

The social environment plays a large role in reproductive behavior. Fish couples tend not to like the presence of rivals of the same species during the preliminaries to mating, preferring to avoid the "audience effect" and seeking discretion. Males of shortfin molly *Poecilia mexicana* usually woo females in an environment lacking competitiveness.

On the contrary, the presence of other males, conspecific rivals, disrupts their courtship behavior, leading them to abandon the company of the female that they had initially chosen and to attend a less-preferred female, perhaps to deceive these competitors due to the risk to being copied. The presence of spectators is therefore prejudicial to the smooth conduct of a process of seduction and males prefer tranquility to better concentrate on their single objective: to seduce a female and mate with it. In fact, they cannot divide their attention between the female that they seduce and males whom they must chase out of their territory, which presents a conflict of motivations.

Similarly, the dominant males of the guppy *Poecilia reticulata* interrupt their courtship in the presence of one or several of their own species and will not resume their courtship activity towards the large females whom they prefer until 24 h later, when the danger of sperm competition has disappeared. Coupling decisions, following sexual selection (Volume 2, section 1.1.1) practiced by these poeciliids, therefore depend on the social environment; the presence of male competitors and/or predators disturb the traditional loving behavior. It is not simply modesty which justifies such discretion. Visual obstruction of their environment due to the presence of opaque barriers and dense structures capable of providing couples with real "privacy" promotes courtship behavior and greatly improves reproductive success. Sometimes the trouble caused by voyeurs is reduced in some difficult environments. Thus, while surface-dwelling males show aggressiveness towards their rivals, the cave-dwelling forms, some of who are sighted and who therefore receive visual signals of the existence of spectators, show very reduced aggressiveness and do not seem disturbed, being particularly anxious to save their energy in an extremely dark and toxic environment rich in hydrogen sulfide ($H_2S$).

The sticklebacks *Gasterosteus aculeatus* conceal their love in the nest built by the male (Volume 2, section 2.1.1.5); therefore, they are sheltered from others of their species – both spectators and predators. They also appreciate the discretion and the "secrecy of alcoves": their courtship behavior is more intense – a greater number of zigzags – in an environment hidden from the eyes of rivals. Disruption to intimate relationships between the partners of a couple is also common among the Siamese fighting fish *Betta splendens*. Females of this species are particularly sensitive to the

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presence of other females in their neighborhood; such a presence, referred to as the "audience effect", disrupts their reproductive behavior.

Bibliography: *Anim.Behav.*, 2004, **68**: 465-471 & DOI:10.1016/j.anbehav.2003.08.024, 2005, **69**: 1317-1323 & DOI:10.1016/j.anbehav.2004.10.010, 2006, **72**: 959-964 & DOI:10.1016/j.anbehav.2006.03.007, 2008, **75**: 21-29 & DOI:10.1016/j.anbehav.2007.05.013, *Behav.*, 2010, **147**: 1657-1674 & DOI:10.1163/0005795X528206, *Ethol.,* 2011, **117**: 10-18 & DOI:10.1111/j.1439-0310.2010.011849.x

### *Cuckolds and cuckolders*

"Extramarital" couplings and fertilizations that are the result of couplings "outside established couples" are fairly common in fish. Inter-male competition is exercised in a context of greater sexual freedom, with winners, the cuckolders, and losers, the cuckolds. Indeed, the constitution of a sustainable couple, a situation that is also very rare, may at any time be in question.

Many species practice alternative reproductive strategies (Volume 2, section 1.2.1). In these cases, small subordinate sneaker* males, very active, highly mobile and very maneuverable, are able to steal fertilizations to the detriment of the dominant males whom they cuckold. Among the sand goby *Pomatoschistus minutus*, who are very polygamous, microsatellite* studies of the genome of embryos and larvae enable us to judge the respective fertilization success of male nest-owners and of sneakers*. These have highlighted that the fertilization success of the latter is considerable, since half of the nests contain eggs of their paternity and 27% of those laid are derived from them. The practice of such cuckoldry reduces the chances of monopolization of females by guardian males, which has the effect of limiting the role of sexual selection. Nesting males also sometimes steal fertilizations by pirating the nests of their neighbors. The frequency of these criminal acts does not depend on the scarcity of spawning nests and is equal among male owners of a nest, whether it contains eggs or not, and among male *sneakers** who possess no nest.

In addition to the considerable risk that the guardian male incurs to his progeny during his absence, even of short duration, it is particularly dangerous for him to leave his nest and thus be exposed to predators. The need to exploit all opportunities for coupling to maximize their reproductive success by extramarital fertilizations is therefore the strongest, and the thirst for adventure affects even these fathers of families. In the bluegill *Lepomis macrochirus*, parental males who are builders of nests and qualified as "bourgeois" must face competition – sperm competition – from small *sneaker** males, who seek to enter furtively into the nest and fertilize some of the oocytes spawned by females that are found there. Large male owners of

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offspring from that of their cuckolders, and manage to restore good order by destroying the eggs considered illegitimate. Molecular analysis of the genome of the young present in the nests of the damselfish *Chromis chromis* containing, in addition to the dominant and nesting male, the presence of two to seven *sneakers** per nest shows that, if the large male ensures 49% of fertilizations from 2 to 13 females present, each small sneaker* ensures, on its side, approximately 7% of fertilizations, showing evidence of cuckoldry which is responsible for high genetic diversity in the population.

This strategy of cuckoldry is flexible and often limited in quantitative terms of success of fatherhoods: the rates of paternity for sneakers* are, in some cases and in contradiction with a previous statement, lower than those of large males, as exemplified by the plainfin midshipman *Porichthys notatus* in which nesting males provide the bulk of fatherhoods.

However, such liberalism of morals and similar generalized cuckoldry prove to be beneficial, because these behaviors provide wide genetic intermixing which promotes gene flow and ensures a greater genetic diversity of populations.

Bibliography: *Behav.,* 2014, **151**: 1029-1227 & DOI:10.10163/1568539X-00003180, *Biol.Lett.,* 2013, **9**: 20130658, *J.Evol.Biol,* 2006, **19**: 1641-1650, *J.Fish Biol.,* 2016, **89**: 2643-2657 & DOI: 10.1111/jfb.13130, *Proc.Nat.Acad.Sci*, 2001, **98**: 9151-9156, *Ethol.*, 2005, **111**: 425-438,

## *Hermaphrodites*

### 1.2.9.1. *Doing without a sexual partner*

Rare species are capable of self-fertilization, thanks to the possession of mixed gonads, the ovotestes*, in which occurs a synchronous maturation of the two categories of gametes. The spermatozoids provide fertilization for the oocytes present. Such hermaphrodite self-fertilizations are found in the mangrove killifish *Kryptolebias marmoratus* of the United States. These functional hermaphrodites are, however, not alone, since they coexist, in the same galleries dug by crabs in which they establish themselves, with a small number of males, sometimes 2% of the population, who mate with them in order to ensure a certain genetic mixing and gene renewal essential to the sustainability of the populations that, without them, would be victims of depletion of their genomes. The cohabitation of 25 individuals per gallery corresponds to a social facilitation of crossed couplings. The males, of an orange-pink color pattern, are preferentially attracted, thanks to olfactory signals related to the major histocompatibility complex (MHC)* (Volume 2, section 1.1.1), to hermaphrodites of mottled brown color whose genomes are most dissimilar to

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ensuring avoidance of any genetic depression. Similarly, the hermaphrodites prefer to mate with males rather than with other hermaphrodites. The assortment and coupling choices between males and hermaphrodites then determine the genetic future of each population.

Bibliography: *Ethol*., 2011, **117**: 586-596 & DOI:10.1111/j.1439-0310.2011.01916.x, *Mol.Ecol*.2013, **22**: 2292-2300 & DOI:10.1111/mec.12238, *The Amer.Natur.,* 2013, **181** & DOI:10.1086/670304

The need, in this same species of killifish and in view of maintaining a certain genetic diversity of the population, to avoid self-fertilization and ensure heterosexual crosses, is so compelling that the hermaphrodites compete for the favors of the few males present in the burrows. The lower the number of the latter (2–20% depending on the population, with a maximum of 25% in Belize), the fiercer the competition between the hermaphrodites who, to obtain from these males the new genes necessary for their descendants, have recourse to aggression. This belligerent behavior leads to the establishment of a social hierarchy in each of the holes of these small cyprinodonts, with the largest – maximum 60 mm – and the most aggressive hermaphrodites enjoying the greatest number of matings with males and the greatest genetic diversity of their progeny. Their ability to sense by smell the degree of genetic familiarity of the males present leads them to select original candidates and to avoid wasting their time and energy in coupling with males who lack genetic originality; thus, a rejection of those of their close family is considered to be too genetically similar to them. Homozygous individuals* are also few in number, because they are the most vulnerable to parasitic infestations due to a weakening of their immune defenses.

Bibliography: *J.Fish Biol.,* 2007, **71**: 1383-1392 & DOI:10.1111/j.1095-8649.2007.01603.x

### 1.2.9.2. *Cross-fertilization*

Among hermaphrodites called “simultaneous”, such as the American perch *Diplectrum formosum*, the coexistence, in a single ovotestis*, of mature oocytes in its dorsal part and functional sperm in its ventral part, the two territories having no communication, does not enable self-fertilization *in situ*. In this perch, although the simultaneous maturation of the two categories of mature gametes renders self-fertilization possible in open water, there would be no self-fertilization, because synchronous maturation does not imply synchronous emission of gametes. Cross-fertilizations between these hermaphrodites occur during mixed couplings, during which alternating and opposite emission of male and female gametes by each partner occurs, leading to populational heterozygosity*. These heterozygotes generally constitute 25% of the population.

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Bibliography: *J.Fish Biol*, 2010, **77**: 676-691 & DOI:10.1111/j.1095-8649.2010.02710.x

## 1.2.10. *Transsexuals*

### 1.2.10.1. *Ordinary hermaphroditic fish*

Hermaphroditic fish have long been zoological curiosities. We know today that it is only, contrary to what was long thought, a common biological phenomenon that we encounter in 27 families and seven orders of teleosts, in particular of tropic marine percids, reflecting a certain lability of sex and usually responding to demographic drivers within some populations.

Two forms are distinguished: simultaneous or synchronous hermaphrodism and successive or sequential hermaphrodism, with generally flexible modalities of more or less mixed gonads which are the ovotestes*, sexual allocations being very diversified, under endocrine control, and often in response to populational imbalances.

The ovotestes of the painted comber *Serranus scriba* are constituted of a dorsal ovarian part containing oocytes and a ventral testicular part, completely independent, consisting of seminiferous cysts which ripen at the same time: synchronous hermaphrodism.

The ovotestes of various sparidae, including the gilt-head bream *Sparus aurata*, are also made up of two distinct territories which operate alternately during the life of the fish: a functional dorsal ovary and a latent ventral testis, or a latent dorsal ovary latent and functional ventral testis, which reflects successive hermaphrodism.

Bibliography: *Fish Fish.*, 2008, **9**: 12-43, *J.Fish Biol.*, 2007, **71**: 1383-1392.

The ovotestes of the dusky grouper *Epinephelus marginatus*, like that of *Labrus* , do not show sectorization of sexual territories: it is the whole of the gonad which is involved in changing sex. At a given time in the life of the fish, female sexual cells or oocytes which, among the young, occupy the gonad in ovarian lamellae are replaced among older individuals, from undifferentiated stem cells, the primordial germ cells (CGPM)*, by male cells in which spermatozoids mature within seminiferous cysts. Such sexual inversion concerns a successive differentiation of the various categories of sexual cells inside the gonad, under hormonal induction.

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Bibliography: S.Bruslé, 1982: *Contribution à la connaissance de la sexualité de poissons marins hermaphrodites, Doctoral thesis at the University of Perpignan, 360 p.*

### 1.2.10.2. *Fish that lead a double sexual life*

Cases of sequential or successive hermaphrodism are interesting, because they reflect the existence of a double sexual life, sometimes even a triple life led by certain individuals who spend the first part of their lives with one functional sex, which then, as a result of sexual inversion, spend a second part or even, more exceptionally, a third, with the other sex just as functional. Such an ability to change gender is not rare, since it involves more than 350 species belonging to 27 families: sparids, serranids, labrids, scarids, pomacentrids, etc.

### 1.2.10.3. *Why change sex?*

Such a sex change is not simply a fantasy intended for a certain individual comfort. Its interest is populational and mainly reflects a social requirement: maintaining an operational sex ratio* and ensuring, in all circumstances, fertilizations enabling the production of progeny.

If the reproductive success of a fish increases with its size or age more quickly with one sex than with another, it can change sex in the appropriate direction in order to obtain higher reproductive success than if it did not change sex. If the gain of reproductive success is higher for a male, in relation to its size or age, than if it remains a female, a protogynous type sex change (♀→♂) seems favorable: a large older male, which dominates the social group, monopolizes couplings with many young females as in the case of harems where he is the winner of the sperm competition by ensuring the majority of fatherhoods. The opposite situation called protandry* (♂→♀) enables the emergence of large females having higher fertility rates than those of small females. Such changes of sex in two directions are consistent with a model called “size advantage”.

If a sex change may provide certain populational benefits for certain species, it should also be noted that the effects of overfishing may prove to be quite harmful to some of them when subject to an over-intensive fishing effort which, by reducing the number of spawners of the sex more dangerously exposed to capture, generally the large specimens, causes a deficit in representatives of a particular sex and limits the reproductive success of the population. Compensation may be obtained by rapid sexual inversion of males in the case of protandry* or of females in protogyny*, with the appearance of increasingly young spawners in order to maintain or restore a sex ratio* compatible with the survival of the population.

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The clown-fish *Amphiprion ocellaris* are protandrous* and the social organization of the couple is dominated by the female, the larger of the social group. Second-class individuals are male, and others do not reproduce. The dominance of the female is reflected in terms of aggressiveness, and dominated third-class individuals undergo permanent stress that causes a delay in their growth as well as sexual inhibition, following a low rate of *11-KT-testosterone* which causes temporary castration.

The gag grouper *Mycteroperca microlepis* is a successive protogynous* hermaphrodite (♀→♂), among which a deficit in the number of males can become critical. In fact, males, which are larger and older than females, are caught more than the latter by fishers and are more vulnerable to fishing gear, especially when they form spawning aggregations on their breeding sites (Volume 2, section 1.1.6). Unable to ensure fertilization of the many females present, these males are collectively victims of a certain shortage of sperm, which can only induce, by way of consequence, a certain collapse of stocks. Only a sexual inversion of females may compensate for this deficit in males, therefore a return to a more balanced sex ratio*, guaranteeing the survival of the population.

In another protogynous species, the tropical reef parrotfish *Chlorurus spilurus*, the sex ratio* is often unbalanced in favor of females, especially in sites where populations are dense and a sex change is late. This is in contrast to highly fished areas which translate into a reduction of male individuals and by a sex change with earlier masculinization, at smaller sizes. There is an urgent need to equip the population with new males, making possible the plasticity with which this phenomenon can occur. But this rule can sometimes admit a few exceptions. Thus, in the bucktooth parrotfish *Sparisoma radians* of Panama, classically viewed as a protogyne*, some older females of larger size than males forget to change sex, in order to maintain strong reproductive potential within the harem. They grow faster and live longer than males who suffer greater mortality by predation, which may justify a quite exceptional social organization. This case is closer to that of the Mediterranean rainbow wrasse *Coris julis*, among whom some females do not change sex. Among the protandrous gilt-head bream *Sparus aurata*, a deficit in females of large size may induce early compensatory feminizations of males.

Most of these changes of sex are carried out in accordance with a model of "size advantage" which recalls the natural preferences of species that usually choose sexual partners of large size.

These examples highlight the interest in developing protected areas designed to preserve these precious males (protogyny), and of course these precious females (protandry), without which the populations would be threatened with disappearance.

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conservation of a sufficient number of spawners of a population, by being very vigilant with regard to the larger and older specimens, among many of the protogynous* hermaphroditic species of groupers of the genera *Mycteroperca*, *Epinephelus*, etc., parrotfish of the genus *Scarus*, snapper of the genus *Pagrus*, or wrasses of the genus *Labrus*, as well as among the protandrous* species such clown-fish of the genus *Amphiprion* or even the gilt-head bream of the genus *Sparus*.

Changing sex is conditioned by social and demographic influences among the protogynous* black sea bass *Centropristis striatus*. A ratio of 9 females to 0 males maintained in a basin for several months causes a sexual inversion or masculinization of some females, the larger ones, while a ratio of 6♀/2♂ and 4♀/4♂ causes no sex change. A treatment with the *androgen 11-KT* accelerates this phenomenon of sexual inversion, while that of the *estrogen* $E_2$ inhibits it. Such sexual inversion can be boosted, in nature, by overfishing responsible for a deficit in one of the two sexes.

Bibliography: *Anim.Behav.,* 2007, DOI:10.1016/j.anbehav.2007.06.025, *J.Fish Biol*., 2006, **69**:1491-1503 & DOI:10.1111/j.1095-8649.2006.01212.x, *Proc.Roy.Soc.B,* 2014, **281**: 20132423 & DOI:10.1098/rspb.2013.2423, *The Amer.Natur.*, 2003, **161**: 749-761, 2009, **174**: n°3 & DOI:10.1086/603611

### 1.2.10.4. *Endocrine control of a sex change*

A sex change is controlled, from the endocrine point of view, by *sex steroids* and initiated by neuronal brain secretions: *gonadotropin releasing hormone* (*GnRH**) *arginine vasotocine* (*AVT**). Thus, among the protogynous* honeycomb grouper *Epinephelus merra*, the *steroid hormones* play a decisive role in the sex change from female to male. After a decline in the concentration of the *estrogen -estradiol* ($E_2$) and an increase in the concentration of the *androgen 11-ketotestosterone* (*KT*), the latter playing a decisive role in masculinization following a regression of the ovaries and development of the testes, the 11-KT causes inhibition of the enzyme *aromatase P450* which controls the synthesis of $E_2$. The *androgenic hormone 11-KT*, catalyzed by a steroidogenic* enzyme, the *cytochrome -hydroxylase*, is also involved in the testicular differentiation of a protandrous male as in the yellow-tail clownfish *Amphiprion clarkii.* Populations of the wrasses *Halichoeres poecilopterus* and *H. trimaculatus* contain two types of male: primary males, whose testicular development is direct, and secondary males, who are masculinized former females; such a situation is referred to as diandry*. This sex change or masculinization is under the endocrine control of *androgen hormones – testosterone* – or instead consecutive to treatment with an inhibitor of aromatase, the enzyme* which affects the biosynthesis of the female hormone *17β-estradiol* ($E_2$). Conversely, primary males undergoing an experimental implantation of $E_2$ develop

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ovarian tissue in 51–63 days among *H. poecilopterus*, demonstrating the lability of sexual differentiation.

The masculinization of the adult female mosquitofish *Gambusia affinis* occurs under the effect of treatment by the stress hormone, *cortisol*; the anal fins of these neomales transform themselves into gonopods under the effect of *androgens*. Their behavior is reflected by attempts at copulation with females.

A feminization of embryos of the Japanese medaka *Oryzias latipes* is obtained by immersion in a solution of the *hormone estrogen 17β-estradiol*. All newborn babies are females and 50% have a male genotype XY.

Bibliography: *Biol.Lett*., 2010, **7**: 150-152 & DOI:10.1098/rspb.2010.0514, *Coral Reefs*, 2007, **26**: 189-197 & DOI:10.10007/s00338-0183-9, *Gen.Comp.Endocr.,* 1999, **116**: 141-152, *J.Exp.Zool*., **303A**: 497-503 & DOI:10.1002:jez.a.178, *J.Fish Biol*., 2007, **70**: 1898-1906 & DOI:10.1111/j.1095-8649.2007.01464.x, *Rev.Fish Biol. Fish,* 2004, **14**: 481-499 & DOI:10.1007/s11160-005-3586-8, *Zool.Sci*.2005, **22**: 1163-1167, 2006, **23**: 65-69 & DOI:10.2108/zsj.23.65*,* 2008, **25**: 123-128 & DOI:10.2108/zsj.25.123, 220-224 & DOI:10.2108/zsj.25.220

### 1.2.10.5. *Reversible sex change*

A sex change may not be definitive as in the haremic, protogynous* dwarf hawkfish *Cirrhitichthys falco* of the Japanese coral reefs. Neomales or secondary males can return to their original sex and therefore become females when the harem is of too low a size, being a victim of a deficit in females: i.e. one or two females present, while in normal conditions, there can be 7 to 1 male. In these conditions of mating deficit, these single males use this optional tactic of a bi-directional sex change, in order to achieve a status of spawner and have opportunities to participate once again in couplings in the form of females. The environmental context and the social environment are determinants.

The tail-spot wrasse *Halichoeres melanurus* is also a protogynous* species in which females are capable of becoming males in 2–3 weeks when all males in their territory are removed, which enables them to rapidly maintain the social system of functional reproduction which the population needs in an emergency in order to avoid a power vacuum. An experimental return of males to the population led these ex-females to leave their role of males which they had momentarily adopted to return to their initial sex and to once again lay eggs. This experience of removal and return demonstrates that their sex is reversible and depends on the social status of the population. Change of gonadal gender is generally preceded by a behavioral change; the neomales are capable of courting females before even having acquired functional testes.

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A similar plasticity and identical reversibility meet in the Japanese rusty angelfish *Centropyge ferrugata*, among whom, when the dominant male who monopolizes the females in the harem disappears, the largest of the females undergoes masculinization in 2–3 weeks. However, when cohabitation with a new large dominant male occurs consecutively to an introduction, placing him in a situation of subordination and making him lose the fight, this male returns to being a female.

The bluestreak cleaner wrasse *Labroides dimidiatus*, another haremic proterogyne*, also practice a return to their initial sex when neomales, in a situation of inter-male competition and with a status of subordinates*, become females. Their ovarian development requires 53–77 days, but their behavior of simulation of spawning begins much earlier, as soon as the second day.

A bi-directional sex change is common among various Japanese gobies such as *Trimma okinawae*, a protogyne* among whom the relationship between the respective number of males and females within the social groups is the social determinant of sexual inductions into one or the other gender, in populations where natural mortality is high and the sexual balance is constantly compromised. The search for the maintenance of a social hierarchy – α and β individuals – within the population is also the factor inducing bidirectional change of gender among other tropical gobies such as *Lythrypnus dalli*; a sex change requires a period of approximately 2 weeks.

Bibliography: *Ethol.*, 2002, **108**: 443-450, 2012, **118**: 226-234 & DOI:10.1111/j.1439-0310.2011.02005.x, *J.Ethol*, 2002, **20**: 101-105, 2007, **25**: 133-137 & DOI:10.1007/s10164-006-0007-y, *J.Fish Biol.*, 2007, **70**: 600-609 & DOI:10.1111/j.1095-8649.2007.01338.x, 1660-1668 & DOI:10.1111/j.1095-8649.2007.01427.x, *The Biol.Bull.*, 2005, **208**: 120-126, *Zool.Sci.*, 2000, **17**: 967-970, 2003, **20**: 627-633.

### 1.2.10.6. *Sensory change associated with a sex change*

Masculinization of females in the cylindrical sand perch *Parapercis cylindrica* of the coral reefs in the Indo-Pacific region is accompanied by auditory sensory changes, otolith *growth, between the 6th and 20th day of the sex change, to optimize the perception of ambient sounds.

Bibliography: *Biol.Lett.*, 2009, **5**: 73-76 & DOI:10.1098/rsbl.2008.0555

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## 1.2.11. *Unisex populations*

### 1.2.11.1. *All-female clones*

Some populations of the Amazon molly *Poecilia formosa* present the originality of having no males. These females result from crosses between them and the males of two neighboring species, *P. mexicana* and *P. latipinna*, which provide the semen to activate their oocytes without, however, adding their genome. Although they do not expect any genetic benefit from the attendance of males of these species, they manifest certain preferences for those of large size as well as for those with whom they have been raised. Such gynogenesis*, under the dependence of heterospecific male sperm donors, perpetuates successive lines of females. The two or three populations of these species live in sympatry* in the same habitats and are therefore in competition for the exploitation of trophic resources. However, this food competition in no way needs to lead to the exclusion of one of them for the benefit of the other. Hence, there exists a balanced system of management of resources, in which intraspecific competition is stronger than interspecific competition, even in a situation of strong deficit of food. The unisexual species has, in fact, an advantage on its counterparts, since it makes a saving on the production of males. The growth of its unisexual populations is accordingly more rapid than that of the host species that are complementary, who suffer from the handicap of producing males.

It is surprising that these females of the unisexual mollies *P. formosa* are sensitive to the possession of prosthetic swords made of colored plastic which are artificially attached to some males of *P. mexicana* or *P. latipinna*. These swords are similar to those of swordtails of the genus *Xiphophorus*, something which neither of the two parental species possesses in nature. Is this penchant to be attributed to a strong atavism which has been maintained in the family of poeciliids?

The cost of these couplings is such that males of *P. mexicana* and *P. latipinna* avoid these heterospecific females and prefer to mate normally with females of their respective species, as reflected in the higher amount of semen that they allocate to the latter, even though they are small in size and the males naturally prefer to mate with large females. Another original case concerns the populations of the Prussian *Carassius gibelio* which consist essentially of clones* of triploid females* that can also reproduce by gynogenesis* (Volume 2, section 1.2.12.3). They also include a small number (2–3%) of triploid males* with 156 chromosomes and tetraploids* with 200 chromosomes who are fertile. However, their descent is made almost exclusively female, because the genetic material on the paternal side, just as that resulting from crosses with males of species such as the goldfish *C. auratus*, is eliminated and therefore provides no genomic contribution; such males are genetically unnecessary.

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Bibliography: *Behav.,* 2009, **146**: 907-931 & DOI:10.1163/156853908396719, *Biol.Lett.,* 2008, **4**: 266-269 & DOI:101098/j.anbehav.2008.0019*, Ethol.,* 2006, **112**: 448-457 & DOI:10.1111/j.1439-0310.2005.01175.x, *J.Fish Biol.,* 2008, **73**: 323-328 & DOI:10.1111/j.1095-8649.2008.01937.x, 2010, **77**: 570-584 & DOI:10.1111/j.1065-8649.2010.02699.x

#### 1.2.11.2. *Males by accident*

In the *all-female* populations of the Amazon molly *Poecilia formosa*, various experimental interventions can produce different types of male: hormonal males by treatment of newborns with *androgenic hormones KT* who do not have normal testes, but intersexual gonads or ovotestes*; pseudomales who are females having been masculinized by various shocks such as high temperature or high density, and who are unable to mate because of a gonopodal disability due to a lack of muscle not allowing gonopod* thrusts; triploid* males whose sperm show reduced activity ascribed to a lack of motivation and which suffer from chromosomal accidents during meiosis*.

Bibliography: *J.Fish Biol*., 2010, **77**: 1459-1487 & DOI:10.1111/j.1095-8649.2010.02766.x

### 1.2.12. *Fatherless fish by parthenogenesis*

#### 1.2.12.1. *Females isolated in aquaria and deprived of any contact with a*

Rare cases of reproduction in which newborns are not the result of a cooperation between paternal gametes and maternal gametes, corresponding to the phenomenon of parthenogenesis*, have been reported in sharks such as the blacktip reef shark *Carcharhinus limbatus*. An embryo has been examined in Virginia from a female isolated for 8 years in a basin, without the slightest contact with a male partner. Its diploidy* is the result of the merger of the maternal oocyte with a polar globule* issuing from meiosis – automixis* – and its genome was homozygous*, exclusively of the maternal type, showing evidence of the absence of paternal intervention. Such a situation is probably rare in nature, but may be the result of the isolation of females in basins of marine aquaria. In Florida, a female of the hammerhead shark *Sphyrna*

has also given birth to a newborn when she had had no contact with a male for several years. The XX genome of this newborn, identical to that of its mother, confirms its homozygosity* and the absence of a paternal genome. Comparative genetic analysis between a newborn and its mother in the whitetip reef shark *Triaenodon obesus* confirms the existence of a parthenogenetic origin* of this newborn; the size of its genome is half of that of the mother in which the nuclear volume* is 1.73 times larger, which suggests a haploidy* resulting from the

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development of an unfertilized oocyte in the absence of a regulation of diploidy*. These females know how to do without a partner.

Bibliography: *Biol. Lett*., 2007, **3**: 425-457 & DOI:10.1098/rsbl.2007.0189, *J.Fish Biol*., 2008, **73**: 1473-1477 & DOI:10.1111/j.1095.8649.2008.02018.x, 2014, **85**: 502-508 & DOI:10.1111/jfb.12415

### 1.2.12.2. *Reproduction without a male genome performed in the lab…*

Reproduction of females without the genetic input of a male is also possible under experimental conditions, when spawning males are subjected to a UV* treatment which destroys the *DNA** genetic heritage of their sperm while maintaining their ability to activate oocytes which, undergoing spontaneous diploidization*, generate viable descendants as in the Sterlet sturgeon *Acipenser ruthenu*s. Such gynogenesis* induced experimentally by UV, $\beta$ or $\gamma$ irradiation is achievable in the laboratory for multiple species, confirming the feasibility of the phenomenon. Remember that gynogenesis* is also practiced in the natural environment in several species, including the Prussian carp *Carassius gibelio*. In this case, it is the sperm of another cyprinid species which activate the oocytes of the carp, but after activation, the genetic material of the sperm is rejected and therefore does not participate in the formation of the offspring, which are composed solely of females in the complete absence of the paternal genome which has become useless.

Whether natural or artificial, all these gynogenetic* individuals can be seen as being genetically fatherless. Their substitute fathers, suppliers of activating sperm, are at the origin of their existence, since, in their absence, the oocytes of their mother would remain sterile.

Bibliography: *Aquacult.,* 2007, **26**: 54-58, *Caryol.,* 2007, **60**: 315-318.

### 1.2.12.3. *… or another genesis, without a female genome*

Androgenesis is the obtainment of an organism without maternal genome. This is experimentally feasible in various cyprinids such as the ide *Leuciscus idus*. For this purpose, the oocytes are treated with *X-ray*, $\lambda$ or *UV* radiation which destroy their chromosomes, and then put in contact with sperm of the chub *L. cephalus* that trigger an oocyte activation process. They are then subjected to thermal shock (3 h at 36°C), in order to cause duplication of the paternal genetic material.

However, no natural androgenesis had ever been described up to the recent discovery, in Portugal, of the case of a cyprinid *Squalius alburnoides* whose genome is exclusively of paternal origin, with any maternal *DNA* being completely absent. Examples of males capable of generating descendants by themselves, giving birth to individuals who are then the clones of their paternal spawners were until this day

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only known among some insects (bees, wasps, ants, etc.), following neutralization or natural elimination of the maternal chromosomes. It would therefore be the first proven cases of androgenesis in a vertebrate species and evidence of remarkable capabilities of substitution.

Bibliography: *Arch.Pol.Fish.,* 2008, **16**: 453-457 & DOI:10.2478/s10086-008-0032-2, *Roy.Soc.Open Sci*, 2017, **4** & DOI:10.1098/rsos.170200

#### 1.2.12.4. *Cases of optional natural parthenogenesis, less rare than expected*

Multiple births by isolated females are reported in multiple examples, in different species of elasmobranchs such as the swellshark *Cephaloscyllum ventriosum*, the white-spotted bamboo shark *Chyloscyllum plagiosum*, as well as among the eagle ray *Aetobatus narinari* and small-tooth sawfish *Pristis pectinata* which show themselves able to perform optional parthenogenesis in the natural environment, as evidenced by the presence of homozygous females on the coasts of Florida. One of the descendants of a parthenogenetic female bamboo shark itself has, in turn, demonstrated similar capabilities of unisexual reproduction. Optional parthenogenesis over two successive generations is considered as an alternative means of reproduction.

Such cases are often the object of microsatellite analysis* of their genome that confirms this mode of uniparental reproduction. They demonstrate that fish that routinely practice sexual reproduction are also able to reproduce by parthenogenesis* when their populations are in low numbers and dangerously threatened with extinction thanks to a parthenogenesis of survival based on a single

Bibliography: *Curr.Biol.*2015, **25**, 11, open archive, *J.Fish.Biol*., 2016, **88**: 668-675 & DOI:10.1111/jfb.12862, 741-744 & DOI:10.1111/jfb.12819, 2017, **90**: 1047-1053 & DOI:10.1111/jfb.13202, *Sci.Avenir*, janv.2009

### 1.2.13. *Posthumous paternity*

#### 1.2.13.1. *Natural storage of semen by females*

The human species is proud to display its biotechnological progress in the field of human reproduction with the establishment of sperm banks that permit an individual to produce offspring long after his death. Some fish possess the same capabilities naturally. Thus, in the guppies of Trinidad *Poecilia reticulata*, life spans are different between the two sexes, with females being more long-lived (15–18 months) than males (3 months). However, the latter can compensate for the relative brevity of their life with a hope of natural procreation that extends beyond their

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During the couplings that are real copulations, semen deposited by males in the genital tract of females by using their copulatory organ, the gonopod*, consisting of several modified rays of the anal fins, is stored by the latter in their ovarian cavity and used to fertilize their oocytes at a later time. The duration of survival of the sperm thus kept and nourished by ovarian secretions is several months (up to 10 months to 1 year): although the lifespan of sperm is equal to those of females, their fertilizing power gradually decreases due to their dilution with fresh sperm acquired in successive copulations later experienced by the females. The latter are also able to selectively control their use: such a choice is qualified as cryptic*, because it is carried out without the knowledge of their partners. Deceased males contribute to a significant proportion of the offspring of their companions as evidenced by genetic studies. Nearly 30% of the males involved in the reproduction of the populations do so having been dead for 8–12 months. These males therefore participate posthumously in the transfer of their genes to descendants that they will never know, and play an important role in the dynamics of populations, as demonstrated by demographic studies.

Some scorpaenids such as *Heliconus dactylopterus* of the Mediterranean practice internal fertilization, and sperm are stored in the ovaries of females. These male gametes have an original morphology with elongated heads: this type, termed "introspermatozoid" or introsperm, is characteristic of fish practicing internal fertilization, while the heads of spermatozoa of fish practicing external fertilization in open water, termed "aquaspermatozoids" or aquasperm, are spherical. In addition, they are wrapped in nourishing cytoplasm that permits a long storage of more than 10 months in the ovarian crypts* until their use for fertilization of the oocytes; their cytoplasmic sac is then exhausted and their hydrodynamic form is acquired. They are protected during their intraovarian stay from the immune defense system of the females that would tend to destroy them – they are non-self – thanks to a cellular apparatus of tight junctions or desmosomes* which prohibit any passage of destructive antibodies*. Such a safeguard of cellular interlocking maintains the viability of the sperm.

Female sharks also have the ability to store for a long time, in oviductary cavities, the sperm of their partners. The record for sperm longevity, with 45 months, seems to belong to the bamboo shark *Chiloscyllium punctatum* maintained in aquaria.

Bibliography: *J.Exp.Biol*., 2013, **216**: iv & DOI:10.12.42/jeb.084475, *J.Fish Biol*., 2007, **71**: 596-609 & DOI:10.1111/j.10958649.2007.01525.x, *Proc.Roy.Soc.B*, 2013, **280**, 1763 & DOI:10.1098/rspb.2013.1116, 2015, **86**: 1171-1176 & DOI:10.1111/jfb.12606

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### 1.2.13.2. *Cryogenic conservation of sperm*

A technique of sperm conservation by cold is artificially feasible in fish. A process for cryopreservation* of the sperm of the giant grouper *Epinephelus lanceolatus*, a Pacific species which is vulnerable and endangered, enables, through the use of the cryoprotectant *dimethyl sulfoxide* (*DMSO*), the retention of semen in *liquid nitrogen* at –196°C, with high rates of motility of the sperm and a strong fertilizing power, with respectively 91 and 93% success compared to fresh semen, which raises the hope of repopulation from juveniles produced in nurseries.

Such cryogenic* methods are applicable to many species. Semen can be frozen even 8 h after the death of the fish, while maintaining its fertilizing power *post-mortem*, which is the case for the rohu *Labeo rohita*. Semen of the gilt-head bream *Sparus aurata*, retained more than 5 years in liquid nitrogen and then thawed, enables the preservation of a total sperm motility of 85% and a swimming speed of m/s, in comparison with respective values of 95% and 350 μm/s for fresh sperm.

The aim of these cryopreservation techniques is to store semen of good quality in order to achieve artificial fertilization in rearing centers or hatcheries. This also raises, through the constitution of gene banks, the hope of restoring endangered species.

Bibliography: *Aquacult. Res.,* 2008, 1-9 & DOI:10.1111/j.1365-2109.2008.02031.x, *J.appl.Ichthyol.,* 2014, **30**: 334-339 & DOI:10.1111/jai.12321, 2015, **31**: 104-107 & DOI: 10.1111/jai.2015.31.issue-S1/issue toc

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# 2

# Reproductive Behavior: Parents

Having completed their role as spawners, the partners will often take their leave of each other, abandoning their eggs. However, some continue their common or solitary lives by taking care of their eggs and then eventually their offspring, who are vulnerable to predation. It is appropriate to protect these and sometimes to feed them with nutrients and respiratory gases, as well as to educate them in order to enable them not only to survive but also to prepare for a life full of pitfalls.

Many ovuliparous species do not wait for mating to take on these parental tasks. In anticipation, they prepare formidable welcoming structures that will be appreciated by their sexual partners and which will count in their favor during the period of sexual selection (Volume 2, section 1.1.1). The construction of spawning nests (Volume 2, section 2.1.1) thus contributes greatly to the success in love of males of various species. These males are capable of responding to a multitude of demands from their female partners, and their parental phase begins early, only to be completed when the young have survived.

Some of developments that follow could perfectly well find a place in Chapter 1, if we were to respect to the letter the chronological order of reproductive events. However, the early construction of nests and the late practice of parental care (respectively before and after spawning) constitute a set of activities with a common purpose for the benefit of eggs, embryos, larvae and juveniles, which justifies the choice we have made to locate them in this Chapter 2.

## 2.1. The post-spawning phase: the future of the offspring

### *Nest builders*

Nesting areas or spawning grounds are chosen by spawners in order to ensure for

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accessible food resources, protection against predators, optimum temperatures ensuring their development and growth, etc. These areas of reproduction are generally traditional, located close to their feeding habitats (Volume 1, section 1.2) or alternatively located at more or less significant distances, which require spawners to undertake reproductive migration of a larger or smaller distance. They are occupied by successive generations of spawners who perpetuate the "traditions" specific to each species, who have used them to their benefit since time immemorial.

The interest of some of these breeding areas lies in the fact that "spawning nests" are constructed by the spawners, acting as builders of more or less developed structures that promote the protection of eggs, and then sometimes also larvae.

#### 2.1.1.1. *Architects and urbanists anxious to please their demanding companions*

Birds are often taken as models of inventive nesting capacities in vertebrates. Yet sometimes, fish have nothing to envy of them. They were even, from a chronological point of view in the course of evolution, the initiators.

There are behaviors prefiguring nesting, such as those of silversides, such as *Atherina boyeri*, who seek out branching algae such as *Gracilaria* on which to hang their eggs which will then be immediately abandoned by the spawners. Other species are content to choose an overhang of rock to which to attach their clutches without making specific accommodations, clutches which they leave behind.

When there is preparation of a spawning space or construction of a nest intended to host the offspring of couples, it is generally the male who does this work. These nests have a dual function: they protect the clutches and the fry resulting from their hatching, thanks to their robustness (resistance to mechanical shock), their ease of defending (visually accessible location) by the male owner of the nest, the difficulty of penetration by predators (orientation and size of openings), but they are also attractive to the females who are invited to enter there to deposit their oocytes. The latter are generally demanding and prefer the largest nests which are capable of hosting a large number of eggs, the best located and protected in relation to the hydraulic currents, the best concealed from the view of potential predators and whose low opening is the most obstructive to penetration. Males must therefore integrate all these constraints into their urban planning and in the choice of their architecture. They seek to make best use of the mineral, vegetable or animal resources of their near environment, always showing creativity and never reproducing nests identically, in a stereotypical manner. They take into account the local hydraulic constraints, the availability of materials as well as forecasts of the activities of guardianship that are complementary to their efforts of nesting (Volume 2, section 2.1.1).

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Note the case of the addition of a final touch brought to the nests by the male builders: some gobiids cover the internal walls of their nests, before attracting females, with semen rich in sperm embedded in a mucus rich in *nutrients* with bactericidal and fungicidal components.

#### 2.1.1.2. *Mineral nests*

Some species use natural cavities available in their habitats. The male of the barred-chin blenny *Rhabdoblennius ellipes* does not build a nest in the strict sense, merely using cavities dug into the coastal rocks by shellfish or burrowing worms. The choice of cavity must respond to a security objective: having an entry carefully adapted to the cephalic size of the nesting fish in such a way as to prohibit any space allowing the entry of a potential predator. This nest being perfectly matched to the size of its guardian, the latter changes habitat during its growth. It is from this entryway that he courts passing females, by nods of the head, in order to invite them to enter the nest. Females' preference, upon their first visit – one-step decision – or after several consecutive visits in the case of sequential choice, is both a function of the quality of the nest and that of its guardian, those with a well-developed cephalic ridge (Volume 2, section 1.1.1) having the most success.

The benthic* sculpins endemic to Lake Baikal *Cottus kneri* and *C. kessleri* use rocky, hard bottoms and look for overhanging stones for spawning nests. Competition between them is severe and the number of favorable microhabitats often insufficient, so that it is common to find nests used jointly by the two species. Males of *C. kneri* are however able to discern the foreign eggs of *C. kessleri* and cannibalize them.

Males of the Amur goby *Rhinogobius* sp. of Japanese water courses build nests by digging in the sand or gravel below a stone, with a space intended to accommodate the clutches of the multiple females that they attract into this nest. Their reproductive success, measured by the number of eggs deposited, depends on both the size of the nest, in favor of larger ones, and their topographic position in the current. Those located in more rapid currents are the most appreciated for two reasons: they demonstrate the constructor's great swimming skills and they offer the clutches better oxygenation. These are the large, oldest males of 3 years who, although constituting only 36% of the population, are entrusted with reproductive success by becoming predominantly, by 70%, the guardians of clutches. The males of the American hornyhead chub *Nocomis biguttatus* build, in the upper Mississippi, nests at depth, in a moderate current. These nests in the shape of a dome are the result of an accumulation of approximately 3,000 pebbles and stones for a total weight of 11 kg. These are of small diameter (6–8 mm) in order to reduce the energy cost of transport, but dense in order to avoid a risk of dispersion by the current while ensuring a good protection of clutches as well as their oxygenation by means of

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percolation* by a current of water. Collection of materials, performed by mouth, is done over a radius of several meters. Totaling up the comings and goings, the path traveled in transporting pebbles for the construction of such a nest would be around 25 km, remarkable in a small fish of 15 cm in length. The neighboring species *N. micropogon* does even better: a nest of 40 kg of materials.

Male cichlid fish, such as tilapia *Oreochromis niloticus*, use the substrate of African lakes to make nests where the clutches will be laid. They choose, following buccal inspection, the most favorable type of substrate, preferably homogeneous, soft and whose elements are transportable – sand or gravel. They then proceed to preparation of the nest, digging and moving the mineral elements with their mouth so as to create a regularly circular depression. Vertical constructions in the sand which are clearly more elaborate in the form of towers ending in a platform are produced by the utaka cichlids of Lake Malawi of the genus *Copadichromis*. Their height, diameter and the inclination of the walls of these small volcanoes that are used during courtship behavior and for spawning vary according to a dozen construction plans which are rigorously specific. They thereby demonstrate a certain innate sense of geometry, which is a good way for the fine conservative females to recognize males of their species. These characteristics thus serve as a signal of recognition for spawners of each species in order to induce homospecific couplings. Females use the criteria of tower size in favor of larger ones, following a gain of height of 1 cm/day and more than 2 weeks' work, and of localization, their most central position in the lek*. In addition, the aggressiveness of males who mobilize to defend nests is taken into consideration by the females, in order to choose those who seem worthy to earn their favors: the largest, the strongest and most dominant, and the best architects.

Bibliography: *J.Fish Biol.,* 2002, **60**: 981-988 & DOI:10.1006/jfbi.2002.1907, 2006, **68**: 185-195 & DOI:10.1111/j.1095-8649.2005.00887.x, 2007, **71**: 77-89 & DOI:10.1111/j.1095-8649.2007.01466.x, 2008, **72**: 93-102 & DOI:10.1111/j.1095-8649.2007.01656.x, 2009, **75**: 1577-1585 & DOI:10.1111/j.1095-8649.2009.02384.x

### 2.1.1.3. *Spawning nests dug in the beds of water courses*

Salmonids are considered to be lithophiles*, because the females lay their eggs in the gravel of the upstream beds of water courses. These clutches are simply dispersed at their emission on the surface of the substrate, before drifting due to gravity into interstices between the stones, for the Arctic char *Salvelinus namaycush*. Their attractiveness for predators is linked to chemical signals, and they are subject to fairly strong predation in lake spawning grounds. In contrast, among trout and salmon, clutches are buried in spawning nests following digging into the substrate of the gravel by sweeping, carried out by beats of the female's tail. Covering up of spawning nests with gravel often occurs during the digging of a new spawning nest

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are used to cover newly deposited eggs which are immediately fertilized by males who patrol in the vicinity.

Strong competition for occupation of spawning grounds is frequent among lake-dwelling brook trout *Salvelinus fontinalis* of Canada, among whom three-quarters of spawning sites are used successively by several females, but losses of eggs remain limited to 20–40% because large females lay eggs earlier and bury their eggs more deeply than those following them. However, the physical quality of spawning habitats based on the rate of flow of groundwater is responsible in itself for the loss of eggs often rising as high as 67–91%.

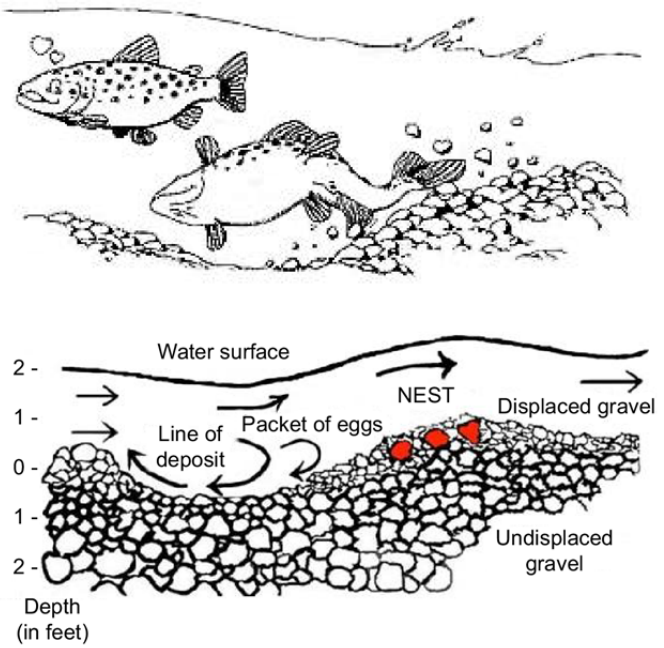



**Figure 2.1.** *Couple of salmonids (top), where the female "sweeps" the substrate of gravel on the bed of a watercourse to eliminate fine particles; spawning nest (bottom) whose eggs are oxygenated by percolation of water through the gravel. For a color version of the figures in this book see www.iste.co.uk/bruslé/fish1.zip*

In the chinook salmon *O. tsawytscha* of Alaska, the females dig, in the tributaries of lakes, a series of spawning nests by sweeping the substrate of gravel with side-to-side beats of their caudal peduncle, an operation which is costly in energy. They preferentially opt for shallow areas traversed by flowing water allowing strong embryonic survival, but are sometimes constrained, under the pressure of stronger

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and more dominant rivals, to retreat to deeper but less favorable areas. Similarly, among sockeye salmon *O. nerka*, females generally opt for spawning grounds corresponding to a compromise between the benefits of a shallow and well-oxygenated site and the costs induced by the strong competition associated with it, being forced then to fall back on deeper spawning grounds. The males reduce their movements to a perimeter of 30–50 cm, which promotes a certain reproductive isolation. Competition for occupation of these mineral spawning grounds actually occurs frequently between salmonids, both conspecific and heterospecific, in particular between trout and salmon who have common requirements for quality of spawning grounds in gravel areas relating to the interstitial movement of water.

Competition may also exist between the trout *Salmo trutta* and the sea lamprey *Petromyzon marinus* which are sympatric*. The spawning nests of the salmonid are sometimes victims, in up to 83% of nests, of digging activities by the petromyzonid, which uses the same reproductive microhabitats, after departure of the trout who abandon their nests after oviposition. This establishes competition to the benefit of the last spawner, which reduces the risk of over-digging of its spawning nests.

Male cichlid fish, such as tilapia *Oreochromis niloticus*, prepare their spawning nests in the substrate by cleaning it of coarse elements, rocks and plant debris that he collects with his mouth so that the depression that he digs is composed only of fine and homogeneous sandy-clay particles. Females inspect this nest before depositing in it their eggs which, after fertilization, will be taken into the mouth for mouth-brooding.

In the flood plains of the Amazon in Brazil, the piracuru *Arapaima gigas* establishes its spawning nests, 190–670 mm in diameter, near the banks of forest areas. The couple dig with their mouths, over 3–5 days, holes in shallower areas, with the maximum depth being 1.20 m and a slow current of 0.12 m/second, in a sandy substrate cleaned of debris of leaves and branches. This improves visibility around the nests kept by parents and provides protection against currents and predators.

Bibliography: *Anim.Behav*., 2006, **71**: 971-981, *Can.J.Fish.Aquat.Sci*, 2005, **62**: 2694-2705 & DOI:10.1139/F05-176, *Env.Biol.Fish*., 2014, **97**: 385-399 & DOI:10.1007/s10641-013-0159-x, *J.Fish Biol*., 2008, **72**: 1520-1528 & DOI:10.1111/j.1095-8649.2007.01778.x, 2010, **77**: 1439-1445 & DOI:10.1111/j.1095-8649.2010.02754.x, 2358-2372 & DOI:10.1111/j.1095-8649.2010.02818.x, 2014, **84**: 1562-1573 & DOI:10.1111/jfb.12388

### 2.1.1.4. *Shell nests*

Various species, adept at recycling natural resources, use the empty shells of

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*Pomatoschistus minutus* carefully choose their nesting sites and camouflage the latter due to risks of predation. Thus, in the presence of shrimps *Crangon crangon* which eat eggs, the largest males turn a bivalve shell so that its concave side faces the soil, under which they dig in order to create a space large enough to accommodate their partners. They then conceal this shell by covering it with a layer of sand, all the more important as the predatory shrimp who lurk in the vicinity of the nest are numerous. The males carry these materials with the aid of their mouth. This camouflage is costly in energy, thus hardly achievable by small males who are less popular with females and who experience lower reproductive success.

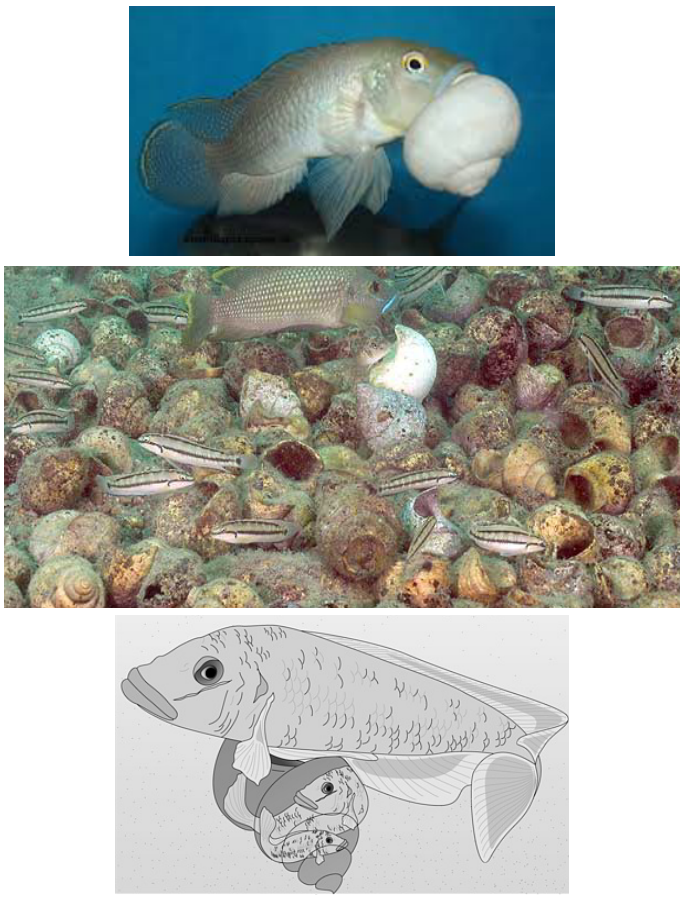


**Figure 2.2.** *Lamprologue* Lamprologus *sp. carrying with his mouth a snail shell towards a place of concentration of shell nests (top); female installed in a shell where she spawns (middle); as for the male, too large, he remains outside (bottom)*

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Such spawning nests consist, in the lagoon of Venice, of cavities located under stones, under the shells of bivalves – mussels, oysters, clams, etc. – that are dug out from below and covered with sand from above. Such an accumulation of sand piled above the nest, in addition to its role of camouflage vis-a-vis potential predators of eggs, favors the transmission of male courtship songs in the form of acoustic waves in the frequency range of 80–300 Hz*, which are then amplified by 20–25 dB*, as measured by hydrophones. Nests made of large shells covered with a large layer of sand which are made by larger males are the most conductive to great reproductive success. Females, who listen for these vocalizations, do not resist these invitations to love, and small nests, weakly covered with sand, are neglected.

The number of nests of the common goby *P. microps* also depends on that of the valves of mollusks available in the Atlantic estuaries, just as in the Mediterranean lagoons, which determines their reproductive success. Nesting sites and the availability of empty shells are subject to strong inter-male competition.

Among the lamprologue cichlids *Lamprologus callipterus* of the African Great Lakes, males attract females by collecting and defending empty shells of the gastropods *Neothauma tanganicense* in which they are invited to lay eggs. The latter prefer large shells. Yet, males also collect shells of small size that females never use. Such disagreement between the choices of males and of females suggests that the shells exert a function other than simple host structures for spawning. A form of artistic activity? The question is open (Volume 2, Chapter 3, section 3.5).

Bibliography: *Anim.Behav.,* 2005, **70**: 539-549 & DOI:10.1016/j.anbehav.2004.11.010, 2006, **71**: 879-884, 2013, **86**: 867-871 & DOI:10.1016/j.anbehav.2013.08.005, *Env.Biol.Fish,* 2013, **96**: 1003-1012 & DOI:10.1007/s.10641-012-0097-z, 2014, **97**: 701-715 & DOI:10.1007/s10641-013-0172-0, *Ethol*., 2008, **114**: 575-581 & DOI:10.1111/j.1439-0310.2008.01500.x, *J.Compil. Eur.Soc.Evol.Biol.,* 2006, **19**: 1641-1650 & DOI:10.1111/j.1420-9101.2006.01114.x

### 2.1.1.5. *Vegetable nests*

A large availability of plant material – algae and various seed plants – justifies its wide use by nesting fish. The most famous are the males of the three-spined stickleback *Gasterosteus aculeatus*, remarkable builders of nests which they construct among aquatic plants from varied plant material, by combining fibers in a genuine weaving that gives this nest flexibility and resistance. They are also known to use waste plastic to make their nests. A mucous secretion of a sticky substance, spiggin*, by the kidney, under the control of the androgenic hormones *11-keto-testosterone* (*11-KT*), enables gluing together of these fibers and promotes their cohesion, which varies according to local hydrodynamics: lake or river with a lentic* or lotic* flow. In addition, mucous secretions with antibiotic properties

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infections. The male is very concerned with the sanitary quality of his nest from which he carefully eliminates sick or dead eggs.

The construction of a nest has, among the sticklebacks, a dual function: accommodation of clutches and juveniles, which are thus protected from predators, and, before that, the attraction of females who are very sensitive to the qualities of the builder and who choose, as a mating partner, that one who presents a nest which is the most beautiful, the largest, the most welcoming, the most solid and the best located to exclude both predators and the risk of hydrodynamic accidents. Each male therefore sets to this work in order to attract the favors of the largest number of females. Each nest is an original individual creation showing a variability of size from 1 to 8 and in composition of 1 to 18 in the number of vegetable fibers used, which depends directly on the size and the energetic and hormonal potential of the *androgens* in this male. There is an inheritable genetic component relating to building skill. Any individual which is parasitized by the cestode *Schistocephalus solidus* shows weaker construction activity; its secretion of spiggin* is reduced since the parasite exercises a castrating function.



**Figure 2.3.** *Nest of the stickleback* Gasterosteus aculeatus *made of woven and pasted plant debris in which the female deposits her eggs*

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In the Amazon fresh waters of Brazil, piranhas *Serrasalmus brandtii* build nests of algal and phanerogamic material on sites rich in vegetation, favoring the fixing of eggs onto plant surfaces, the structure of their egg envelope consisting of filaments coated with adhesive secretions.

The choice of nesting sites by male wrasses of the genus *Symphodus* such as *S. roissali*, a marine builder which uses fragments of algae cut and assembled in the manner of a bird's nest, at the same time impacts its mating success – as females perform their choice among males based on the quality of their nests – and its reproductive success, because the survival of its progeny depends on the security offered by this nest. On the rocky Catalan coast, these nests are established on hard substrates. Physical characteristics relating to a depth of −6 to −10 m, a low slope, proximity of adjacent sandy areas, border zones being better visible for females, and especially their degree of protection or exposure to the mechanical and destructive action of the waves, condition their nesting success. These males must satisfy many requirements.

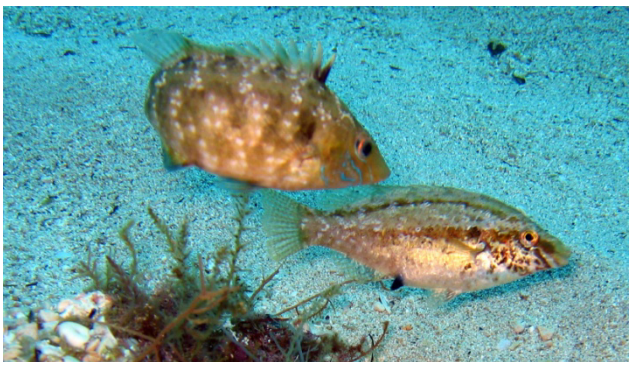


**Figure 2.4.** *Couple of wrasses* Symphodus cinereus *on their nest of algae (source: S. Ruitton)*

Bibliography: *Anim.Behav.,* 2008, **75**: 547-553 & DOI:10.1016/j.anbehav. 2007.06.011, *Behav.,* 2004, **141**: 1499-1510, 2005, **142**: 979-996, *J.Fish Biol.,* 2005: 1400-141. & DOI:10.1111/j.1095-8649.2005.000691.x, 2006, **68**: 305-309 & DOI:10.1111/j.1095-8649.2005.00885.x, **69**: 870-882 & DOI:10.1111/j.1095-8649.2006.01164.x, 2007, **71**: 298-303 & DOI:10.1111/j.1095-8649.2007.01495.x, 2009, **73**: 746-752 & DOI:10.1111/j.1095-8649.2008.01970.x, **75**: 2095-2107 & DOI:10.1111/j.1095-8649.20009.02411.x

### 2.1.1.6. *Sterile nests*

The male of the peacock blenny *Salaria pavo* secretes, from a pair of anal

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properties, which ensure protection of the health of the clutches in a sanitized nest and promote embryonic and larval survival. As we have discussed previously, male sticklebacks also secrete mucus rich in antibiotics and antifungal substances that ensure the development of eggs and larvae in good sanitary conditions.

Bibliography: *Anim.Behav*., 2008, **75**: 379-389 & DOI:10.1016/j.anbehav. 2007.05.018, *Biol.Lett*., 2006, **2**: 330-3333 & DOI:10.1098/rsbl.2006, 0492, *Funct.Ethol*., 2010, **24**: 141-148 & DOI:10.1111/j.1365-2435.2009.01608.x, *J.Fish Biol*., 2008, **73**: 1790-1798 & DOI:10.1111/j.1095-8649.2008.02025.x

### 2.1.1.7. *Bubble nests*

The male of the Siamese fighting fish *Betta splendens* builds a nest made of air bubbles color patterned with mucus, by expectorating air via a pharyngeal organ containing mucus cells which are rich in glycoproteins*. These bubbles accumulate at the surface of the water and constitute a cradle for the female's clutches which are deposited below, well protected from surface predators. The male of the paradise *Macropodus opercularis* of Taiwan also builds one to three nests made of bubbles among floating vegetation. These bubbles are produced by a labyrinthiform organ which enables him to suck in, then to expel air bubbles coated with mucus. Approximately 300 to 500 eggs are in this way well protected and hidden among floating aquatic plants in waters which are generally opaque.



**Figure 2.5.** *Male of the Siamese fighting fish* Betta splendens *expectorating mucus bubbles (left); floating bubble nest (right), underneath which the eggs are protected*

The male of the atipa *Hoplosternum littorale*, a South American catfish, sometimes helped by a female, builds, during a single night, in areas of the flood plain, a floating nest, a mixture of air bubbles and plants, 30 cm in diameter and 6 cm thick. These bubbles provide at the same time flotation, thermal regulation of eggs and protection against predators. As a significant proportion, 48%, of these

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nests contain no eggs, it has been suggested that inter-male competition may have been too high, or that the population suffered from a deficit of females.

Bibliography: *Aquat Living.Res*., 1998, **11**: 173-185, *Zool.Sci.*, 2010, **27**: 861-866, *Zool.Stud*., 2006, **45**: 475-482.

### 2.1.1.8. *Animal nests*

Another form of protection of clutches and descendants is to isolate them from predators in an organic cavity (Volume 2, section 2.1.4), either one's own (oral cavity, ovarian and/or genital cavity) or in that of another organism (the gill cavity of crabs, the pallial cavity of shellfish, etc.) which becomes the host, most often against its will, of foreign eggs in accordance with a form of parasitism or mutualism* (Volume 1, section 3.4).

### 2.1.1.9. *Constructions with a purpose other than a simple spawning nest*

The construction of nests has very often, as mentioned above in the case of the cichlid *Copadichromis*, a purpose other than that of simple protection of clutches and juveniles: that of serving as a criterion of the quality of the male builders, the females using this as a positive signal in sexual selection (Volume 2, section 1.1.1). This concern with being agreeable to females is sometimes very strong and has become a priority in the male cichlids of Lake Malawi *Hemitilapia oxyrhynchus*. In fact, these build sand castles which are geometrically circular, with towers whose height and central position in the lek* are a function of their size and their valor and which, accordingly, play an important role in sexual selection.

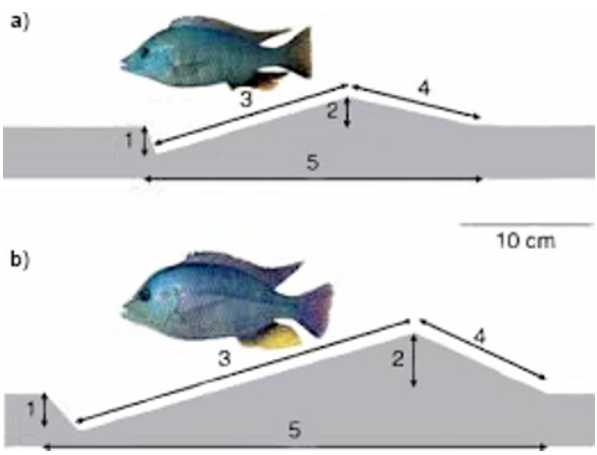



**Figure 2.6.** *Nests of cichlid fish whose morphological characteristics (dimensions and slope) are different: Hemitilapia (top); Protomelas*

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This sand is transported by mouth, then shaped by the fins so that the architectural type (general form of the tower, inclination of the walls, etc.) is rigorously specific (see the difference in construction between a *Hemitilapia*, at the top, and a *Protomelas*, at the bottom).

In addition to their demonstration of specific usefulness for their recognition and the attraction that they exert on females, these constructions are also intended to display dominance vis-a-vis other, rival males. Large males, owners of higher towers, produce more abundant sperm and enjoy the maximum of reproductive success. These are also the least contested by competitors, without forgetting the artistic "masterpiece", i.e. the circular and sculpted sandy nest of the fugu *Takifugu rubripes* (Volume 2, section 3.5).

Bibliography: *Behav.*, 2009, **146**: 963-978 & DOI:10.1163/156853908X396836, *J.Evol.Biol.*, 2008, **21**: 1387-1396 & DOI:10.1111/j.1420-9101.2008.01558.x, 2014, **27**: 2629-2643 & DOI:10.1111/jeb.12522, *Mol.Ecol.*, 2006, **15**: 459-478 & DOI:10.1111/j.1365-294X.2005.02787.x

### *Incubating clutches in the mouth*

#### 2.1.2.1. *Priority: ensuring the survival of progeny*

While pelagic species* and many nectonic* and nectobenthic* species abandon their eggs in open water without worrying about their fate, some demersal* and benthic* species are concerned to ensure the security of their progeny and thus grant them a guarantee of a better survival rate. Modalities of parental protection are very varied, involving one or both of the parents. The most common practice concerns the construction of spawning nests as we have just seen and the dispensing of parental care (Volume 2, section 2.2). These protective behaviors are generally effective, although subject to the risks of desertion of the nests (Volume 2, section 2.1.3), at risk of predation or destruction by hydroclimatic events. A higher degree of protection is provided by those species that practice buccal incubation; one or the other of the parents is entrusted with this mission, the supreme protection being the prerogative of viviparous species.

#### 2.1.2.2. *Female incubators*

Females of many cichlids such as *Simochromis pleurospilus* of Lake Tanganyika are mothers who are very concerned with the survival of their eggs, then of their larvae. They will host in their mouth the clutches fertilized by a small number of males – a weak polyandry*, since 70% of clutches are fertilized by a single male – which constitutes a very secure refuge against predators.

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Young issuing from the maternal oral cradle continue, after emerging, to remain faithful to their mother's mouth in which they take refuge at the slightest danger. The beneficial effects of this maternal protection are limited to a short critical period in the development of their offspring. Young who live in an environment at a high risk of predation show accelerated growth during their first month of life in response to an activation of maternal origin of the growth hormone (GH) gene and are already of suitable size when they definitively depart from their mother's mouth. In addition, they possess an innate olfactory capacity to recognize predators and to differentiate them from species which are not dangerous.

With females generally living in small groups (up to eight females), unfamiliar fry at risk of predation hastily find shelter in a non-maternal mouth (14% of foreign broods). Is such a mixture of juveniles a well-accepted form of solidarity, or is it accidental maternal adoption? Its existence presupposes that the host mother does not know how to sort between its own progeny and that of another, or that the cost of this accommodation being low, it is not necessary to perform such discrimination.

In another cichlid, *Tropheus moori* of Lake Tanganyika, the female of size 10 cm lays large eggs of 0.045 g, which are among the largest spawned by fish, then incubates them in her mouth, the larvae being protected and fed in her mouth by microalgae that she cultivates. This brooding lasts 6 weeks during which the female fasts, a period costly in energy, but which offers the advantage of producing young of large size, vigorous and good swimmers – a speed greater by 20% in comparison with larvae of the same age who are not fed – and whose survival rates are high, the mother saving herself the effort of seeking out and defending a spawning territory, but with less energy to escape predators.



**Figure 2.7.** *Fry of cichlid fish who take refuge in the maternal mouth in case of danger*

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The female of another cichlid *Ctenochromis horei* adapts the duration of its oral incubation to the risks of predation incurred by the young, extending their intrabuccal stay to more than 7 days post-hatching when the danger is great. Its progeny, which continues during this time to grow in size to +15% in 4 days, is thus in part secured against risk of predation when it leaves this safe harbor, but the female then undergoes a delay in its later reproductive cycle.

Bibliography: *Anim.Behav*., 2004, **68**: 1275-1281 & DOI:10.1016/j.anbehav.2004.03.005, *Funct.Ecol*., 2014, **28**: 944-953 & DOI:10.1111/1365-2435.1222, *Mol.Ecol*., 2012, **21**: 2805-2815 & DOI:10.1111/j.1365-294X.05573.x

### 2.1.2.3. *Male mouth-incubators, sometimes cannibalistic*



**Figure 2.8.** *Male of the Apogon sp. practicing buccal incubation of clutches (source: S. Ruitton)*

Male cardinalfish *Apogon doederleinii* of the Great Barrier Reef in Australia, like all species of *Apogon* in the world, are also oral incubators. Their bony mouth morphology – osteology* – is different from that of females; their head and, in particular, their jaws are lengthened so as to constitute a cradle for the eggs. The brooding of eggs does not, however, prohibit their taking food and does not compromise the respiratory role of the buccal pump. Reproduction and feeding being closely coupled, species with a piscivorous diet produce smaller clutches and a lesser number of eggs, the latter being of smaller size, compared to species with an invertivore diet* who consume small invertebrate prey, corresponding to a judicious physiological compromise between feeding and hatching. Among the Mediterranean cardinalfish *A. imberbis*, the male practice courtship behavior by circular swimming, then the female lays its eggs, 4,000 to 6,000, which are fertilized and immediately taken into the mouth by the father who shelters them from predators for 5 to 7 days, during which he is deprived of exogenous food. He thus consumes a certain number

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of eggs, up to 30% of the clutch, in order to keep in shape. Such filial cannibalism which in the end spares a lot of eggs therefore remains a good plan for the couple.

The males of some cichlids of Lake Tanganyika also practice oral incubation of clutches, but such a dual function of their mouth (feeding + reproduction) has consequences for the geometric characteristics of their craniofacial structures. The cephalic elongation and enlargement linked to this brooding is reflected by a swimming disability in the Nile tilapia *Oreochromis niloticus*. This completely new functional coupling, perhaps derived from an ancestor practicing surveillance of clutches on the substrate and which has an evolutionary diversifying effect on the skulls of incubator species, constitutes a new research topic for understanding the evolutionary path of these African cichlids.

Bibliography: *Biol.Lett*., 2015, DOI:10.1098/rsbl.2014.1053, *Proc.Roy.Soc.B*, 2012, **279**: 2426-2432 & DOI:10.1098/rspb.2011.2670, *Vie Milieu*, 2008, **58**: 63-66.

#### 2.1.2.4. *Cooperation of the two sexes*

Among the cichlid *Eretmodus cyanostictus* of Lake Tanganyika, the female begins buccal incubation during the first 7–10 days, then the male takes over during the 12–16 days following. This male manifests more defensive activity than his companion. Such sharing of the energy investment promotes the early preparation of a new spawning cycle by the female, a week later when it is released from its parental obligations. Such a transfer of responsibility therefore seems optimal at the reproductive level.

Bibliography: *Anim.Behav.*, 2004, **68**: 1283-1289 & DOI:10.1016/j.anbehav.2004.03.007

### *Deserters*

#### 2.1.3.1. *Abandonment of nests*

Males of many species are exemplary parents, entirely dedicated to the construction and defense of spawning nests, as well as to the care of their offspring. This remarkable behavior of paternal care however sometimes shows a few limitations. It is not rare that the male guardian of a nest leaves the latter and, tempted by new adventures, abandons the eggs and young to their sad fate. Males are led to wonder about the best strategy to adopt: to protect their present offspring or to seek new opportunities which may be potentially more profitable.

Bibliography: *Biol.Lett.*, 2007, **3**: 234-236 & DOI:10.1098/rsbl.2006.0616

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### 2.1.3.2. *Males who, for attractive females, become infanticidal*

The gestating male black-striped pipefish *Syngnathus abaster* of Portugal interrupt the "brooding" of the embryos present in their incubation pouch when they visually perceive the presence of a female more attractive than the one with which they have previously coupled. Any female of "better quality" (larger size, more "sexy" color patterns) is so attractive as to cause him to abandon the gestation of their embryos. These are then eliminated from the incubation pouch, which becomes available for a new generation.

Bibliography: *Proc.Roy.Soc.B*, 2018, **285** & DOI.org/10.1098/rspb.1335

### 2.1.3.3. *Stay or leave? A serious risk to take*

Such paternal desertion occurs in the largemouth bass *Micropterus salmoides* and is more frequent among the young of small size than among older fathers. Abandonment of nests appears to be correlated with an estimate of the apparent value of the offspring by the male, which relates to the number of eggs, the quality of the spawning and his personal involvement in the paternity, since the question is: is it not more interesting to leave the nest to found a new family, which has the advantage of being of better quality? The prospect of new couplings is a powerful engine, raising hopes of progeny gifted with greater *fitness**. Sometimes, it is environmental factors that induce a departure. A sudden change of temperature, a drop of −2°C following a storm, for example, causes a frequent desertion of nests by guardian males in the neighboring species smallmouth bass and *M. dolomieu*, which also anticipates an embryonic mortality resulting from this heat stress.

Females are very attentive to the faithful behavior of male guardians of nests and usually choose as partners those who appear to be the most dedicated.

Bibliography: *J.Fish Biol.*, 2014, **84**: & 1863-1875 DOI:10.1111/jfb.12404

### 2.1.3.4. *Collective resignation*

A whole population can temporarily cease to reproduce when environmental conditions are unfavorable. The cod *Gadus morhua* of the Arctic may practice cessation of spawning when they have suffered a restriction of food which weakens their energy reserves. An ovocytic atresia* enables them to recover the vitelline material which will be usable through metabolic recycling during a future spawning

Bibliography: *Can.J.Fish. Aquat.Sci*., 2009, **66**: 1582-1596 & DOI:10.1139/F09-102

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### Gestation

Bringing live young into the world is not only the prerogative of mammals. Some fish, more than 1,000 species, 2–3% of teleosts and 50% of elasmobranchs, are also capable of producing offspring which have remained a certain time in the genital tract of females: the ovary or oviduct in the absence of a uterus, which is specific to the placental mammals. Internal fertilization and embryonic development assume that, when coupling, a transfer of sperm occurs in the genital tract of the female. This transfer is done by simple contact between the genital pores of the male and female (pseudocopulation) or using a male intromittent organ named the urogenital papilla, ichthyophallus, pseudopenis, gonopod (Volume 2, section 1.1.2.6.2; Figure 1.1) or pterygopod (Volume 2, section 1.2.4; Figure 1.7), depending on its origin and its morphoanatomy. This transfer of sperm by phallic copulation or by contact does not necessarily imply the existence of gestation, nor even of fertilization.

Thus, among the Japanese sculpin *Alcichthys elongatus*, there is intromission of sperm within the genital tract of the female, but fertilization takes place in open water after the joint expulsion of gametes. The intromission of semen is usually followed by fertilizations which generate eggs (oviparity), or these eggs are retained in the ovary or the genital tract until the birth of the larvae (viviparity). Sometimes, it is embryonated eggs which are expelled (ovoviviparity). A particular case is that Malabar ricefish, *Horaichthys setnai*, in which the male equipped with a gonopod does not introduce the spermatozoa into the genital tract of the female but attaches a spermatozeugma containing these gametes near to her genital opening. This spermatozeugma liberates its sperm, which penetrate into the genital tract of the female and fertilize the oocytes. Intromission of semen by simple contact of the genital orifices is very exceptionally followed by gestation (viviparity), the most famous being that of the West Indian Ocean coelacanth *Latimeria chalumnae*. Another very original mode of fertilization concerns the bronze corydoras *Corydoras aeneus* who practice sperm-drinking: the female, when coupling, absorbs the semen of her partner by mouth and the sperm, after having moved quickly in the digestive tract, emerge intact at the level of the anal orifice to fertilize oocytes which are simultaneously spawned.

Among elasmobranchs as in teleosts, viviparity is associated with a phallic intromission of semen into the genital tract of the female, with one exception: that of syngnathids, who have reversed sexual behavior (Volume 2, section 1.1.4). The exit of the newborn from the maternal organism is termed ovoviviparity* or viviparity*, the degree of maternotrophic relations between the embryo and the maternal organism and their duration varying considerably according to family and species.

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The black surfperch *Embiotica jacksoni*, a North American embioticid of fresh waters (lakes and rivers), also practices internal fertilization resulting from copulation followed by gestation. Spermatozeugmas consisting of agglomerated sperm are transferred into the genital tract of females via one of two intromittent organs located on either side of the anterior part of the anal fin, the contraction of smooth muscles ensuring this insemination.

Bibliography: *Bull.Fish Biol.*, 2015, **15**: 9-31, *J.Fish Biol.*, 1995, **47**: 171-173, *Bull.South.Calif.Acad.Sci.*, 2017, **116**: 219-226 & scholar.oxy.edu/scas/vol116:iss3/7

### 2.1.4.1. *Variable materno-fetal exchanges*

Nutrient supplies made to the fetus by the maternal organism, or maternotrophy*, vary according to the species as a function of the type of exchange through the intermediary of an omphaloplacenta* and the gestation duration. Some inputs are limited to water and mineral salts, as in the Portuguese dogfish *Centroscymnus coelolepis*, when at the end of the gestation period of more than a year, the uterine epithelium decreases in thickness, which increases its vascularization, allowing a gain of wet mass for the fetuses from +37% to +44%. No contribution of organic material occurs, the latter only originating from the ovarian vitelline sac: lecithotrophy*. Similarly, among the sand devil *Squatina dumerili* of the Gulf of Mexico, ovoviviparity* is purely lecithotrophic*: the embryos are only fed from the vitellus* of the egg, which is stored in their vitelline sac, up to its exhaustion (for approximately 12 months).

Among many other species of viviparous fish*, maternotrophic inputs are of greater importance, involving *proteins, amino acids*, fats* and *fatty acids*. Among scalloped hammerhead *Sphyrna lewini* and the blacktip shark *Carcharhinus limbatus* of the Gulf of Mexico, the transfer of nutrients* of maternal origin to embryos is demonstrated by marking the latter with the stable *isotopes** $^{15}N/^{14}N$ and $C$, reflecting a very active maternotrophy*.

Bibliography: *J.Fish Biol.*, 2008, **72**: 1675-1689 & DOI:10.1111/j.1095-8649.2008.01843.x, 2010, **76**: 1682-1695 & DOI:10.1111/j.1095-8649.2010.02608.x, **77**: 1724-1727 & DOI:10.1111/j.1095-8649.2010.02813.x, *Mar.Biol.*, 2010, **157**, DOI:10.1007/s00227-010-1568-4

### 2.1.4.2. *Gestating mothers who modulate their energy effort*

Among the least killifish *Heterandria formosa*, a poeciliid of fresh waters in the United States, the embryos, numbering from 4 to 31, are fed by the maternal organism during the course of a gestation period lasting 27–35 days. This maternotrophy, ensured by exchanges taking place at the level of a follicular placenta, varies as a function of the feeding and social environment. The number and

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competition (from 20 up to 5,000 individuals/$m^3$) and stress factors. Round-bellied females possess the ability to modulate their use of energy by varying the number and the size of their descendants, adjusting their energy investment depending on the circumstances, knowing that the body weight of an embryo between fertilization and birth multiplies by a factor of 50 and that there coexist, in the maternal organism, several successive broods of embryos (up to six of different ages), in various stages of development, which corresponds to a superfetation* involving up to 30 embryos. The production of juveniles who are large at birth and thus likely to have the highest rates of survival is a means, for females, of ensuring the fitness* of their progeny. In contrast, abortions occur in the case of hybrid crosses (Volume 2, section 1.2.5).

An evolution of types of placentation has been linked, among poeciliids of the *Poeciliopsis*, to the size of females during their first cycle of reproduction, the number of descendants increasing as a function of viviparity*, which is earlier or later according to the population, hence the formulation of a hypothesis of "facilitation" of reproduction linked to maternotrophy*.

Bibliography: *Biol.Lett.*, 2013, **9**: 20130327 & DOI:10.1098/rsbl.2013.0327, *Curr.Biol*., 2014, **24**: R805-R808 & DOI:10.1016/j.cub.2014.07.039, *Evol*., 2009, **63**: 2805-2815 & DOI:10.1111/j.1558-5646.2009.00763.x, *Funct.Ecol*., 2011, **25**: 757-768 & DOI:10.1111/j.1365 -2435.2011.01842.x, 2014, **28**: 999-1010 & DOI:10.1111/1365-2435.12233

### 2.1.4.3. *Ensuring her progeny by viviparity stimulates maternal fighting spirit*

Females of the eastern mosquitofish *Gambusia holbrooki*, usually subject to strong inter-female competition to the advantage of the dominant who tend to exclude the subordinate*, become more aggressive, increasing their number of pursuits and bites. An increase in their stress occurs over the course of their gestation. They adopt increasingly risky behaviors, allowing them to win fights, although this behavior is costly in energy (increase in consumption of oxygen and ATP*; higher metabolism, particularly cardiovascular). Their reproductive success is not affected by this decline in the availability of energy resources.

Bibliography: *J.Exp.Biol.*, 2013, **216**: 771-776 & DOI:10.1242/jeb.07009756

### 2.1.4.4. *Variable length of gestation depending on the environment*

The durations of gestation of sharks vary according to species and their environment, generally around 1 year: 12 months in *Carcharhinus albimarginatus* *C. amblyrhynchos*, 10–12 months in *C. brevipinna*, 10–11 months in *C. leucas*, 8–10 months in *C. melanopterus* and 12–13 months in *C. limbatus*. These durations are a function of the temperature of the waters during gestation and females seek out areas of warm waters located in their area of distribution or close to them. The

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newborn infant after a gestation period of 1 year. Such a weak fertility rate and such lengthy gestation make these species very vulnerable to overfishing.

Bibliography: *J.Fish Biol*., 2007, **71**: 1512-1540 & DOI:10.1111/j.1095-8649.2007.01623.x, 2010, **77**: 169-190 & DOI:10.1111/j.10958649.2010.02669.x

### 2.1.4.5. *Variable number of embryos per litter*

The fecundity of female sharks is generally reduced, the number of embryos per litter ranging from one to several dozen. This number depends not only on the species, the size of the female and its ovarian fertility but also sometimes on the intensity of intra-oviductary cannibalism (Volume 1, section 1.2.3). It is the case of the Japanese viviparous tawny nurse shark *Nebrius ferrigeaneus* whose embryos show the particularity of being mobile, unlike the "sedentary" embryos of mammals, as shown by ultrasonic images. They move to one uterus to another (from left to right and vice versa) to cannibalize their sibling embryos. Such embryonic mobility is more than rare: this is the only known case in the animal kingdom.

Bibliography: *Ethol*., 2018, **125**: 122-126 & DOI.10.111/eth.12828, *J.Fish Biol*., 2008, **73**: 732-739 & DOI:10.1111/j.1095-8649.2008.01951.x

### 2.1.4.6. *Immunological problems related to gestation*

The fetuses express a portion of the paternal genome, which is considered a "foreign body" by the maternal organism at the level of the major histocompatibility* complex MHC (Volume 2, section 1.1.1), which induces in the latter an immunological defense reaction which, if not neutralized, may cause immunological rejection resulting in an abortion. Well known in mammals, this phenomenon of mother–child immunological compatibility is also seen in fish. In the Japanese viviparous surfperch *Neoditrema ransonnetii*, which has a gestation duration of more than 6 months, the embryos who depend almost exclusively on maternal nutrient supplies ingest the liquid of the ovarian cavity in which they develop, which exerts an inhibitory effect on maternal immune defense cells: absence of phagocytosis* linked to suppression of the cytotoxic activity of maternal leukocytes* following a production of immunomodulating cytokines. Such immunoregulation is crucial for embryos and entirely comparable with that developed by placental mammals.

Bibliography: *J.Fish Biol.*, 2015, **86**: 139-147 & DOI:10.1111/jfb.12549

### 2.1.4.7. *Gestating males*

Males of the various species of syngnathids including pipefish, seahorses and sea-dragons have the originality of performing a genuine gestation of embryos.

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oxygenation for developing embryos in their marsupial pouch which is comparable to the marsupium of kangaroos. Among these syngnathids, the females, at the time of mating, lay their eggs in the marsupial pouch of the male in which they develop and the embryos are released in a parturition*.

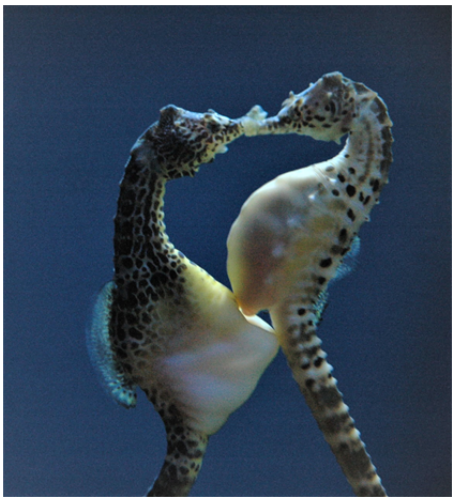


**Figure 2.9.** *Ventral coupling of seahorses* Hippocampus abdominalis*: the female deposits its oocytes in the ventral pouch of the male*

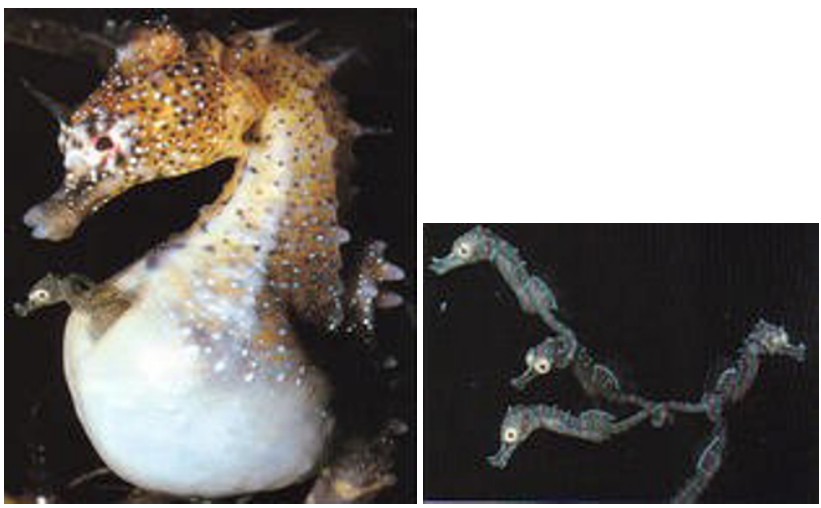


**Figure 2.10.** *Male hippocampus performing gestation of eggs in his*

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The reproduction of the broadnosed pipefish *Syngnathus typhle* is characterized, as in seahorses, by exemplary paternal care by males who perform, in a pouch, the incubation of clutches laid by a female who then abandons them. These males are gravid for 30 days and more, up to the exit of the newborns during a paternal childbirth. It has been highlighted in this pipefish that, during their period of gravidity, males move very little and sometimes cease to feed, so that their gestation is costly in energy. In effect, rich vascular structures resembling those of a mammalian placenta are found at the level of contact between the embryos and the epithelium of the incubation pouch, which enables paternotrophic exchanges in the form of nutrition of embryos by nutrients* of paternal origin. In *S. fuscus* of the American coasts, it has been shown that specialized vascular structures which develop around the embryos ensure a maximum of transfer of nutrients* via blood flow and begin to regress shortly before the release of newborns. Also, the supply of *oxygen* becomes limited while the embryos' demand increases in the course of their development, which creates a certain degree of hypoxia* that only larger males manage to avoid.

Bibliography: *J.Exp.Biol*., 2015, **218**: 1615 & DOI:10.1242/eb.125195, 1639-1346 & DOI:10.1242/jeb.120907, *J.Fish Biol*., 2010, **77**: 67-79 & DOI10.1111/j.1095.8649. 2010.02659.x, *Proc.Roy.Soc.B*, 2010, **277**: 971-977 & DOI:10.1098/rspb.2009.1767

### 2.1.4.8. *A parent exceptionally fed by their offspring*

Trophic exchanges can, surprisingly, also occur in the reverse direction: egg or embryo → father, as evidenced by a transfer of $C^{14}$-marked amino acids from the eggs contained in the incubation pouch to the liver and the muscles of the paternal broadnosed pipefish *Syngnathus typhle*, as well as towards the developing embryos.

*amino acids* are derived from the lysis of some eggs and embryos. This practice ensures reproductive success in producing well-formed hatchlings and maintaining a male in good condition, capable of quickly ensuring a new cycle of reproduction.

The females also show themselves sometimes to be cannibalistic, preferentially targeting, at the moment of childbirth, the offspring of others of their species. Such cross-cohort cannibalism thus tends to preserve their own descendants.

### 2.1.4.9. *Ancestral viviparity*

It has long been accepted that, in the history of the animal species, the spawning of oocytes or ovuliparity* far precedes in time the spawning of eggs or oviparity and the bringing into the world of live newborns or viviparity. This conception has been challenged with the discovery of an Australian fossil, *Masterpiscis attenboroughi*, a placoderm dating from the end of the Devonian 380 million years ago. This gravid female contained an intra-uterine embryo connected to the maternal organism by an

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umbilical cord, which suggests that "the mother of fish" experienced a successful copulation, more than 300 million years ago. The subsequent discovery, also in Australia, of a male placoderm *Microbrachius dicki* possessing a bony appendix assimilated to a copulatory organ allowing the insemination of females has confirmed such ancient origin.

## 2.2. Parental care

### *Providing parental care*

#### 2.2.1.1. *A minimum interest in progeny*

The males of many species are wholly uninterested in the future of their descendants, but are mainly concerned with the act of procreation and do not make any effort to ensure their survival, while the clutches and the newborns are the object of considerable risk of predation. Dominant male brown trout *Salmo trutta* behave a little better and provide protection to freshly laid and fertilized eggs on the gravel beds, by chasing away other, so-called "peripheral" males who are tempted to cannibalize them. Such chases, whose number is correlated with that of potential predators, are of short duration (generally a few minutes), because these males are quick to go courting new females and seeking to produce new progeny. This delay is however sufficient to limit cannibalism (Volume 1, section 1.2.3), time enough for the eggs to be quickly covered with soft sediments of sand and gravel by beats of the females' tail which sweep the spawning nests, or to insinuate naturally into the inter-gravel spaces, thus circumventing the greed of hungry oophages*.

Many other species show interest in their offspring, similar to birds who follow brooding with care (protection, feeding) and in contrast to reptiles (turtles, snakes, lizards, iguanas, etc.) who abandon their clutches.

The origin and evolution of parental care in fish have been widely documented as a function of benefits to the offspring during the various modalities of single- or bi-parental intervention.

Bibliography: *Evol.*, 2009, **64**: 823-835 & DOI:10.1111/j.05585646.2009.00854.x

#### 2.2.1.2. *Hard-working females*

Among the Japanese marine sculpin *Radulinopsis taranetzi*, females lay a thousand eggs on a sandy substrate, then cover their clutches with sand by beating their pectoral and caudal fins and, unlike most other cottids, they perform guardianship of the eggs. A disk formed by lengthening the mandibular and supramaxillary bones creates a suction cup structure, allowing them to suck water

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from the surface of the eggs to ensure their oxygenation during the 23–26 days until they hatch. This is the only example of maternal care in this family. In addition, it is the only known case in fish where females are equipped with such an unusually modified mouth.

Females of the cichlid *Simochromis pleurospilus* who incubate their eggs in their mouth (Volume 2, section 2.1.2) anticipate the risks of fasting and predation of their progeny by producing eggs of greater size, and thus juveniles who are 8.8% larger, when they previously lived in environments poor in food and threatened by predators in Lake Tanganyika. Among honduran red point cichlid *Amatitlania* , the parental care developed by females is dependent on the quality of their partner. In the presence of large males of high quality, they increase their maternal care, as if strengthening ties between the couple, increasing the hopes for development of beautiful progeny and ensuring future reproductive success.

Bibliography: *Biol.Lett.*, 2006, **2**: 225-228 & DOI:10.1016/rsbl.2005.0422,
*J. Fish Biol.*, 2005, **67**: 201-212 & DOI:10.1111/j.1095.8649.2005.00728.x

### 2.2.1.3. *Bi-parental care*

Not content to offer their offspring shelter in nests that they have made, many spawners look after them by providing supportive and defensive care, so as to ensure their reproductive success. There is a large diversity of situations, with varying degrees of parental investment ranging sometimes even up to a certain sacrifice and varying levels of care, therefore of benefit for descendants. The two partners of the couple are sometimes jointly mobilized, but generally the males are more available, driven to the task and more devoted.

Among the daffodil cichlid *Neolamprologus pulcher* of Lake Tanganyika, the two reproductive parents vigorously defend their nests, more than the servitors do (Volume 1, section 3.6). Females are more aggressive than males towards an intruder and are the best defenders of their offspring. These behaviors reflect the existence of cooperative defense of the territory, with different levels of commitment by females who are particularly active. A size difference exists between dominant males and subordinate* males, as a result of social mechanisms of inhibition. The growth of the latter, of second and third ranks, is accelerated after removal of the dominant male. Such a size limitation prevents these subordinate* males from being punished by the dominant, their submission sparing them from aggression and risk of injury. Such inhibition of growth does not apply to females.

On the other hand, a hepatic dimorphism is reported, these small subordinates possessing a more voluminous liver in relation to their size. Unrelated to eating activity, this characteristic may be linked to differences in energy expenditure. The

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depends very much on the assistance provided by the servitors or helpers*, varying in particular as a function of the various social interactions and especially the sex of these subordinates* who are more or less devoted to their service (Volume 1, section 3.6). The aggressiveness of each member of the couple is directed especially against individuals of their own sex. The male shows aggression towards all small males who are likely to later constitute sexual rivals and compromise their future reproductive success. As subordinates* of female sex do not constitute a direct threat to them, they benefit from greater leniency on their part, but are victims of aggression from the dominant female which maintains the sustainability of a social hierarchy.

In the species *Julidochromis marlieri*, the julies females who are of larger size than males provide most of the defense of the territory, while small males are confined to the role of guardians of the progeny inside the nests. The aggressiveness of the female towards an intruder is all the greater when she is dominant by size in the couple. Optimum efficiency is observable in favor of the male defender if he is the greatest.

The ability to provide care, very developed among the cichlids of the African Great Lakes, is correlated with strong brain development in one or the other sex engaged in these parenting practices. Those of females who solely provide care are more developed than those of females in couples whose care is bi-parental, while the brains of males show no difference between providers and non-providers of care. It would therefore seem that females cerebralize their parental function, thus the existence of intersexual differences of "cerebrotypes".

Among the convict cichlids of Central America *Amatitlania nigrofasciata* (formerly *Archocentrus nigrofasciatus*), males and females of each couple deliver care together to their offspring, housed in a nest which they have previously made. Such care extends up to an age of 6 weeks. There is traditionally a division of labor, each parent contributing to all the parental activities and to a distribution of roles which sees males focus on the activities of external defense of the nest and females taking care of the household, spending more time in the nest in contact with their offspring. Each of the parents prefer to follow the roles consistent with their sex in everyday life, but are able to compensate for the absence of their partner when it disappears, the victim of predation or tempted by desertion (Volume 2, section 2.1.4). There is, however, an asymmetry between male and female aptitudes for performing, in need and urgency, with the females being more gifted in all roles due to their greater behavioral flexibility. They are however not usually able to fully perform the defensive function which is usually devolved to males. However, males do not do well in recovering their descendants when dispersed outside of the nest at a short distance, the females have better rates of success. The males however are the

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best gatherers of the young when they are very distant from the nest. This care may sometimes benefit young foreigners, who are thus adopted.

Among the cichlid *Julidochromis ornatus* of Lake Tanganyika who spawn on a rocky substrate, the priority is defense. Bi-parental care is dimorphic; large females are paired with small males in 80% of couples. Although the two sexes are able to assume either role, both defense of the territory and parental care for young people, it is common that females take charge of the defensive function against intruders who are aggressively attacked, and they leave domestic care to the males, who remain in the nest and care for – cleaning, oxygenation – the clutches and the young. This case reflects a reversal of traditional roles with fathers at home and mothers fighting. Such plasticity of function shows that the role of defense of the territory is a priority and must be performed by the largest partner of the couple, whether a female or not. Moreover, in couples where the male is larger than the female – in 20% of cases – it is he who ensures the defensive role. Aggressive behavior is not determined by gonadal sex, but is dependent on the size of the combatant who is most able to ensure the security of clutches and juveniles. It is therefore the relative size of the two parents and not gender which determines their roles and the type of care provided, with a priority for defense.

Sometimes the parents offload the defense of their nest onto auxiliaries, upon whom rests the bulk of responsibilities. Such a transfer of security duties towards subordinates* referred to as helpers*, of whom up to five may perform guard duties during 94% of the time, means that parental guardianship then remains limited. The presence of subordinates* therefore changes the role of the couple, although all members of the group often cooperate in the defense of the nest.

On the other hand, parental behaviors depend on the experience gained previously by the females: those who have already reproduced are quicker to form couples, lay eggs earlier and better divide their time between care of the eggs and the young and defense of the nest when the male has been experimentally removed. In contrast, ex-virgin and inexperienced females, in the same situation, allocate the bulk of their time to parental care. Defensive aggression is higher in experienced females who are most able to rapidly adopt a typically-male defensive role. The permanent aggression that males display towards them seems to prepare them for this role of future combatants. Behavioral differences between females which are interpreted as differences in personality (Volume 2, section 3.7) are expressed at the level of their color pattern: individuals who are more active in aggressiveness, courage and taking initiatives in defensive parental care are distinguished by their dark coloration made of melanistic black bands with a lesser development of bright dots of orange color on their abdomen.

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The two parents of the cichlid *Pelvicachromis taeniatus* of Cameroon adjust their parental investment to the quality and the vulnerability of their litters, reducing their efforts when these are of low value – number, age, size and quality of offspring. In such cases, the mothers show less aggression during their defense of the nest and also towards the 4th week after hatching when the juveniles have acquired greater capabilities to flee.



**Figure 2.11.** *Larvae of the discus feeding on mucous secretions lactated from the skin of their parents*

The two parents of the Amazon discus *Symphysodon* provide food for their larvae over approximately 1 month with skin secretions from their flanks. This mucus made of mucins* provides them, in addition to nutrients* rich in proteins, with a contribution of antibodies*, an analogy with the colostrum of the lactic secretions of female mammals. As if the production of milk secretions had been "invented" by fish, and then resumed in the pigeon – milk secreted by the crop – and particularly by mammals provided with mammary glands? Parental mucous secretions are, however, sometimes vectors of transfers of chemical contaminants such as *cadmium Cd*.

Bibliography: *Anim.Behav*., 2005, **69**: 95-105 & DOI:10.1016/j.anbehax.2003.12.027, 2006, **71**: 449-456 & DOI:10.1016/j.anbehav.200506.011, 2010, **79**: 621-630 &

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2010.04.001, 2014, **93**: 201-206, **105**: 201-209, *Behav.*, 2004, **141**: 1135-1149, 2008, **145**: 313-325, 2009, **146**: 457-464 & DOI:10.1111/j.1439-0310.2009.01625.x, 1665-1686 & DOI:10.1163/0005579509X, 2014, **151**: 1389-1411 & DOI:10.1163/1568539X-00003190, *Behav.Proc.*, 2009, **82**: 25-29 & DOI:10.1016/j.beproc.2009.03.005, *Ethol.*, 2010, **116**: 257-269 & DOI:10.1111/j.1439-0310.2009.01738.x, 316-328 & DOI:10.1111/j.1439-0310.2009.01735.x, 2014, **120**: 483-491 & DOI:10.1111/eth.12221, 540-550 & DOI:10.1111/eth.12227, *Ethol.Ecol.Evol.*, 2005, **17**: 1-15 & DOI:10.1080/08927014.2005.9522611, *J.Exp.Biol.*, 2010, **213**: 3787-3795, 2013, **216**: 3587-3590 & DOI:10.1242/jeb.089102, *J.Fish Biol.*, 2009, **75**: 1-16 & DOI:10.1111/j.1095.8649.2009.02234.x, *Proc.Roy.Soc.*, 2009, **76**: 161-167 & DOI:10.1098/rspb.2008.0979, 2019, **286**, 1904 & DOI.org/10.1098/rspb,2019.0760

### 2.2.1.4. *Paternal care: a means of seduction*

Females of many species who provide parental care are very sensitive to the quality of paternal care deployed by males and choose them willingly as partners. Cases of single-parent care are many as among the sunfish *Lepomis gibbosus* and *L. macrochirus* of the Canadian lakes in which the male builds a nest and performs the defense and protection of clutches and larvae alone. This paternal care is adapted to the environmental threat: the stronger the predation pressure by the smallmouth *Micropterus dolomieu*, the better the nests are protected, by the male sunfish who invest an expensive energy expenditure in these defensive exercises.

Males of the three-spined stickleback *Gasterosteus aculeatus* are all the more appreciated by the females to the extent that their nests are well filled with eggs and that they provide good parental care – ventilation of clutches, absence of parasitized and dead eggs – this behavior participating in sexual selection (Volume 2, section 1.1.1). Spiggin* secreted by the kidneys of these males, which acts as glue for the purposes of consolidation of the assembly of vegetable fibers (Volume 2, section 2.1.1.5) has, in addition, an antifungal, antimicrobial and antibacterial health function, thus leading to an improvement in the rate of embryonic survival.

The male of the Venetian goby *Zosterissessor ophiocephalus* secretes from a gland in its spermiduct* an abundant mucus made of *mucins** and rich in antimicrobial substances such as *lysozyme*, containing *immunoglobulins** that it paints onto the walls of its nest and which is intended to protect from microbial infections the clutches deposited into this nest dug into the sediment of the lagoon.

The males of the sand goby *Pomatoschistus minutus* who build nests in two types of habitats, on rocky hard bottoms or on soft sandy bottoms, expend more energy for ventilation of the clutches in the latter habitat than in the former, because it is less well oxygenated. These males, guardians of their nests, must sometimes face a double threat: that of predators of eggs, the gastropods *Nassarius nitidus*, and that of mating competitors, small *sneaker** males who are always quick to steal

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fertilizations (Volume 2, section 1.2.1). It is appropriate for them to find a compromise to share their energy between defense of their rates of paternity and of their offspring. In addition, they must ensure the maintenance of the nests, in which they take care of the eggs by ensuring their cleanliness. Females avoid spawning eggs in nests impregnated with the odors of mold, in the case of eggs infected by the fungus *Saprolegnia*. Similarly, in the Caribbean beaugregory *Stegastes leucostictus*, it is common that males have to choose between several priorities for activity: defense of their nest and their offspring from predators such as wrasses, inter-male competition and/or courtship behavior with respect to females. A clear preference is shown by females of the neighbor species the scissortail sergeant *Abudefduf sexfasciatus* for males who are judged to be good fathers based on the eggs that they guard, protect, maintain by cleaning and ventilate, and among which the hatching rates are higher.

The male of the North American tessellated darter *Etheostoma olmstedi* dispenses his care by releasing, also, a mucus rich in antifungal components that protect the eggs from infections by microscopic fungi, not because they are concerned about the protection and future of their offspring, but rather as a means of sexual selection in order to attract the favors of females who are sensitive to such a demonstration of quality. These males even push their zeal so far as to perform cleaning and guardianship of eggs which are not their own and which have been fertilized, and then abandoned by other males who have deserted their nests. They thus prefer, playing the role of "step-fathers", to occupy strangers' nests containing eggs rather than to suffer from the absence of a nest. For them, the essential thing is to adopt behavior which is attractive to females and which brings hopes of coupling.

The male of the Lusitanian toadfish *Halobatrachus didactylus* vigilantly watches over the clutches contained in his nest, whether he is their father or the eggs are foreign, testimony to his marital woes. Their visual and acoustic demonstrations corresponding to a wide vocal repertoire and intended to chase away any intruders in the vicinity of the nest are identical, whether the clutches are autoparental or alloparental, and the survival rates of eggs are similar, indicating that their surveillance and defense do not vary as a function of the rates of paternity of the guardian, who therefore accepts the role of stepfather. However, he is rewarded, since females appreciate males who have many eggs in the nest, which reflects their qualities as guardians and they mate more willingly with them.

It is also the male of the butterfly blenny *Blennius ocellaris* who bears the obligation to provide parental care: oxygenation by ventilation of clutches and defense of the eggs deposited in the nest from predators. Their reproductive success is high, because the larger the number of eggs present in the nest, the more females prefer to mate with these males who are good parents and have already experienced

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Portugal, also reflects the success of males and therefore their attractiveness for females in search of a ripe male.

The parental care of the threespot damselfish *Stegastes planifrons* is ensured by the males: ventilation of eggs and guardianship of the clutches and larvae. Such an investment in energy, already substantial among healthy individuals, becomes unbearable for those who are the victims of parasitic infestation by a dactylogyrid monogene, which is responsible for injuries to the gill that induce a respiratory deficit. They are less resistant to fasting and thus attempt to compensate for this nutritional deficit, either by deserting the nests to seek food (Volume 2, section 2.1.3) or by cannibalizing the clutches in a filial cannibalism (Volume 1, section 1.2.4). Having thus reacquired better physical condition and higher potential energy, they become attractive to females.

Bibliography: *Anim.Behav.*, 2005, **69**: 661-668, 2009, **78**: 25-33 & DOI:101016/j.anbehav.2009.03.006, 2010, **79**: 237-242 & DOI:10.1016/j.anbehav.2009.11.006, *Ecol.Freshwat.Fish*, 2008, **17**: 71-77 & DOI:10.1111/j.16000-0633.2007.00260.x, 628-638 & DOI:10.1111/j.1600-0633.2008.00314.x, *Env.Biol.Fish*, 2008, **83**: 391-395 & DOI:10.1007/s10641-008-9359.1, *J.Exp.Biol.*, 2010, **213**: 2997-3004 & DOI:10.1242/jeb.044586, 2012, **434**: 58-62, *J.Fish Biol.*, 2006, **68**: 1215-1221 & DOI:10.1111/j.1095-8649.2006.01010.x, **69**: 1164-1177 & DOI:10.1111/j.1095-8649.2006.01194.x, 2008, **73**: 1823-1828 & DOI:10.1111/j.1095-8649.2008.02069.x, 2380-2389 & DOI:10.1111/j.1095-8649.2008.02086.x, *J.Zool.*, 2011, **283**: 269-275 & DOI:10.1111/j.1469.2011.00788.x, *Proc.Roy.Soc.B*, 2012, **279**: 1784-1790 & DOI:10.1098/rspb.2011.2237

### 2.2.1.5. *Male ventilators*

Male guardians of spawning nests have the responsibility of monitoring and defending the clutches which are deposited successively by several of their companions, but they are also the providers of paternal care for their offspring. They must particularly ensure a good oxygenation of eggs inside the nest where, as the opening to the outside is reduced in order to avoid intrusion of predators who will steal clutches, water circulation is limited. It is therefore appropriate, in order to avoid asphyxiation of the eggs, to regularly accelerate the movement of the water inside the nest by actively ventilating. To do this, the males proceed to rapidly beat their pectoral fins; this ventilation of nests is more important in the sandy habitats than in the rocky habitats of the sand goby *Pomatoschistus minutus*. Among the round goby *Neogobius melanostomus*, the male has long pectoral fins whose growth is induced, in the reproductive period, by a high rate of androgenic hormones *11-keto-testosterone* (*11-KT*). This anatomophysiological particularity begins even before spawning: each male displays his ventilatory capabilities before the females that he courts, and these females appreciate the best ventilators who, being the most vigorous, will probably be the best lovers and the best fathers. The flow of water

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created by such beating of the fins conveys, in addition, chemical messages *pheromones** emitted by the male for females which inform them of his personal quality. An energy deficit resulting from a parasitic infestation has the consequence of reducing ventilation activity, which translates into a lack of interest from females.

The most important paternal care performed by males of the three-spined stickleback *Gasterosteus aculeatus* concerns the ventilation of eggs, which takes up almost 40% of their time and is costly in energy. There are large genetic variations between males as to their capacity to oxygenate the clutches. This characteristic, which participates in sexual selection (Volume 2, section 1.1.1), is highly heritable.

The lungfish *Lepidosiren paradoxa*, an air-breathing fish, pond, lays its eggs, during the wet season, in cavities dug in the ground at the bottom of South American stagnant pools before they dry up over summer. The males perform not only the guardianship of nests but also do more than ventilating the clutches, since they ensure their oxygenation through richly vascular temporary structures which they develop, during the breeding season, at the base of their pelvic fins. At the bottom of the nest, the clutch, then the water-breathing larvae rapidly deplete the *oxygen* dissolved in the relatively warm water. The vascularized pelvic structures capture and release $O_2$ into the spawning nests over 7 weeks, until the larvae have acquired pulmonary respiration. The males renew the *oxygen* concentration of their blood by regular trips to the surface to breathe in, renewing the air content of their lungs which oxygenizes their blood. Such adaptation to life in hypoxic environments is original.

The ventilation efforts of the male flagfish *Jordanella floridae* increase when males are in strong competition in the case of an unbalanced sex ratio*; this criterion favors females making optional choices for the best males in this activity. An increase in water temperature responsible for a lesser concentration of *dissolved oxygen* forces males of the three-spined stickleback *Gasterosteus aculeatus* to additional efforts of ventilation. However, some males fail to ensure proper service, as evidenced by a high rate of embryonic mortality.

Contrary to what occurs in many species such as the beaugregory *Stegastes leucostictus*, who give priority to the sexual rivalry of inter-male competition over the defense of their nest, paternal care provided by males of the ocellated wrasse *Symphodus ocellatus* does not waver when sperm competition is high. The females are in no way appreciative of this beautiful effort in favor of the offspring, since they do not particularly choose those males who devote themselves to necessary and exclusive care. Even worse, cuckoldry (Volume 2, section 1.2.3) affects 100% of

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nests. Males therefore deliver their caring attention to eggs and larvae over which they do not have exclusive paternity.

Bibliography: *Behav*., 2006, **145**: 39-50, 2010, **147**: 37-52 & DOI:10.1163/000579509X12483520922089, 2013, **150**: 1623-1639 & DOI:10.1163/156539X00003113, *Env.Biol.Fish*, 2010 & DOI:10.1007/s10641-010-9724-8, *Proc.Roy.Soc.B*, 2010, **277**: 115-122 & DOI:10.1098/rspb.2009.1425, *Roy.Soc.Open Sci*., 208, **5**, 1 & DOI:10.1098/rsos.171029

#### 2.2.1.6. *Hard-to-replace paternal care*

The quality of parental care not only influences the rate of survival of the offspring. Juveniles of the three-spined stickleback *Gasterosteus aculeatus* who have benefited from paternal care of quality, such as defensive care from predators, and ventilation of the nest for its oxygenation, have more serene and less anxious behavior faced with a predator, such as a pike, than those who have been deprived of paternal affection.

Bibliography: *J.Exp.Biol.*, **218**: 164-165 & DOI:10.1242/jeb.111310

#### 2.2.1.7. *A conversion both physiological and behavioral*

A hormonal change occurs in the male three-spined stickleback *Gasterosteus aculeatus* in the course of its cycle of reproduction. From courting behavior at the beginning of the cycle (Volume 2, section 1.1.2), after mating and egg-laying, he adopts the behavior of the guardian of the spawning nest; this new behavior is correlated with an increase in the secretion of *prolactin PRL* by the pituitary gland. Induction of this behavior can be experimentally produced by an injection of *PRL* and its cessation after that of its inhibitor, *bromocriptine*. A parallel decline in the secretion of *androgen hormones 11-keto-testosterone* (*11-KT*) allows the entry of the ex-spawner into the parental phase of its reproductive cycle. A spawner becoming a parent is a real social conversion. After treatment by the synthetic *estrogen hormone 17β-ethinyl estradiol* $EE_2$, males lose their ability to build nests of quality due to a deficit in spiggin* and to provide paternal care.

Bibliography: *Behav.*, 2004, **141**: 1499-1510, *J.Fish Biol*., 2006, **68**: 1883-1890 & DOI:10.1111/j.1095-8649.2006.01053.x

#### 2.2.1.8. *Differing behavior between ecotypes*

In British Columbia, various ecotypes* of three-spined stickleback *Gasterosteus aculeatus*, benthic* or limnetic*, are found, who show distinct characteristics, not only morphological – cephalic and corporal morphotypes – but also behavioral. The differences involve their courtship behavior, nesting and parental care; their duration of stay in the nest; their defensive vigor and filial cannibalism. This regional

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ecological and ethological flexibility may serve as an indicator of genuine speciation*.

Bibliography: *Ethol*., 2007, **113**: 190-198 & DOI:10.1111/j.1439-0310.2006.01311.x

### 2.2.1.9. *False good solutions?*

Parental care is generally supposed to improve the survival of their offspring. However, it seems not to be always so. *Jordanella floridae* is a flagfish that delivers parental care, the male ensuring the guardianship of some 200 eggs deposited in his nest. The survival of eggs is compromised by its filial cannibalism (Volume 1, section 1.2.4), which is high when it is alone, the presence of females limiting this practice. In addition, the cleaning and ventilation of the clutches it performs appears to be without positive effect on the survival rate of eggs. An unnecessary expense of energy, unless this ventilation is used to attract the attention of females and to court

### 2.2.1.10. *Adoptive parents*

Dispensing parental care is not always exclusively specific and when several nests are contiguous, exchanges of some of the offspring may occur between different species, couples then playing the role of adoptive parents. Among the cichlids *Pundamilia pundamilia* and *P. nyererei* of Lake Victoria, adopted males raised in a lek* which neighbors that of their biological parents do not change their sexual preferences, which remain strictly specific, in contrast to the females who prefer to mate with males of the adoptive species, following visual *imprinting** for a familiar phenotype which was induced during their youth.

Bibliography: *Ethol.*, 2009, **115**: 39-48 & DOI:10.1111/j.14390310.2008.01582.x

### 2.2.1.11. *A relationship between size of eggs and quality of parental care?*

The question of such a relationship has been raised as a result of observations relating to a growing size of eggs in species of cichlids, salmonids and centrarchids who practice parental care compared to most of those (cyprinids, sticklebacks, etc.) that lay their eggs in the open water.

The hypothesis of a safe harbor has been developed, favorable to the idea of evolutionary progress correlating with better fitness* among those species who have developed such protective behaviors towards their progeny.

Bibliography: *J.Fish Biol*., 2005, **66**: 1499-1515 &
DOI:10.1111/j.1095-8649.2005.00777.x

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### *Having good parents*

#### 2.2.2.1. *Non-genetic heredity, very important and long-misunderstood*

The conditions of life encountered during the early stages of embryonic, then larval development greatly affect performances of survival and growth in fish. Parental influence is manifested for their progeny via mechanisms which are not only genetic but also non-genetic. A non-genetic heredity called "parental effect" has, in fact, been recognized, in certain circumstances. Transgenerational parental effects to the benefit of the offspring are measured in terms of the size, weight and survival rate of juveniles.

In addition, if the conditions encountered by an organism during its embryogenesis and at the beginning of its life have lasting effects on its growth and on its subsequent behavior, the experiences of its parents, its mother especially, affect its fate. Such a beneficial influence for their descendants has been observed in various teleosts, in particular in salmonids. These effects relate to the size of the eggs which depends on the feeding of the spawning female, the sex ratio*, the potential for growth and the ability to migrate, social behaviors such as courage or fear faced with a predator, effects demonstrated in 25 marine species exploited by fisheries. In the Australian spiny chromis damselfish *Acanthochromis polyacanthus*, juveniles derived from parents who are well fed and in good physical condition are, at hatching, larger by +6% and heavier by +21% than those whose parents are less well fed and of lesser condition; their survival rates are respectively 100 and 70%. However, these differences are erased in equivalent conditions after 50 days: the so-called compensatory growth enables the smaller to catch up with the larger, and their respective rates of survival are not affected, suggesting that this handicap at birth is not sustainable and that juveniles of a lesser condition are able to compensate by better growth performance.

Chemical *imprinting** is necessary to induce the mutualistic relations between ocellaris clown-fish *Amphiprion ocellaris* and sea anemones that serve as their hosts (Volume 1, section 3.4). It is promoted by early contact between the eggs deposited on the body of anemones; such a system of early recognition is facilitated by the parents.

Bibliography: *Biol.Lett.*, 2009, **5**: 262-265 & DOI:10.1098/rsbl.2008.0642, *J.Fish Biol.*, 2014, **85**: 151-188 & DOI:10.1111/jfb.12432, *J.Exp.Mar.Biol.Ecol.*, 2014, **457**: 160-172.

#### 2.2.2.2. *Maternal effects*

Parental effects generally express maternal quality which manifests itself on several levels and greatly impacts the chances of survival of descendants. The choice

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of spawning grounds of quality on a coarse substrate facilitating optimal circulation of interstitial water is a prerequisite for the survival of eggs and embryos of the lithophilous salmonids* such as the rainbow trout *O. mykiss*. The viability of the embryos of the walleye *Sander vitreum* of Lake Ontario depends essentially on the quality of maternal oocytes and especially on their age of fertilization. Oocytes that have suffered over-maturation before being laid are of lesser quality; such a delay of ovuliposition* is due either to the age of the females or to a very high temperature of the water, which explains the interannual differences in reproductive success.

It has been shown among populations of clownfish *Amphiprion polymnus* of Papua as well as those of *A. chrysopterus* of Polynesia that the number of eggs laid, which may affect the number and the survival of recruits, is correlated with the size of the female. The older and larger ones produce offspring which perform better than those of young females and may provide the bulk of recruitment*, which shows the importance of Big Old Fat Fecund Female Fish (BOFFFF). The duration of partnership of spawning couples could also constitute an important factor in the vital success of populations. Similarly, populations of the northern red snapper *Lutjanus campechanus* of the coasts of Florida have a strong power of resilience* thanks to their many BOFFFFs.

Maternal effects vary with the age of the females. They are more spectacular in a long-lived species (40 years) such as the Pacific Ocean perch *Sebastes alutus* of the north-east of the Pacific – Gulf of Alaska, viviparous with intra-ovarian development of embryos, among which, in the absence of any sign of senescence, the oldest females are the most powerful with respect to the quality and number of viable descendants when compared to the progeny of females aged 4–32 years. Note a lack of menopause in fish, whose females do not cease to be better and better-performing.

Bibliography: *Ecol.Freshwat.Fish*, 2015, **24**: 424-434 & DOI:0.1111/eff.2015.24.issue-3/issuetoc, *J.Fish Biol.*, 2008, **72**: 2634-2644 & DOI:10.1111/j.1095-8649.2008.01879.x, *Proc.Roy.Soc.B*, 2012, **279**: 2116-2121 & DOI:10.1016/rapb.2011.2433, *Roy.Soc.Open Sci.*, 2018, **5**, 1 & DOI: 10.1098/rsos.170966

Several criteria which depend on maternal inputs seem to be advantageous for the progeny: we shall detail them.

### 2.2.2.2.1. Nutrient supplies

The quality of the maternal diet in carotenoids* has been demonstrated in the cichlid *Amatitlania siquia*: an increase in this pigment in the diet of the mother is reflected by an increase in the growth and survival of offspring. Such an allocation *carotenoids** enriches the eggs and, thus, benefits the newborns in terms of

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*Gymnocephalus cernuus* by the size of the eggs, their richness in vitellus* and its chemical composition, all these elements contributing to the size of the larvae at hatching and to their survival, in particular their ability to tolerate brackish water. The viability of embryos of the Arctic char *Salvelinus alpinus* depends on the size of the eggs, which is a function of temperature, which is smaller at 7°C than at 2°C, and the capacity to partly protect them from thermal stress during their incubation. The composition of the eggs in essential fatty acids affects embryonic development, the growth and performance of the embryos and larvae, and thus their survival, then their recruitment*. These *fatty acids* find their origin in the diet of their mother, as shown by tracking of the *arachidonic acid ARA 20:4w-6* among the red drum *Sciaenops ocellatus* whose concentration depends not on body reserves accumulated over a long time but on the maternal diet during the 2–6 days preceding spawning. Survival of descendants depends on the availability of food at the sites of trophic resources of this marine species. Such a rapid transfer of nutrients* justifies the existence, at the time of reproduction, of parental migration towards the richest and most productive coastal areas. Females of the cichlid *Bagrus meridionalis* of Lake Malawi adopt a very original behavior: they expel oocytes above the nest which feed their newborns. Such spawning for purely trophic purposes has been described only in this species.

Bibliography: *Funct.Ecol*., 2014, **28**: 612-620 & DOI:10.1111/1365-2435.12205

### 2.2.2.2.2. Sex ratio*

When they mate with attractive males that they like, females of the guppy *Poecilia reticulata* give birth to more males. How do they manipulate in this way the sex ratio of their offspring? A diet of high nutritional quality provided to female swordtails *Xiphophorus multilineatus* favors production by the latter of large males with rapid growth, for whom sexual maturity is reached at a high size, thus their strong attractiveness to females and their great reproductive success. Having great energy, they are more courageous and more aggressive than others of their species from mothers who are more poorly fed. *Polyunsaturated fatty acids* (*PUFA*) in food are favorable to the *fitness** of males by controlling the quality of their sperm, while a deficient diet decreases the paternity rates of the guppy *Poecilia reticulata*. Despite females experiencing a period of scarcity, then hyperphagia allowing compensatory growth, they show a decline in fertility (approximately −20%). Among the coral of the Pacific *Plectropomus leopardus*, the size of the eggs and their richness in (3% of fresh weight), which constitute the main energy reserves, are directly correlated with the size of the mother as among many fish. Maternal characteristics are good predictors of the quality of the clutches and the chances of survival of their offspring, in particular at the critical time of passage from endogenous nutrition by consumption of vitellus* to exogenous feeding corresponding to capture of larval prey, which ensures a greater success of recruitment* (Volume 2, section 2.2.3).

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Bibliography: *Ecol.Freshwat.Fish,* 2006, **15**: 105-110 & DOI:10.1111/j.1600-0633.2006.00138.x, *Ecol.Lett*., 2010, **13**: 998-10007 & DOI:10.1111/j.1461-0248.2010.01491.x, *Ethol.*, 2010, **116**: 524-534 & DOI:10.1111/j.1439-0310.2010.01767.x, *J.Fish Biol*., 2015, **86**: 1286-1304 & DOI:10.1111/jfb.2015.86.pssue-4/issuetoc

### 2.2.2.2.3. Resistance to temperature changes

The beneficial influence of the mother on its progeny is also expressed in the form of better resistance to a warming climate, for example, in marine populations in littoral zones of the three-spined stickleback *Gasterosteus aculeatus* which show an adaptive plasticity resulting from such transgenerational effects: physiological mechanisms involving metabolic capacity, mainly cardiorespiratory and of mitochondrial origin. These translate, in neonates, into better acclimatization to warm waters when their mother has herself been acclimated to these temperatures than if they were to acclimate by themselves. These benefits relate to faster body growth in an early period of their life, up to 30 days post-hatching, which would be due to this maternal physiological legacy. It is therefore the mothers who "block out" the impact of harmful effects of the current global warming. Similarly, the tolerance for cold of the tropical cichlid, the tilapia *Oreochromis aureus*, among whom the optimum temperature is 25–28°C, is the result of maternal effects, as evidenced by the experiences of multiple crosses.

Bibliography: *Env.Biol.Fishes*, 2016, **99**: 975-981 & DOI:10.1017/s10641-016-0539-0, *Funct.Ecol*., 2014, **28**: 1482-1493 & DOI:10.1111/1365-2435.12280

### 2.2.2.2.4. Acclimation to high rates of $CO_2$

Exposure to high levels of $CO_2$ generally affects the swimming performance of fish. These effects are however less if the parents have previously undergone such treatment, which would ensure transgenerational acclimation.

Bibliography: *Proc.Roy.Soc.B*, **281**: 177720132179 & DOI:10.1098/rspb.2013.2179

### 2.2.2.2.5. Lower vulnerability to predators

As vulnerability to predation is very great in recently hatched larvae, it is again the mothers who contribute effectively, via the size of their eggs, to the safeguarding of their offspring in promoting their survival during their first month of life, thanks to rapid growth which, associated with better swimming abilities and achievement of a size not compatible with the oral diameter of some predators, reveals itself to be a lifesaver. Among the stickleback *Gasterosteus culeatus*, a maternal experience of antipredation is transmitted to her descendants who adopt a capacity for narrower grouping. The largest eggs laid with greater richness in *cortisol* prepare the newborn to live in a risky environment. Females of the cichlid *Simochromis pleurospilus* of

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Lake Tanganyika also produce, in the presence of predators, larger eggs which generate larger, less vulnerable larvae. In addition, they indicate to the larvae, by olfactory chemical messages, the presence of a predator. Such an early knowledge of the dangers of predation proves useful in being able to flee quickly. These maternal alerting effects are often decisive during this short critical period of the beginning of their life. The females of *Ctenochromis horei* who practice buccal incubation of eggs, and then of larvae (Volume 2, section 2.1.2) extend the latter so as to enable their progeny to remain protected for longer, and then to release them at a larger size, anticipating better survival.

The small Brazilian poeciliid *Phalloceros harpagos,* when undergoing strong predation pressure, modifies its reproduction parameters in order to increase the number and quality of its descendants: a smaller size at achievement of first sexual maturity, superfetation* when two lots of embryos at different stages of development are in simultaneous gestation and maternotrophy* by a rich maternal supply of *nutrients*, the embryos increasing – multiplying by 4 – their dry mass during the course of their development.

Bibliography: *Ecol.Freshwat.Fish*, 2018: 27: 442-452 & DOI:10.1111/eff.12359, *Funct.Ecol*., 2014, 28: 944-953 & DOI:10.1111/1365-2435.12224

### 2.2.2.2.6. Preparation for competitive behavior

The size and number of descendants often depend on the social conditions of maternal life. Descendants of the females of the least killifish *Heterandria formosa* are of greater size when the mother has been raised in a high population density of 5,000 individuals/$m^2$.

### 2.2.2.2.7. Protection from pathogenic agents

A maternal contribution to the resistance of descendants to bacterial infections by the bacterium *Pseudomonas fluorescens* was identified in the whitefish *Coregonus palaea*, the vulnerability of descendants increasing in the course of development. It has been experimentally demonstrated that a transfer of immune factors such as *immunoglobulins**, lectins such as *lysozyme*, of maternal origin, into the egg, protects embryos from infections at the beginning of their development, but that this immune protection declines during the course of this development. Larval mortality is thus greater after hatching and the surviving larvae have a later hatching, a smaller size and lower swimming capabilities. Such maternal protection of early vulnerability is used only to cover a limited “critical window” during development. The physical condition of the females of migratory species of salmonids such as sockeye salmon *O. nerka* affects the size of the eggs, the growth of fry and their swimming skills, and therefore their survival. Females who are energetically exhausted by their return migration (Volume 1, section 2.1.1), moribund in a

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situation of stress with a high concentration of *cortisol*, give birth to descendants whose sensitivity to stress is high.

Bibliography: *Anim.Behav*., 2015, **102**: 147-151, *Evol.*, 2009, **63**: 1341-1347 & DOI:10.1111/j.1558-5646.2009.00631.x, *Funct.Ecol.*, 2014, **28**: 714-723 & DOI:10.1111/1365-2435.12214, 1482-1493 & DOI:10.1111/1365-2435.12280, *J.Fish Biol.*, 2009, **75**: 1244-1257 & DOI:10.1111/j.1095.8649.2009.02360.x, *Mar.Ecol.Prog.Ser*., 2015, **526**: 125-141, **529**: 249-263 & DOI:10.3354/meps11277, *Proc.Roy.Soc.B*, 2010, **278**: 1753-1759 & DOI:10.1098/rspb.2010.1819

### 2.2.2.3. *Paternal effects*

Parental effects of paternal origin relate to the fitness* brought to the progeny by the father, through the quality of his semen that varies as a function of the inter-male competition during reproduction. In case of very high sperm competition at the time of mating due to the presence of many rival males, males of the zebrafish *Danio* produce more mobile spermatozoa, with a greater swimming speed than those submitted to less competition. These effects of good sperm have immediate consequences for hatching of the eggs, which is more precocious via mechanisms involving *RNA** messengers (*mRNA*) transmitted to the eggs during the fertilization, as well as processes of methylation* of nucleic acids* which control the expression of genes, in this case those that synthesize the protein tetraspanin CD63 secreted by the hatching glands. The action of these proteolytic enzymes accelerates the breaking of the chorion* of the egg and the accelerated exit of the larva. Such acceleration of hatching, associated with higher metabolic activity, constitutes a fitness* advantage as regards the larvae's competition for food, to the benefit of the first hatched. Such epigenetic effects* often turn out to be decisive in terms of early survival.

Paternal effects were also observed in Atlantic salmon *Salmo salar*, among whom a variation in longevity between sperm cells, which compete within the same ejaculation and who have a power of fertilization of about 1 min, leads to differences of fitness* – vigor and survival – in the progeny. In fact, differences in earliness of hatching in favor of the first fry to emerge from the gravel are reflected by better occupation of habitats for protection and feeding.

Other effects involve the impact on the progeny of parasitic infestations by the nematode *Carnallanus* sp. affecting males of the three-spined stickleback *Gasterosteus aculeatus* who have spermatic deficiencies corresponding to a lesser motility of their sperm and reduced reproductive success. Their progeny suffers from lower rates of hatching and survival, but enjoys, unlike that of others of their species born to healthy parents, greater immunological resistance to parasites, following the non-genetic transmission of *proteins* – or other molecules? – from the

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The size of male defenders of spawning nests is a predictive criterion of successful survival of larvae, the largest ones enjoying the best reproductive success among the convict cichlid *Amatitlania nigrofasciata* (formerly *Archocentrus nigrofasciatus*).

Bibliography: *Biol.Lett.*, 2014, **10**: 20131040 & DOI:10.1098/rsbl.2013.1040, *Ecol.Lett.*, 2014, **17**: 1409-1417 & DOI:10.1111/ele.12344, *J.Fish Biol.*, 2006, **69**: 1239-1244 & DOI:10.1111/j.1095-8649.2006.01174.x, *Proc.Roy.Soc.B*, 2014, **281**: 20140422 & DOI:10.1098/rspb.2014.0422

#### 2.2.2.4. *Bi-parental sacrifice*

Is it not the best gift that parents can give to their offspring to ensure a quality food supply during their younger years? That is what is done by American salmon of the genus *Oncorhynchus*, who die on the spawning grounds in the upstream part of the rivers, their reproductive duty accomplished. The bodies of these spawners who "die for love" remain on site and are subject to gradual decomposition that not only brings happiness, in the short term, for bears, eagles and flies (their maggots at least), but also benefits mainly, in the long term, the young salmon that will use aquatic invertebrates (insects especially: mayflies, caddisflies, etc.) to ensure their growth. Thus, the nutrients* *nitrogen* (*N*) and *phosphorus P* of marine origin, because acquired in oceanic feeding areas frequented by spawners and thus parents, enrich the freshwater ecosystems*, and even the riparian forests benefit from them! Tracking these nutrients* in Alaska by means of isotopes* marked $\delta^{13}C$ and $\delta^{15}N$ shows that, in addition to the decomposition of leaf litter, richness in benthic* aquatic insects – chironomids, stoneflies, caddisflies, etc. – is high 1–50 m downstream of the dead bodies of these spawners, thus the idea of adding carcasses to enrich the environment, which will benefit the young salmon. Such a flow of nutrients* of marine origin which benefits the whole freshwater ecosystem would be seriously affected by a decrease of salmon stocks caused by anthropogenic* interventions: overfishing, habitat degradation, pollution, etc.

Bibliography: *Can.J.Fish.Aquat.Sci.*, 2006, **63**: 1230-1241 & DOI:10.1139/F06-029, 2543-2552 & DOI:10.1139/F06-144, *J.Fish Biol.*, 2010, **76**: 2558-2570 & DOI:10.1111/j.1095-8649.2010.02648.x

### *Larval recruitment*

To participate in the maintenance and sometimes increase in stocks of their species, planktonic larvae, whether derived from marine or pelagoplanktonic or benthic freshwater spawning of many species, must find either their original biotope, or at least sites favorable to their installation in order to complete their vital cycle (nursery). This recruitment* in these favorable places must be done shortly before

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their metamorphosis, which consists of a morpho-anatomical, physiological and behavioral remodeling allowing them to experience the juvenile and adult phases of their life cycle. The recruitment stage has the same importance as the later life of larvae during both the juvenile and adult stages, whether it takes place in open water in the pelagic ecosystem (tuna, sardine, etc.) or on or near the bottom (sole, red scorpionfish, sea bream, etc.). The larval dispersion of saddled seabream *Oblada melanura* has been studied in the south-west of the Mediterranean by following variations in the chemical composition of their otoliths* during the phases of their development during their pelagic larval migration, which can reach 90 km and which is followed by their benthic installation.

Bibliography: *Mar.Ecol.Prog.Ser.*, 2016, **544**: 213-224 & DOI:10.3354/meps11609

### 2.2.3.1. *Recruitment on soft bottoms*

The passage from planktonic* life to benthonectonic* or benthic* life is a crucial step in the larval life of some species such as flatfish. Selection of the type of substrate occurs in the flounder *Platichthys flesus* whose larvae, in their nurseries on the Danish coasts, seek bare sandy bottoms and avoid those cluttered by a vegetation of filamentous macroalgae *Enteromorpha* sp. The particle size of these sandy shores is important for larval survival, because it must allow rapid burial to avoid predation by shrimp, *Crangon crangon*.

Transfer of the pelagic larvae of various families – mullet, sole, sea bream, etc. – occurs in a sandy bay in South Africa: these take advantage of breaking waves to "surf" onto the beach, in the absence of predators. There may be a positive influence of the wind and waves on larval recruitment.

In spite of dispersion of eggs and larvae, the recruitment of Atlantic cod *Gadus morhua* on the Norwegian coast is evidence of fidelity to the protected habitats represented by certain fjords.

Bibliography: *J.Fish Biol.*, 2014, **84**: 1354-1376 & DOI:10.1111/jfb.12360, *Mar.Ecol.Prog.Ser.*, 2014, **511**: 153-163 & DOI:10.3354/meps 10944

### 2.2.3.2. *Recruitment on coral reefs*

On the coral reefs of the island of Moorea in Polynesia, the pelagic larvae of many species, 27 of them belonging to 14 families including pomacentrids, acanthurids, snapper, serranids, etc., swim actively, mostly on the surface in the upper 30 cm, while surfing, during the night, in order to be able to recruit further, beyond the fringing reef. The position of the larvae in the water column depends on their recruiting* site and the beginning of their benthic* existence. Those who swim near the bottom settle first at the entrance of the lagoon according to the

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first-encounter-first-stop model. The larvae of groupers such as the white-streaked grouper *Epinephelus ongus* are dependent on ocean currents, as well as have freedom of movement, thanks to the contraction or expansion of their dorsal and pelvic spines, giving them autonomy of swimming movement and a certain individual control of hydrodynamic forces.

Olfactory stimuli of *amino acids* at low concentrations of $10^{-5}$–$10^{-6}$ M and acoustic stimuli in relation to a sensitivity to noise of 100–2,000 Hz* frequency with peaks at 100, 200, and 600 Hz* participate in attracting larvae of the coral trout *Plectropomus leopardus* onto the reefs of the Great Barrier Reef in Australia. Their metamorphosis in view of a demersal* life takes place after 19–31 days of pelagic

On the reefs of the Red Sea at Eilat, the pelagic larvae* of the green *Chromis* settle preferentially in response to perceptions of olfactory and auditory cues emanating from adults of the same species who are already settled on sites rich in the branching coral *Acropora* sp. Tests of olfactory choices carried out on three species of damselfish (*Dascyllus melanurus*, *D. reticulatus* and *Chrysiptera arnazae*) show that each of them has a clear preference for waters containing chemical messages emanating from members of the same species and, on the contrary, an aversion to those of heterospecific origin. Such chemical signals of homospecific attraction and heterospecific aversion seem to be responsible for the distributions of juveniles on the coral reefs. Such a selection of the best microhabitats affects the success of recruitments*, although the intraspecific competition for habitat and food that new entrants undergo may be difficult for

It seems clear that the larvae of some species of pomacentrids who recruit on the Great Barrier Reef use celestial markers to guide themselves; the accuracy of their orientation is variable over the day, modified by cloud cover and variations in polarization of sunlight (Volume 1, section 2.2.2).

Sensitivity to submarine noises of the larvae of tropical species who recruit* on coral reefs varies considerably depending on the species; some species such as the lagoon triggerfish *Rhinecanthus aculeatus* are attracted by certain sounds and repelled by others. Larvae of the bridled cardinalfish *Pristiapogon frœnatus* are not attracted by any noise but are repelled by those emanating from the bays and mangroves*, and finally others, such as those of the convict surgeonfish *Acanthurus triostegus*, are insensitive to all sounds. Strategies for installation on the reefs thus obey distinct and quite separate rules of attraction–repulsion, which determine their final spatial distribution. Larvae of the mangrove snapper *Lutjanus griseus* off the coast of Florida who use acoustic signals to orient themselves in the direction of the reefs are also able in their turn to issue sounds which are likely to maintain the cohesion of groups during the night among these “sound-making” larvae.

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Bibliography: *Biol.Lett*., 2014, **10**: 20140643 & DOI:10.1098/rsbl.2014.0643, *J.Fish Biol*., 2008, **72**: 2543-2556 & DOI:10.1111/j.1095-8649.2008.01864.x, 2707-2713 & DOI:10.1111/j.1095-8649.2008.01868.x, **73**: 1005-1018 & DOI:10.1111/j.1095-8649.2008.02003.x, 2014, **85**: 1757-1765 & DOI:10.1111/jfb.12502, 2015, **86**: 1507-1518 & DOI:10.1111/jfb.2015.86.issue-5/issuetoc, *Mar.Ecol.Prog.Ser*., 2014, **505**: 193-208 & DOI:10.3354/meps10792

#### 2.2.3.3. *Massive mortalities*

Larval dispersal of reef species is conditioned by general oceanographic movements of upwelling* of ocean currents and local hydrographic movements of tidal currents, which ensure larval transport and determine both their journey and the success of recruitment*. Larval survival during installation or *settlement* on coral reefs is generally very random, which is primarily a function of predation intensity. That of the Ambon damselfish *Pomacentrus amboinensis* of the Great Barrier Reef in Australia is correlated with the size of the larvae. Mortality rates are lower, in the first 10 days, among large larvae than among small ones (12.3 mm vs. 11.9 mm), but may still reach 25% on the first day. Above all, remember that the survival rate of larvae capable of reaching the stage of metamorphosis into juveniles is always low, approximately less than 1% and sometimes even more than 1‰.

Bibliography: *Biol.Lett*., 2014, **10**: 20140643 & DOI:10.1098/rsbl.2014.0643, 2015, DOI:10.1098/rspb.2014.0746*, Mar.Biol*., 2014, **161**: 1905-1918 & DOI:10.1007/S00227-014-2473-z, *Oikos*, 2004, **106**: 225-242.

#### 2.2.3.4. *The devastating effects of a tsunami*

The ecological impact of the tsunami which, in March 2011, struck the eastern coast of Japan, flooding 400 $km^2$ and devastating the whole coastline, has had very negative effects on larval populations of ayu *Prosopium altivelis* with a selective mortality of newly hatched larvae that were present on these sites. A microchemical examination of surviving larval otoliths shows that those that were in the sea were less vulnerable than those occupying estuaries, which were victims of severe erosion.

Bibliography: *Env.Biol.Fishes*, 2016, **99**: 527-538 & DOI: 10.1007/s10641-016-0495-8

### *Metamorphoses*

It is not only insects who present themselves in many forms (caterpillar → chrysalis in a cocoon → butterfly) between larva and adult. Amphibians also move through aquatic larval stages, or tadpoles, before becoming adult amphibians. Some

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and adopting different types of behavior in relation to profound changes in their main vital functions and their living environments. Such metamorphoses often involve profound changes, morphological, physiological and behavioral, experienced by larvae before reaching the adult stage.

#### 2.2.4.1. *Primary metamorphoses during development*

These metamorphoses correspond to changes in shape (or morphological metamorphoses), as well as to changes in anatomy and mode of life between planktonic larvae and pelagic, nectobenthic or benthic adults. The case of the European eel *Anguilla anguilla* is well known: first, leptocephale larvae which are adapted due to their willow-leaf shape to pelagoplanktonic* life in the open ocean during transatlantic migration from the Sargasso Sea where they are born to the continental shelf of Western Europe. Then, larvae (elvers) who undertake the colonization of continental environments, estuaries, lagoons, rivers, etc., before becoming yellow eels who are more or less settled in fresh water, then migratory adult silver eels who will spawn in the Sargasso Sea. The metamorphoses of flatfish such as common sole *Solea solea*, plaice *Pleuronectes platessa* or the turbot *Psetta maxima* are just as spectacular. After a phase of pelagoplanktonic* life during which their symmetry is bilateral, these larvae become benthic* with a quite asymmetrical morphology in order to lie on their side, in contact with the sedimentary substrate. The eye migrates from the side which must rest on the ground to their upper side, called zenithal, which is pigmented; the lower side, called nadiral, in contact with the substrate becomes blind and depigmented.

#### 2.2.4.2. *Secondary metamorphoses in anticipation of a new life*

Such metamorphoses are physiological. They enable the body to prepare for a change of environment: on the one hand, from marine to fresh water as in spawning adult salmon, sea trout, shad or even lampreys, when they return from marine migration to spawn, and, on the other hand, from fresh water to marine water to feed themselves, as in juvenile salmon, shads and lampreys, as well as silver eels for reproduction. The physiological process of smoltification* of migratory salmonids (Volume 1, section 2.2.1) and silvering* or acquisition of silver color pattern among eels consists of anticipatory preparation for occupying environments of fresh water seawater which are characterized by differences in the concentration of *mineral salts and ions* $Na^+$ and $Cl^-$, justifying the development of so-called osmoregulatory mechanisms which are under hormonal control – thyroid, inter-renal gland – and which affect their survival. This metamorphosis is much more than a simple change of look and reflects complete transformation of a body which, shedding its original apparel, prepares to lead another life. The second metamorphosis of the eel, the passage of the yellow eel to become a silver eel, is not limited to the acquisition of silvering by deposit of guanine* crystals in the skin and osmoregulatory

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anatomo-morphological (increase in the diameter of the eye, development of the vascular network around the swim bladder, involution of the digestive tube, etc.) and physiological (onset of puberty under the effect of *gonadotropic hormone GTH* under the control of *thyroxine* $T_4$), in the context of preparation for the great Sargasso voyage (Volume 1, section 2.2.1).

Bibliography: *Cybium*, 2013, **37**: 216, *J.Fish Biol.*, 2005, **66**: 1025-1043 & DOI:10.1111/j.0022-1112.2005.0062.x, *Neuro-Endocr.*, 2005, **82**: 221-232 & DOI:10.1159/00092642

### *Miniaturized fish*

Gobies and blennies, the dominant representatives of benthic* populations of the coral reefs in which they are camouflaged (Volume 1, section 1.3.4) generally have active reproduction, but a short life, as seen in the adoned dwarf goby *Eviota sigillata*, who live 59 days and produce up to 7.4 successive generations/year, and kuna goby *Coryphopterus kuna*, whose adult life is shorter than their larval life.

Rare species, in particular of goby, are distinguished, in addition to their small size, by the conservation of larval characters throughout their life.

They show a simplified anatomy which preserves juvenile characteristics such as a transparent body deprived of scales, and their reproduction takes place at a very early stage of their development, known as paedomorphosis*. This type of reproduction from a morphologically non-adult parental body which has preserved larval or juvenile characteristics is called neoteny*.

Among the Indo-Pacific goby *Schindleria praematura*, which is among the smallest vertebrates, females breed to a size of 7.5 mm for a mass of 2–6 mg. Their life is brief: 3 months. Among the Mediterranean transparent goby *Aphia minuta*, these childhood characteristics are considered an adaptation to pelagic* life and a short life span of less than 1 year, with the achievement of two clutches of eggs during this brief period which precedes their death in the autumn. These are short-lived fish.

Bibliography: *Curr.Biol.*, 2017, **27**: R453-R454, *J.Fish Biol.*, 2000, **58**: 656-669 & DOI:10.1016/jfbi.2000.1478, 2005, **66**: 378-391 & DOI:10.1111/j.1095-8649.2004.00603.x, 2008, **72**: 1539-1543 & DOI:10.1111.j.1095-8649.2008.01811

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# 3

# Remarkable Capabilities

## 3.1. Aces of ballistics

### *Stronger than William Tell?*

Recall the quite original and particularly clever hunting strategy of the spotted archerfish *Toxotes chatareus* which feeds on aerial prey (insects) which it targets on the foliage of plants along the banks of Australian rivers and destabilizes with a jet of water from its mouth to make them fall into the aquatic environment (Volume 1, section 1.2.2).

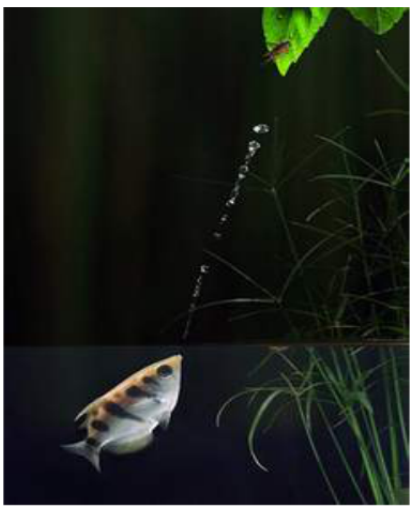


**Figure 3.1.** *Archerfish Toxotes sp. projecting a water jet, like a blowgun, in the direction of aerial prey in order to destabilize it. For a color*

Fish Behavior 2: Ethophysiology,
First Edition. Jacques Bruslé and Jean-Pierre Quignard.
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### *Using a stream of water to hunt*

Another specialist in oral projection of a hydraulic stream is the tropical triggerfish *Pseudobalistes fuscus*, which destabilizes sea urchins from their rocky positions and turns them over to reveal their most vulnerable, oral side, which is usually oriented towards the substratum. This then becomes directly accessible and easier to break in order to access the genital glands upon which they feast. As for the river stingray *Potamotrygon castexi*, in the aquarium, it can manage to use a jet of water to extract coveted prey from a plastic tube. Not foolish at all, the ray is able to solve, through the use of hydraulics, a food strategy problem.

Bibliography: *Anim.Behav.*, 2013, **86**: 1265-1274, *Curr.Biol*., 2015, **25**: R585-R599, *J.Exp.Biol.*, 2013, **216**: 3096-3103 & 3450-3460, 2014, **217**: 2816 & 2866-287

## 3.2. Possession of a black box

Each fish unknowingly possesses systems for recording a number of its vital activities and behaviors from embryonic life to death. Its “past” is revealed, on the one hand by its otoliths, on the other hand, by its parasites.

### *An inviolable personal identity card*

Otoliths* are mineralized pieces of a fish’s inner ear, of varying size, shape and orientation, which play a role in its hearing and balance, but on which are also recorded its whole past and its whole life history. Such a fish has no secrets for who knows how to “read”.

These “ear-stones”, numbering three pairs – sagitta*, asteriscus, lapillus – consist *calcium carbonate* $CaCO_3$ crystallized in the form of *aragonite*, of *calcite* and of *valerite* whose biomineralization obeys diurnal as well as nocturnal, lunar or seasonal annual rhythms, that record all the environmental events of its life: the cold, the heat, as well as diet and its variations, fasting, changes of environment during migrations, diseases, sex change among hermaphrodites*, egg-laying, etc. Otoliths, like other mineralized pieces such as scales, vertebrae, operculum or teeth that exhibit variations in their rhythms of biomineralization, can thus, through a reading of their streaks of variable increases in width and density separated by zones of discontinuity related to environmental and physiological changes, be used to date the main events of the life of the fish, to reconstitute in particular its growth rates and to estimate its age as well as its wild or hatchery origin and the succession of environments in which it has lived. These are precise biological markers.

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It should be noted that otolith chemistry does not simply reflect the chemistry of water, but depends on other ambient conditions – such as temperature – that affect the incorporation of mineral elements into the organic structure of the otolith.

### *Traveling leaves traces, like a real passport*

Magnetic resonance (MR) spectroscopy studies of otoliths* enable analysis of the processes of their bio-integration and their biocrystallization, such as the incorporation of *manganese* $Mn^{2+}$ during their biomineralization, which differs according to the salinity of the water and according to metabolic differences. A comparison of 12 species of Brazilian croakers such as *Stellifer rastrifer* shows that the elongated sagittae* of certain populations are richer in *manganese* than round sagittae*, the lower concentrations of the latter corresponding to a more coastal lifestyle under the influence of desalinated waters of continental origin. This modern method of chemical analysis of otoliths* provides useful information on the geographical origins of the various stocks of these fish of economic interest in South America and which are subject to marine, freshwater or mixed influences.

The "otolithary signature" enables us, in migratory species such as the American salmon *Oncorhynchus* sp., to identify their wide behavioral variations of descent or catadromy* towards the estuaries during their transformation from *parr** into *. It also enables, in those which are diadromous* like char *Salvelinus* sp., to differentiate between amphidromes*, freshwater residents and estuarine/marine residents based on the concentrations of their otoliths* in *strontium* $^{87}Sr/^{86}Sr$. In obligate diadromous migrants, the values of the ratios *Ba/Ca* and especially *Sr/Ca* retrospectively reconstruct the early migration stages of their lives; the concentration *strontium Sr* is more than eight times greater in marine waters than in fresh waters, as in the case of shad *Alosa alosa* who alternate between residence in fresh water, estuarine crossing, then marine migration during their movements in the haline* gradients of the successive compartments of the Dordogne-Garonne-Gironde hydrological system. These signs are irrefutable.

The chemical composition of the otolith* is rich in information about the movements of reef fish such as the sweetlip emperor *Lethrinus miniatus* along the Great Barrier Reef between 18 °S and 22 °S. Indeed, compared rates of *isotopes** of *oxygen* $\delta^{18}O$ and *carbon* $\delta^{13}C$ in their otoliths* are environmental markers characteristic of their past, whether sedentary or migratory. These isotopic* values increase with latitude; these signatures are a function of the ambient temperatures. Marking is different between the nucleus of the otolith and its marginal peripheral part in those individuals who have during their life undergone latitudinal displacements towards warmer or cooler waters, while no difference is detectable

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among those who have settled. Such a black box is useful for the management of marine fisheries.

The microchemistry of otoliths also reveals the life history of fish in the Amazon Basin, which is rich in a complex network of terrestrial and aquatic interconnections and a wide variety of geochemically complex environments, within which many species move. Through measurement of various otolithic chemical markers – *manganese Mn*, *selenium Se*, etc. – and their isotopic ratios *Sr/Ca*, *Mn/Ca*, *Zn/Ca*, etc., we have confirmed the sedentarity of the piracuru *Arapaima gigas* and specified the complex migratory movements of the sciaenid *Plagioscion* sp. and the catfish *Brachyplatystoma* sp.

Bibliography: *Aquat.Liv.Res,* 2005, **18**: 291-300 & DOI:10.1051/alr.2005033, *Fish Fisheries*, 2018, **19**: 441-454 & DOI:10.1111/faf12264, *J.Exp.Mar.Biol.Ecol.,* 2014, **456**: 18-25, *J.Fish Biol*., 2008, **72**: 946-960 & DOI:10.1111/j.1095-8649.2007.01776.x, 2014, **85**: 987-1004 & DOI:10.1111/jfb.2014.12468, *Mol.Ecol*., 2014, **23**: 1000-1013, *Roy.Soc.Open Sci*., 2016, **3** & DOI:10.1098/rsos.160206

### *A birth certificate*

The otolith* can also be used to measure the age of the larvae, based on a hatching mark, and to assess the duration of their marine migration. Thus, counting of microstructures in the form of daily increment streaks in the leptocephale larvae, then the elvers of the European eel *Anguilla anguilla* indicate a transatlantic migration lasting about 7 to 9 months. This value is called into question by other current technological approaches that argue for a longer duration of about 2 years, as the daily rhythm of deposits of *aragonite* materialized in a growth line has never been able to be validated.

### *Proof of diet*

The microstructure of the otolith* may also provide data on the trophic past of an individual which, for example, at the juvenile stage, has undergone a sudden change in diet as a result of a difference in abundance of larval prey that rapidly induces, in 4 days, an otolithic response in the form of the deposit of a generally detectable growth ring, as has been successfully practiced in the roach *Rutilus rutilus.* Diet quickly influences the microstructure of the otolith of the Australian smelt *Retropinna semoni*, which enables the reconstitution of its early growth according to the availability of food. However, the chemical composition of the otolith may be misleading, as it may sometimes only reflect the origin of prey consumed before its movements and not the movements of the consumer itself.

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Bibliography: *J.Fish Biol.,* 2008, **73**: 853-860 & DOI:10.1111/j.1095-8649.2008.01976.x

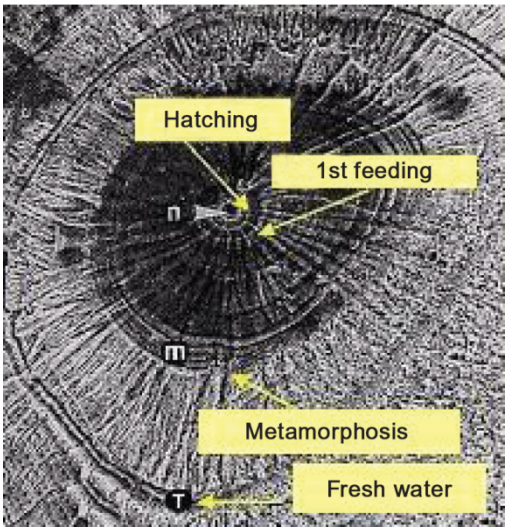



**Figure 3.2.** *Otolith of eel Anguilla anguilla: different growth streaks tracing the stages of its previous life (source: R. Lecomte)*

### *Belonging to a stock*

For a very long time, it has been known that the morphology of otoliths has a specific value and that, therefore, these parts can be used in systematic*. More recently, it has been shown that the shape of the sagittae* enables us, in addition to its use in the identification of species, to discriminate between populations – stocks – which are components of a species present in a given geographical area. The knowledge thus provided to fisheries* by this intraspecific population approach is essential for the development of fisheries management strategies for the sustainable exploitation of this living resource. Thus, the use of such descriptors has made it possible to understand the population structure of the lagunomarine silverside *Atherina boyeri* of the western Mediterranean, the cod *Gadus morhua* of the Baltic Sea and the Faroe Islands and the annular seabream *Diplodus annularis* of the Tunisian coasts. On the other hand, the same approach has shown that swordfish *Xiphias gladius* form a single stock in the Indian Ocean.

Bibliography: *Acta Icht.Piscat.*, 2015, **45**: 363-372, *Can. J. Fish. Aquat. Sci*., 1986, **43**: 1228-1234, 2015, **72**: 10-20, 2016, **73** & DOI:10.1139/cjfas.2015-0332, *Ital.J. Zol*. 2015, **82**: 446-453, *J.Fish Biol*., 2016 & DOI:10.111/jfb.1311, *Mar. Ecol. Progr.*

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### *Parasites used as biological markers*

If otoliths* and scales can be used as intrinsic markers of the life events of each *post mortem*, there also exist extrinsic markers for characterizing an individual and a population: their external parasites attached to their skin and gills or those present in their digestive tract.

Thus, three populations of blackspot seabream *Pagellus bogaraveo* are identifiable in the western Atlantic: Azores, Portugal and Madeira, by comparing their respective parasitic infestations of digenous trematodes such as *Diphterostomium* sp., acanthocephalans such as *Bolbosoma* sp. and nematodes such *Anisakis* sp., which are quite precise markers of their zoogeographic origin.

As we have just seen, multiple methods of investigation concern the previous life of each fish. It is quite difficult for a fish to hide its past and its private life; ichthyologists can always know everything and read them "like a book".

Bibliography: *Fish.Fish.,* 2010, **11**: 289-306, *J.Exp.Mar.Bio.Ecol*., 2014, **456**: 18-52, *J.Fish Biol*., 2008, **72**: 1023-1034, **77**: 2454-2459, *J.Mar.Biol.Ass.UK,* 2013, **93**: 1973-1980, *Sci.Mar*., 2013, **77**: 607-61570.

## 3.3. Using tools

A tool is defined as "an external functional object corresponding to an extension of the body used for a specific purpose". Encountered in various species of mammals and birds who know how to use them, their use by fish has rarely been observed. The ability to use a tool is, for ethologists and neurologists, proof of the existence of a practical form of "animal intelligence". Man is not alone in this category; birds and mammals, especially primates, are the heroes in this practical sense, whose function is to solve a problem stemming from a certain rational reflection. This concept, which has been widely used by anthropologists to analyze the emergence of intelligence in humans about 2.5 Myr* ago, has evolved during the last decades as regards its extension to various animal groups, from invertebrates: ants, wasps, octopuses, etc., to vertebrates, including fish.

### *A form of intelligence from which fish are not excluded*

The use of tools by fish is complicated, partly because of the absence of members able to grasp objects – anatomical constraints – and, on the other hand, the characteristics of their living environment – physical constraints related to the viscosity of water, which is much higher than that of air, as well as the buoyancy of

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and protecting offspring as practiced by nearly 9,000 species of fish, a third of them, already represents a performance involving a certain "know-how". Such builders (Volume 2, section 2.2.1), whether it be a three-spined stickleback *Gasterosteus aculeatus* who weaves a plant nest by calibrating plant fibers, an American cyprinid *Nocomis* sp. who selects, transports and assembles pebbles to make a mineral nest or gourami *Colisa* sp. who produces mucus-wrapped air bubbles to form a floating nest, all of which demonstrate a certain kind of intelligence on these occasions. In the absence of a prehensile limb, their mouth is used as a hand for transporting and assembling the constituent materials of the nests. Some architects and builders are properly "tooled up" thanks to elaborate oral and pharyngeal devices.

### Using an anvil

Some species even do much better by designing a tool that demonstrates long-term and largely underestimated cognitive abilities. Our consideration of such capabilities is recent, for example, when actively manipulating certain objects with their mouths and the use of a hard substrate as an anvil.

Some wrasses, consumers of hard prey protected by a shell (bivalve mollusks such as mussels and cockles) or mineralized tests (sea urchins), work to break these protective external elements in order to access their contents: the flesh and the viscera upon which they feast. A precise observation accompanied by convincing photographs concerns the tropical tuskfish *Chœrodon schoenleinii* who, on the Australian reefs, has been seen using a pebble carried in the mouth to hit a bivalve mollusk to break its shell, using as an anvil a rock located in its feeding area, until this quite robust shell bursts. The amount of shelly debris on this chosen site attests to the feeding activity of this fish. Other tropical wrasses of the genera *Halichoeres*, *Cheilinus* or *Thalassoma* also succeed by using pebbles, which they project onto sea urchins to break their mineralized envelope, which constitutes the test in order to consume their viscera. Similarly, the sixbar wrasse *Thalassoma hardwicke* has been observed in the aquarium, carrying in its mouth a pebble intended to crush dry granules, which were provided for its food, but which were too large and too hard to be swallowed in their existing state. It can repeat the process of crushing pellets* 15 times until they become consumable. *Pisces faber*.

### Capabilities related to the size of their brains?

The behavioral abilities of fish have often been related to the size of their brain, particularly that of their telencephalic optical roof (Volume 2, section 4.3), which varies according to environmental and social factors. Those wrasses which use tools actually have a brain larger than the average of their counterparts who do not use tools.

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It is remarkable that the use of tools has occurred many times during the course of fish evolution, involving diverse families without relations between them, but in connection with the emergence of superior cognitive abilities. We must be smart to design and use a tool.

Bibliography: *J.Fish Fish*, 2012, **13**: 105-115 & DOI:10.1111/j.1467-2979.2011.00451.x, *Zoo.Biol*, 2010, **29**: 767-773.

## 3.4. Capacity to play

### *Expression of a certain well-being*

Play is interpreted as evidence of a certain well-being in the individuals who practice it, because it is linked to the existence of "positive emotions" (Volume 2, section 4.1). It seems to correspond to favorable moments of relaxation from survival activities (absence of external threat, satisfaction of trophic needs, etc.).

Young white spotted cichlids *Tropheus duboisi* seem to thus engage in a "social game" by practicing, with other cichlids *Labeotropheu*s sp., movements of approaching and touching, rubbing, nibbling of flanks and lateral parades without purpose other than a certain "free play". Such "teasing", which often occurs between juveniles and parents, seems to reflect the existence of a harmonious family balance.

Even the great white shark *Carcharodon carcharias* seems to pursue prey that it does not consume. Just for "fun". On the other hand, the behaviors of jumping out of the water and aerial capers, which are common to some sharks, rays and skates, in the same manner as dolphins, orca or whales, could be likened to playful forms of behavior and could express a certain happiness.

### *A toy in an aquarium*

Behavior considered enigmatic and similar to a game was reported and even filmed, performed repeatedly by three males of the white spotted cichlid *Tropheus duboisi* who, in their aquarium, attacked and struck a ballasted thermometer, seeking to turn it upside down when it invariably resumed its vertical position like a "Weeble", while they showed no interest in other objects – pebbles, plants – placed in their environment. They were therefore totally able to take an interest in this object without any value for them and thus considered to be a toy.

Indeed, this behavior of play with the thermometer can neither be assimilated to feeding behavior, with their usual food being algal, nor to a sexual behavior, no

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given its remoteness and the apparent absence of stress in their small basins. In contrast, their congeners placed in large numbers in large basins with predators are mainly concerned with problems of intraspecific competition and feeding, which are stress inducers. It may therefore be concluded that, responding positively to all the criteria for defining play, our three players, freed from any constraint of feeding or anti-predation and could devote themselves fully to such fun activities. A thermometer able to bounce back when pushed: what a fascinating toy! This is play behavior worthy of a higher organism.

Bibliography: *Curr.Sci*., 2015, **25**: R9-R10 & DOI:10.1016/j.cub.2014.10.027, *Ethol.,* 2015, **121**: 38-44 & DOI:10.1111/eth.12312, *Fishes*, 2019, **4**, 31: 1-14.

## 3.5. Artists

If the playing abilities demonstrated in fish may already seem astonishing, what to say about convincing testimony of the possession, in certain other species, of a certain "aesthetic sense".

In their effort to seduce females, the males of some species appeal to a rich imagination and build not only very elaborate nests (Volume 2, section 2.2.1), but are also capable of producing structures deemed artistic to which they seem to have sensitivity.



**Figure 3.3.** *Spawning nest of the Japanese fugu Takifugu rubripes forming a decorated geometric circle*

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The male of the tropical fugu or pufferfish *Takifugu* (formerly *Fugu) rubripes* in southern Japan settles on the bottom and shakes its fins to sculpt the sandy loose substrate, then carries shells and stones with its mouth that it places in a geometric circle of nearly 2 meters in diameter, thus producing a "work of art" whose quality determines the choice of mating females that reward the best artists. This small fish makes, day and night, a considerable effort to develop such a nest that will gather the clutches deposited in the sand, with shells around its perimeter to slow the water currents that might sweep away the eggs, proof of the existence of practical sense combined with an artistic sense. A seducer inspired by love who is not limited to producing utility but combines with it a sense of artistic geometry.

In the lamprologue cichlid *Lamprologus callipterus* of the African Great Lakes, males attract females by collecting in their territory, then defending, empty shells of gastropods in which the females are invited to lay. Although the latter prefer to lay eggs in large shells that offer better egg quality, males collect small shells that are never used by females. Such discord between male and female choices suggests that small shells have a function other than that of being mere egg-receiving structures. Why not a decorative role? There seem to be different artistic tastes between the sexes: the males are anxious to offer decoration for the cradles of their offspring.

Bibliography: *Anim. Behav.*, 2014, **95**: 131-137*, Int.Business Times*, 20/11/2014

## 3.6. Counting

It has long been believed that humans are the only species capable of counting, except perhaps clever dogs. Various animal species – birds, mammals – are now known for their ability to differentiate between two quantities and perform a quantitative analysis of distinguishing small quantities from large quantities. And why not fish?

### *Quantitative knowledge of their environment*

Several examples make it possible to admit that fish possess some quantitative knowledge of their environment.

Thus, females of the swordtail *Xiphophorus helleri* are able to compare the size, number and volume of groups of their congeners (Volume 1, section 3.3) by choosing to join the larger ones, but without making a truly numerical evaluation, only differentiating between a larger group and a smaller group. Males of the mosquito fish *Gambusia holbrooki* choose their sexual partners from among the quantitatively largest groups of females. In the guppy *Pœcilia reticulata*, two

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distinct mechanisms are involved in this numerical diagnosis: one is a precise system for comparing small quantities, up to three to four elements, and the other, an approximate system that is used to estimate orders of magnitude of groups of objects: $5 \neq 10$, $8 \neq 16$, but not $8 \neq 12$, which is useful in a social context, for example, for joining schools of one's congeners.

Such abilities are quite comparable to those known in non-human primates and in human children. Guppies are also able, under experimental conditions, to discriminate numerically between four and five batches of small objects placed on the bottom of basins and which give rise to a food reward, a performance of which many birds and mammals are not capable. Such cognitive abilities, which are both innate and result from training, give rise to discussion among specialists around the often-complex modalities of the testing operations. These fish seem gifted with an approximate number system (ANS).

Numerous tests carried out on various primates and in humans demonstrate their common mental abilities to spontaneously evaluate quantities in increasing numbers. Chickens do the same, hence the idea that this mental representation of quantities in space or mental number line (MNL) is an innate cognitive ability common to mammals, birds and fish that has been conserved in the vertebrate lineage during evolution. It enables them to acquire useful information for their foraging – the number of prey – and their social behavior – the size of groups. These are essential operations in everyday life.

The guppies are able to discriminate between two quantities of food when it is in a ratio of 1:2 or 2:4, but not 2:3 or 3:4, preferring to feed, in the first two cases, on the largest quantities accessible to them based on their cumulative surface area. Such a choice seems to be dictated by the constraints related to life in groups and schools which has selected for cognitive mechanisms favoring a fast and efficient choice of the most profitable food. This is the key to feeding success.

Tests applied to about 20 females of bluestreak cleaner wrasse *Labroides dimidiatus*, a species capable of discriminating the number of its "clients" (Volume 1, section 3.5) and to evaluate the amount of ectoparasites distributed on each of them, reveal that they have a great capacity to discriminate between small quantities (2 against 5) or larger ones (5 against 8). On the other hand, they fail to recognize these numbers in space according to their spatial location – the difference between right and left – and to evaluate quantities such as surface areas and densities, which has led to doubts about their actual MNL capability. The demonstration is thus made that fish possess a capacity to apprehend "numerical information".

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Bibliography: *Anim.Behav*., 2015, **107**: 183-191 & DOI:10.1016/j.anbehav.2015.06.019, *Anim.Cogn*., 2012, **15**: 215-221, 2014, 285-291 & DOI:10.1007/s10071-011-0447-9**,** **17**:1413-1419, 2015, **18**: 1007-1017 & DOI:10.1007/s10071-015-0868-y, 2017, **20**: 187-198 & DOI:10.1007/s10071-1037.7, *Behav*., 2007, **144**: 1333-1346, 2017, **20**: 187-198 & DOI:10.1007/s10071-1037.7, 2018, **21**: 99-107 & DOI 10.1007/s10071-017-1143-1, *Behav.Proc.,* 2017, **141**: 161-171 & DOI:10.1016/beproc.2017.02.001, *Ethol*., 2008, **114**: 479-488 & DOI:10.1111/j.1439-0310.2008.01493.x, *E thol.Ecol.Evol.,* 2016, **28**: 211-220 & DOI:10.1080/03949370.2015.1029011

### *Innate quantitative knowledge which is perfected*

The ability to make quantitative estimates is not unique to mature and experienced fish. Juveniles of the guppy *Pœcilia reticulata* aged 4–9 days are already able to discriminate between small groups of their congeners. Their numerical information improves according to the social context, association with other guppies helping them to make progress in calculation. Isolated fish are able to join groups made up of the largest number of individuals, distinguishing between those of four and those of six individuals.

Bibliography: *Dev.Psychobiol.,* 2014, **56**: 529-536 & DOI:10.1002/dev.v56.3/issuetoc, *Ethol*., 2016, **122**: 481-491 & DOI:10.1111/eth.12498

### *Clever fish*

Some fish also have a rudimentary ability to discriminate between numbers such as quantities of food, other fish, rivals or sexual partners, in order to adapt their behavior to these numeric data. The recognition of members of the same species according to the number of lateral colored bands of their color patterns and the number of these fish, namely $1 \neq 2$, $2 \neq 3$, $3 \neq 4$, $8 \neq 16$, etc., has been demonstrated eastern mosquito fish *Gambusia holbrooki*. A performance comparable to a numerical sense concerns the swordtail *Xiphophorus multilineatus* in which females have a mating preference for males whose color patterns contain a number of symmetrical vertical bars. This tendency is increased in those from small litters as well as those fed with high-quality diets, while those who have consumed a diet of low quality are content to choose between males according to their size, as if a rich diet boosted their counting performance.

Similarly, three-spined sticklebacks *Gasterosteus aculeatus* are able to make decisions quickly when joining a group based on its numerical size, distinguishing between groups which differ by a single unit: $1 \neq 2$, $2 \neq 3$, $3 \neq 4$, $4 \neq 5$, etc., and

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even 6 ≠ 7, making it one of the most talented fish. They thus always prefer to associate with the group with the largest number of members. This ability to make such subtle numerical distinctions between small groups is spontaneous and requires no learning. Its significance seems to lie in providing anti-predator protection based on a risk dilution benefit (Volume 1, section 1.1.3). Quantitative distinction between large groups, 8 ≠ 12 and 40 ≠ 60, seems easier, a subtlety also detected in the fathead minnow *Pimephales promelas* who can discriminate 18 ≠ 23.

The angelfish *Pterophyllum scalare* forms wild groups of 15 to 20 individuals. These fish have a natural ability to join groups of their congeners and make spontaneous choices of discrimination between small groups smaller than four individuals and larger groups larger than four individuals and more. When they are tested on visually recognition of groups, then kept without vision by deploying shutters creating darkness for 30 seconds in their breeding compartment, they memorize perfectly the position of large groups and forget that of small groups, as if their memory capacities for quantifying groups of their congeners were mixed, using two separate systems of quantitative evaluation favoring larger groups. Such evaluation is useful in case of danger of predation.

Such counting ability seems *a priori* impossible among blind cave-fish like *Phreatichthys andruzzi* who, living in total darkness in the groundwater of Somalia, lost their visual function 2 Myr* ago. However, tests of choice carried out on them reveal an ability to discriminate quantitatively among objects and shapes by differentiating between groups of two objects compared to those of four and six objects present in their environment whose surface area, volume and density differ. Such 3D numeric acuity is enacted by the lateral line* consisting of ciliated sensory cells that are the hair cells* or neuromasts* in these anophthalmic* fish, no matter that they are endowed with a small brain and live in an environment poor in food and congeners and lacking in predators, although this function is significantly inferior in performance to that of sighted fish. A remarkable mechanical sense, a substitute for vision.

Bibliography: *Anim.Cogn,* 2015, **18**: 1125-1131 & DOI:10.1007/s10071-015-0884-y, 2017, **20**: 829-840 & DOI:10.1007/s10071-017-1104-8, *J.Exp.Biol.*, 2014, **217**: 1833-1834 & DOI:10.1242/jeb.107904, 1902-1909 & DOI:10.1242/jeb.101683

### *Inter-individual variability*

An experimental study aimed at establishing a relationship between cognitive skills of numerical discrimination and a series of social behaviors conducted among mosquito fish *Gambusia affinis* in tests of learning of visual numerical discrimination (shapes: rectangles or ellipses, color and orientation of images),

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showed the existence of strong inter-individual variability in both sexes, with some females and males showing high learning capacities, others performing poorly and others finally with zero potential. While the best individuals of both sexes exhibit identical numeric learning abilities, inter-gender behavioral differences include feeding activity, sociability, innovation, exploratory tendencies, predator inspection, anxiety, stress and fear, traits which favor females, with males being bolder, quicker to make decisions and showing more flexible behavior. Such divergences result from phenotypically different sexual selective pressures (experience) in a species that practices sexual coercion (chasing, thrusting of gonopods by males (Volume 2, section 1.2.1), avoidance of sexual harassment in females (Volume 2, section 1.2.3)). A link has been established between cognitive abilities of numeric visualization and behaviors with a tendency to associate social behaviors (sociability) and learning performance. These are personality traits related to the complexity of social relationships.

Inter-sexual differences are observed in guppies *Pœcilia reticulata*. Females are faster than males to pass laboratory tests; the success of one at the beginning of the test is contrasted with later successes of others after several attempts.

Bibliography: *Anim.Cogn.,* 2018 **21**: 37-53 & DOI:10.1007/s100071-017-1134-2, *Ethol*., 2016, **122**: 481-491 & DOI:10.1111/eth.12498

## 3.7. Having a personality

### *Not all fish are identical*

In a given environment, all individuals of the same species, even though they give the appearance of resembling each other and being uniformly formatted, do not all behave identically. Why do some of them adopt different attitudes from their congeners and distinguish themselves from their social group? Any individual facing various demands for food, protection, reproduction, etc. adopts behaviors that are sometimes instinctive and have an innate origin. It may also use two types of available information, either that acquired individually and corresponding to its personal experience or that obtained through observing others by social copying. The respective importance given to each category of information, private or public, depends on the personality of each individual.

### *Individual and inter-sexual differences*

Differences in behavior are equated with differences in personality between individuals in the same population whose behavioral decisions depend on the

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frequent conflict between a situation of benefit and that of a cost which is specific to each individual, according to a personal and individual assessment.

In the three-spined stickleback *Gasterosteus aculeatus*, behavioral responses to the presence of a predator, assimilated to a "behavioral syndrome", vary according to the individual. Some of them, when subjected to tests using dummies of members of their species, are divided into three categories: lovers who essentially practice courtship of females (Volume 2, section 1.1.3), fighters who are aggressive with their rivals and partners, and dividers, which alternate behaviors of seduction and combat. However, behavioral plasticity is such that each individual can, at any time, modify their belonging to one or another of these categories. A relationship between personality traits and food intake has been confirmed in this fish: the boldest individuals, those who take maximum risk, are also those with the highest growth capacities, the best rates of fertility and, correspondingly, the greatest energy needs, which translates into maximum feeding activity.

In the guppy *Pœcilia reticulata*, as with other poeciliids such as the killifish *Brachyrhaphis episcopi*, personality traits are expressed during foraging (isolation or participation in a social group) or threats of predation (demonstration of boldness to confront or fear resulting in a movement of flight and a hasty search for shelter) (Volume 1, section 1.1.3). Males exhibit differential tendencies to express their boldness or fear, their activity or inactivity, their sociability or their independence in various social relations in their immediate environment such as the presence of competitors and/or predators. Females who preferentially use social information from their environment and prefer relations with competing females (Volume 1, section 3.10) are those who are generally the boldest and also those who learn more quickly and better memorize the signals acquired during learning tests. Confirmation has been given of the lower capacity of males and the greater behavioral flexibility of females who, undergoing such tests, learn twice as fast as their partners. Personality traits also include the ability to take advantage of social information when learning; some are content with private experience while others are more open to public information. Males, however, are not all dullards and, among them, some have learning skills to move through a labyrinth, for example, which are superior to those of others. These fast-learning males are attractive and are usually preferred by females. The most intelligent males find success mating with females who know how to detect their intellectual potential, but how do they perceive it?

Bibliography: *Anim.Behav.,* 2004, **68**:1339-1348 &
DOI:10.1016/j.anbehav.2004.05.007, 2009, **78**: 399-406 &
DOI:10.1016/j.anbehav.2009.04.025, 2014, **88**: 99-106 &
DOI:10.1016/anbehav.2013.11.022, *J.Fish Biol*., 2007, **71**: 1590-1601 &
DOI:10.1111/j.1095-8649.2007.01627.x, 2009, **75**: 1323-1330 &
DOI:10.1111/j.1095-8649.2009.02366.x, 2016, **88**: 1661-1668 &

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### Customized food preferences

From a dietary point of view, each species has an aptitude to consume certain prey and, following learning, to remain faithful to a certain type of diet according to the shape, color and/or odor of its familiar prey. When new prey is offered to three-spined sticklebacks *Gasterosteus aculeatus*, guppies *Poecilia* sp. and swordtails *Xiphophorus* sp., some individuals show no interest in them, demonstrating a feeding conservatism that is generally sustainable, while others, more innovative, accept them, thus behaving as adventurous consumers. These differences are both intraspecific and interspecific: while stickleback populations generally have a greater number of risk takers, guppies and swordtails are much less prone to taking risks.

The lamprologue cichlids *Neolamprologus fasciatus* of Lake Tanganyika show dimorphism of both buccal morphology, with no individual being symmetrical, and behavior when catching shrimp, with left-handed and right-handed individuals; the latter are often the best performers. Such an advantage, which has sometimes been linked to the existence of cerebral laterality (Volume 2 section 4.3), should result in the dominance of right-handers in the population. However, this is not the case and the dominant phenotypes vary between left-handed and right-handed from one year to the next.

Such oral dimorphism is not exceptional, since it is found in the scale-eating cichlids *Perissodus strœleni and P.microlepis*, where it facilitates sharing of the food resource (Volume 1, section 1.2.2).

Bibliography: *Anim.Behav.,* 2008, **75**: 2359-1366 &
DOI:10.1016/j.anbehav.2007.09008, *J.Fish Biol.,* 2011, **79**: 776-788 &
DOI:10.1111/j.1095-8649.2011.03064.x

### Differences in risk-taking

Differences in temperament between brave and/or fearful individuals which are measured by the time between their emergence from a refuge after receiving a signal from a predator have also been reported. They depend on both genetic heritage and lived personal experience according to the levels of dangerousness of the environment, based on the pressure of predation. A personal balance is to be found between benefits and risks in each of the given social contexts. Personality differences between mosquitofish *Gambusia affinis* are expressed between resident individuals and so-called “dispersers” such as emigrants, immigrants or colonizers, the latter demonstrating more boldness, aggression and sense of exploration, but less

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sociability than the former. However, in the presence of a high risk of predation, these behavioral characteristics tend to fade. Bold but not foolhardy: when predation risk is high, wisdom is not to show oneself too much and to show more sociability by forming groups or schools (Volume 1, section 3.3).

However, dispersal can also be a form of avoiding predators, and brave and solitary individuals can escape predation in this way, who are less frequently attacked than those who fearfully form groups, but whose schools may become the preferred targets of predators.

Individuals who have undergone physical training by swimming in running water, who are constantly moving, jumping, swimming and leaping, show signs of boldness and aggression that contrasts with the fearful temperament of their congeners raised in still water. Do movement and action predispose to boldness?

In the monogamous cichlid *Pelvicachroma pulcher*, females prefer males whose bold behavior is the most dissimilar to theirs, such unmatched mating ensuring a parental role of transferring behavioral qualities useful for their survival to descendants.

Personality differences are reflected in the eastern mosquito fish *G.holbrooki*, by a differential spatial distribution: the most fearful fish are close to the substrate and the boldest are at the surface of the water where the risks of being attacked are greater – less camouflage, accessibility to avian predators, etc. Comparative tests of boldness against a predator based on the length of stay in a shelter, the time of exit and risk-taking in the presence of the predator, were conducted in European perch *Perca fluviatilis* and personality traits rated based on their size and their characteristic of being solitary or belonging to a group. Male zebrafish *Danio rerio* also show differences in personality traits and behaviors with respect to boldness and aggression, qualities which are appreciated by females, since their reproductive successes are higher than those of shy and timid individuals, as well as lead them to take risks and jeopardize their survival. Their dominant behavior is thus enacted to the detriment of subordinates* who are victims of stress.

Personality differences can also be observed in Australia's Port Jackson shark *Heterodontis portusjacksoni*: the boldest individuals who take more risks than their cowardly counterparts are also the most reactive to stresses of manipulation.

Bibliography: *Anim.Behav.,* 2008, **75**: 509-517 &
DOI:10.1016/j.anbehav.2007.06.007*,* 2012, **83**: 41-46 &
DOI:10.1016/j,anbehav.2011.10.004, 2017, **128**: 117-124 & DOI:
10.1016/j.anbehav.2017.04.007, *Ethol*., 2010, **116**: 96-104 & DOI:10.1111/j.1439-0310.2009.01719.x, *J.Exp.Biol*., 2014, **217**: 2987 & DOI:10.1242/jeb.095026, *J.Fish*

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2016, **89**: 1142-1157 & DOI:10.1111/jfb.129963, *Proc.Roy.Soc.B*, 2013, **280** & DOI:10.1098/rspb.2013.2349

### *Personality changes related to age and parental life*

Personality traits change over time and over the life of the fish. So the males of three-spined stickleback *Gasterosteus aculeatus* have less boldness in dealing with a predation threat when they have reproduced and have parental responsibilities (Volume 2, section 2.2). Fathers of families become cautious. This change is related to a change in the rate of androgenic hormones 11 keto-testosterone 11-KT. This reorganization of their neurohormonal balance is related to their parental status.

Bibliography: *Anim.Behav*., 2016, **112**: 247-254 & DOI:10.1016/j.anbehav.2015.12.002

### *Personality traits varying according to environmental factors*

In the Australian speckled damselfish *Pomacentrus bankanensis*, differences in personality traits are correlated with thermal variations, a rise of 3°C (from 26 to 29°C) modifying behavior: greater activity, an increase in aggression and a 2.5- to 6-fold increase in displays of boldness, which is measured by a briefer retreat into shelters in the presence of predators. Bold behavioral differences are often only justified by hunger, which drives hungry individuals to greater risk-taking, and especially in the early morning hours for this diurnal feeding species. This observation proves that this behavior has nothing to do with any personality criteria.

The behavior of guppies *Pœcilia reticulata* is affected by the presence of molecules of endocrine-disrupting compounds (EDC) in water, risk-taking by males decreasing in the presence of synthetic *estrogen hormones* $EE_2$, while females, on the contrary, increase their searching abilities. Females are boosted by estrogen following interference between natural hormones and synthetic hormones that activates their hormone receptors, which corresponds to a form of doping.

It has been shown that early risk-taking behaviors in the eastern mosquito fish *Gambusia holbrooki* are dependent on the size of the breeding ponds. Juveniles reared in large ponds are more apt to exhibit exploratory behaviors. Adults no longer show differences in ability, regardless of pond size. Only juveniles, who are the most vulnerable, are sensitive to these spatial constraints.

A correlation has been established between manifestations assimilated to evidence of courage such as exploratory behavior, risk-taking in an environment

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bluegill *Lepomis macrochirus*, so-called "bold" individuals have an aerobic breathing capacity higher by 25% measured via a respirometer compared to their fearful counterparts. On the other hand, no difference was found between them with respect to the anaerobic* mechanisms of muscular glycolysis*.

Some observations lead us to question the validity of certain criteria used to define personality traits, whereas they appear to be only occasional and transient physiological responses induced in response to natural or artificial environmental stimuli. Are these false demonstrations of courage?

Bibliography: *Anim.Behav*., 2016, **115**: 127-136 & DOI:10.1016/j.anbehav.03.013, **121**: 175-183 & DOI:10.1016/j.anbehv*J*2016.09.006, *.Anim.Ecol.,* 2008, DOI:10.1111/j.1365-2656.2008.01643.x, *Proc.Roy.Soc.B,* 2010, **277**: 71-77 & DOI:10.1098/rspb.2009.1346

### *Differences in migratory behavior*

Variable individual behaviors occur in migratory salmonids such as sea trout *Salmo trutta trutta* and the Atlantic salmon *Salmo salar*; some individuals become sedentary while most others move to the sea, to areas of feeding and fattening (Volume 1, section 2.2.1), followed by return or homing* (Volume 1, section 2.2.1) to their original habitats. Such alternative behaviors have combined genetic, physiological and phenotypic* causes, based on an energy potential correlated with the size and quantity of energy reserves – fats, glycogen – which condition an aptitude or inaptitude to undertake such a long trip. This plasticity ensures a better potential of survival for the population which is thus always assured of having a reserve of spawners in place, regardless of the risks of a long migration from which not every individual always returns. There are great travelers who love open-sea adventures, as well as "couch potatoes".

### *Personalized mutual relations*

Mutualist relationships between species may exhibit individual variability, for example, in the bluestreak cleaner wrasse *Labroides dimidiatus*, with honest workers who remove ectoparasites* from their clients in accordance with an unspoken agreement between them, while other individuals opt for deception (Volume 2, section 3.9) by feeding on their skin, scales and skin mucus. There are decent fish and cheaters.

Bibliography: *Ethol.,* 2014, **120**: 904-912 & DOI:10.1111/eth.12262

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### *Complex motivations*

Individual differences are apparent in pœciliidae in the gradient of courageous ↔ fearful behaviors according to size, physical condition, age, acquired experience and environmental danger. The hunger factor can, as we have already seen, justify risk-taking in small individuals with low energy reserves.

Individual metabolic performance also explains the behavioral differences observed in carp *Cyprinus carpio*: those with higher endocrine and energetic physiological potential are the most capable of taking risks.

Behavioral changes are often linked to an individual receiving conflicting signals. For example, male Siamese fighting fish *Betta splendens*, owner of a nest of bubbles, focus their attention either exclusively on other rival males by aggression corresponding to fighter behavior or on females by courtship behavior, making them lovers, or yet again by dividing between the two attitudes, which makes them considered to be dividers. Such behavioral plasticity results in variability in decision-making: fighting or courtship on the basis of alternative risks such as losing one's territory or losing opportunities for breeding, or having both territory and access to females. *Love or war?*

Bibliography: *Behav*., 2010, **147**: 805-823 & DOI:10.1163/000579510X493142,
*J.Fish Biol*., 2010, **76**: 1576-1591 & DOI:10.1111/j.1095-8649.2010.02582.x

## 3.7.10. *Different brain potential*

In the guppy *Pœcilia reticulata*, a link has been demonstrated between courage in the face of a predator, the ability to explore a new environment, the ability to socialize and lateralization of the brain that makes it able to use together, simultaneously and independently, the left and right cerebral structures. Such potential is well developed in humans, mammals and birds and has been long ignored in fish (Volume 2, section 4.3). The most lateralized organisms, left-handed or right-handed depending on the case, have a clear advantage in terms of cognitive abilities. It appears that males respond more to this criterion, who are bolder, more active and less sociable than females who are more cautious, more reserved and more sociable. These personality traits differentiate individuals from wild populations and play a role in natural selection. Indeed, behavioral variations between the individuals of the same population are such that, as females prefer to mate with the most active, the most bold and/or the most innovative individuals, this criterion is used in natural sexual selection to the advantage of the most endowed males (Volume 2, section 1.1.1).

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Behavioral differences can also result from chronic stress induced by parasitic infestation. Thus, in the three-spined stickleback *Gasterosteus aculeatus*, individuals infested with larvae of the cestode *Schistocephalus solidus* who are recognizable by the bleaching or fading of their bodily color patterns and their black eye, possess in their telencephalon* reduced levels of cerebral monoamines*, neurotransmitters such as *5-hydroxytryptamine 5HT, dopamine** (*DA*) and *norepinephrine* (*NE*), which translate into alterations of the neuroendocrine system affecting their behavior and their original personality. Their personality is under hormonal control.

Bibliography: *J.Fish Biol.,* 2013, **83**: 311-315 & DOI:10.1111/jfb.12165

### 3.7.11. *Higher metabolic potential*

Personality differences between males of the sailfin molly *Pœcilia latipinna* are linked to their individual size, with larger individuals being both the boldest in the face of a predator (because they know they can count on their swimming speed?) and the best courters (because they know that females have a weakness for their beautiful morphology?). Individual differences in behavior among the Panamanian killifish *Brachyraphis episcopei* are responses to the presence of predators, early exit from a refuge or the ability to explore a new habitat, which are considered evidence of boldness. These personality traits have been related to the large size of individuals who, endowed with a strong metabolism, are gifted with great swimming capacities. A low propensity to take risks characterizes small individuals who remain fearful, a lack of hardiness easily explained by their weak means of escape. Males are generally bolder than females, who are handicapped in their escape reactions to a predator by their ovarian excess weight depending on their fertility and/or their gravidity in relation to their embryonic load in these ovoviviparous fish*. Differences in behavior have been reported in the eastern mosquito fish *Gambusia holbrooki*, in the energetic potential of individuals: those who have high swimming skills following 4 weeks of training in a hydraulic flow system and whose swimming performances have progressed show more boldness against predators, leaving their refuge more quickly, exploring more unfamiliar environments and being more aggressive than their sedentary counterparts. These are the benefits of exercise.

On the other hand, a trophic deficit can provoke a stimulating effect when a diet of low energetic value contributes to inducing aggressive behavior, as has been observed in undernourished female zebrafish *Danio rerio.*

It seems well established that the personality traits of courage, aggression and exploratory behavior are essentially based on physiological bases, with inter-individual differences being linked to differences in metabolic and energetic

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levels. The postulate of the pace-of-life syndrome (POLS) predicts that individuals with high metabolic potential are those who access the greatest amount of food, grow faster and have earlier sexual maturity, maximum risk-taking and reduced longevity. These criteria are not recognized in the study of a population of guppies *Pœcilia reticulata.* The POLS that is unconfirmed in a population leads us to question the validity of this postulate, proof of the difficulty of analyzing a particularly complex process.

Bibliography: *Anim.Behav.,* 2004, **68**:1325-1329 & DOI:10.1016/j.anbehav.2004.04.004, 2005, **70**: 1003-1009 & DOI:10.1016/j.anbehav.2004.12.022, *Behav.,* 2016, **153**: 1517-1543 & DOI: 10.1163/1568539X-00003375

### 3.7.12. *Influence of the genome*

Personality traits are genetically determined and maintained when the individual changes sex. So, the females of the cylindrical sandperch *Parapercis cylindrica* who are most active and most aggressive later become males (Volume 2, section 1.2.10) who are both more active and more aggressive than those developing from females with a less assertive character.

Variations in the expression of genes localized in different regions of their brains account for differences in zebrafish *Danio rerio* and help to adapt it to various environmental situations. Artificial selection of some traits can be achieved after four to seven generations, between lines of brave fish and fearful fish, the first with superior capacities of initiative and rapid swimming abilities – fast-start – in relation to an elongated body profile and a more developed caudal region. This development of personalities induces morpho-physiological changes.

Bibliography: *Anim.Behav.,* 2016, **117**: 79-86 & DOI:10.1096/j.anbehav.2016.04.007, *Mol.Ecol.*, 2013, **22**: 6100- & DOI:10.1111/mec.12556

### 3.7.13. *Early expression of personality*

Personality traits are expressed early in the pike *Esox lucius* whose 21-day-old larvae tested in labyrinths can be classified into two categories: the “proactive” bold and the less enterprising. The timing of the emergence of salmonid fry on the spawning grounds (Volume 2, section 2.1.1.3) expresses early behavioral differences. Those Atlantic salmon *Salmo salar* who emerge from the first layer of spawning nests are bolder and more aggressive than those of late emergence who are more stressed because they have greater difficulty in acquiring secure habitats. They

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*serotonin 5-HT*. Differences in cerebral gene expression determine the future of young salmon, such as occupation of the best habitats (Volume 1, section 1.1.1). The time of emergence has the effect of inducing a more or less bold personality towards risks of predation in young brown trout *Salmo trutta* subjected to tests in start-boxes.

Bibliography: *Env.Biol.Fishes*, 2016, **99**: 105-115 & DOI:10.1007/s10641-015-0459-4, *Ethol*., 2015, **121**: 556-565 & DOI:10.111/eth.2015.121.issue-6/issuetoc, *J.Exp. Biol.,* 2015, **218**: 1077-1083 & DOI:10.1242/jeb.114314

### 3.7.14. *Social influence*

The social behavior of an adult fish may depend on the social environment in which it developed and the social interactions it experienced early in its young years. Thus, the mating behavior of the male bluefin killifish *Lucania goodei* depends on the company it keeps during its early development, being more aggressive towards females when raised in the absence of adults.

The behavior of locating food and choices of quality of shelters and sexual partners in the guppy *Pœcilia reticulata* often depends on its social environment and the quality of the information at its disposal. The boldness and sociability that play an important role in its survival result from a choice of use of private information and social information received from its congeners. Females especially appreciate the presence of congeners who teach them about trophic opportunities, those who are bold and fast learning, and better than those who are shy.

In the daffodil cichlid *Neolamprologus pulcher*, individuals who have been brought up in contact with their parents and siblings, and who have thus acquired social experience, have a lower sensitivity to stress, as evidenced by the low concentration of *corticotrophs – corticotropines*, *glucocorticoids* – in their brain. Individuals from natural environments at high risk of predation are generally bolder than those who have not experienced such pressure. The manifestation of this character of boldness will determine their chances of reproductive success and of survival. Under such conditions, it would seem that bold males who take risks when courting females, as they then relax their anti-predator vigilance, would be subject to higher mortality rates than their female partners.

The importance of experience gained from previous intraspecific disputes and recent conflicts has been shown in the mangrove rivulus *Kryptolebias marmoratus* whose behavior depends very much on the size of the individual, a size advantage of 2–3 millimeters being sufficient to give him a vigor that will make him a winner in later conflicts. However, the effects of an experience of victory – a winner effect – tend to constitute the essential criterion of success, more than the simple advantage

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These multiple examples provide indisputable proof that fish, despite the deceptive appearance of uniformity of all individuals, are not all identical in their behavioral responses and that some of them sometimes even display strong and original personalities, compared to their more commonplace and ordinary counterparts, showing that fish are far from being standardized and robotic with the existence of an "elite" among the anonymous crowd.

Bibliography: *Anim.Behav.,* 2014, **88**: 99-106, *Behav.,* 2007, **144**: 351-371, *Anim.Cogn*., 2016, **19**: 1183-1193 & DOI:10.1007/s10071-016-1028-8, *J.Fish Biol*., 2015, **86**: 1852-1859 & DOI:10.1111/jfb.12674

## 3.8. Disguise

Social relations between fish are not always honest and some behaviors are quite dishonest and guided by a desire for deception, some with a defensive purpose being more morally permissible and others with an offensive purpose that can be seen as a skillfully calculated deception. Adopting disguises is a good example of deception. A clever strategy whose scientific name is mimicry* consists, for one species, of imitating another, in order to avoid becoming the prey of a predator – defensive mimicry – or seeming harmless with regard to coveted prey – offensive mimicry. These forms of deception are exploited by some fish to deceive others. The pinnacle of perversity? Or more simply a form of intelligent tactics developed at the expense of species which are too naive?

### *Offensive mimicry for feeding*

Duping potential prey is successfully practiced in some particularly clever species. So, the Central American cichlid *Parachromis friedrichsthalii* adopts an original hunting strategy, feigning death and mimicking a dead body. Their body lies laterally on the bottom with its frayed fins, which does not fail to attract necrophagous species interested in the prospect of a good meal represented by a decaying fish. The visibility from distance of such a dead body in the beginning of putrefaction is all the more considerable as the waters are generally clear. And the awakening of the dead is dazzling! Such a strategy is also successfully practiced by the African cichlid *Nimbochromis livingstoni* of Lake Malawi. Similarly, the tropical comb grouper *Mycteroperca acutirostris* from southeastern Brazil pretends to be moribund or dead, lying on its side on a substrate of sand or gravel, flippers retracted, in order to catch naive little fish who approach it. This tactic pays off, sometimes being repeated five times in 15 minutes.

The false cleanerfish *Aspidontus tæniatus* of the Great Barrier Reef is a predator

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the color pattern of a peaceful species, the bluestreak cleaner wrasse *Labroides dimidiatus*, which does not inspire any suspicion on the part of many species who, on the contrary, seek and even solicit their cleaning services in order to get rid of their external parasites, small copepod crustaceans (Volume 2, section 3.5). The customers of this cleaner, seeking skin care, are then victims of bites and are robbed of pieces of healthy skin or fragments of fins before discovering the deception of which they are victims. And what about the cichlid *Parachromis friedrichsthalii* who feigns death in order to be approached by naive prey who are killed by their curiosity (Volume 2, section 3.9)?



**Figure 3.4.** *The blenny Aspidontus tæniatus (left), a predator, mimics the color pattern of the harmless bluestreak cleaner wrasse Labroides dimidiatus (right) to deceive prey*

None of these fish, however, have co-operated or trained together. A good example of evolutionary convergence?

Bibliography: *Anim.Behav*., 2014, **88**: 85-90 & DOI:10.1016/j.anbehav.2013.11.006, *Copeia,* 2004, **2**: 403-405, *Ethol*, 2018, **124**, 5 & DOI:10.1111/eth.12743, *J.Fish Biol.,* 2005, **66**: 877-881 & DOI:10.1111/j.1095-8649.2005.00648.x

### *Offensive mimicry for reproductive purposes*

The consumption of preferred prey by females may enable males, by imitating such prey, to approach the females, to attract them and to fertilize their oocytes by surprise. The males of the Venezuelan tropical swordtail characin *Corynopoma riisei* (Volume 2 section 1.1.1) use as a lure, during their courtship behavior, an ornament developed on their operculum, which consists of a filament which ends in an imitation of an insect: an ant, a beetle. This fishing lure, which perfectly mimics a terrestrial insect that regularly falls into the water from riparian plants and becomes a favorite prey in the population's diet, is used as a fishing rod which males wave, like a flag, under the nose of the females. The latter, victims of the sin of gluttony, are attracted by this appetizing lure and come to nibble it, especially if they are hungry. Their positioning near the male enables their insemination in the absence of a gonopod. Fertilization is internal, with the male depositing sperm capsules into the oviduct of the female and fertilization takes place at the time of spawning in the

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absence of the male. This stratagem enables males to successfully "catch girls" and mate briefly with them. Following a multitude of bites, this fragile lure is sometimes damaged and must regenerate, which requires several weeks. However, a partially broken lure continues to attract females, who see it as a criterion of male quality that has often been preferred by other females. A perfect match between the type of lure and the specialized diet of females in each population – terrestrial prey (ant, beetle) or aquatic prey (daphnids, insect larvae such as chironomids and ephemera) – enables males to use the dietary motives of their sexual partners to their benefit. The evolution of shapes of lures reflects differences in the abundance of local prey from different populations – canopy* habitats, which are thus rich in ants that fall from trees, or habitats without a canopy which appeal to aquatic prey – and constitutes a sensory adaptive process. Females are trapped by their greed.

In the Comanche Springs pupfish *Cyprinodon elegans*, male sneakers* try to look like females – same size, same color pattern – in order to approach them while avoiding aggression from the territorial males. These males, however, are difficult to deceive and, knowing how to discriminate and recognize such tricks, chasing the sneakers* ruthlessly. Disguise as a female is a very common trick among sneakers* in very many species, but is too unrefined a trap and generally ineffective.

Another type of subterfuge consists, for males of the cichlid *Astatotilapia burtoni* in Lake Tanganyika, of making females believe that eggs are present in order to attract them. These females practice oral incubation of eggs (Volume 2, section 2.1.2) and usually, after the emission of their oocytes, take a mouthful of the eggs which are then fertilized by the males. The males possess five to nine shiny, orange ovoid spots on their anal fin, which perfectly resembles eggs. These mimic-oocytes, called egg-spots, strongly attract females, and the position of their mouth near the genital opening of the male, following a rapid ejaculation reflex, promotes intra-oral fertilization of the oocytes. This process limits sperm waste and guarantees strong reproductive success. The number and size of these spots vary according to species and even represent a very specific character so that this interspecific variation enables precise recognition of sexual partners among the tens or hundreds of spawning species occupying the littoral zones of the Great African Lakes. Their role in mating selection seems essential as the number of egg-spots is generally higher in large dominant males. This character being inheritable, their sons inherit it and have high reproductive success like that of their father. These egg-spots that function as badges, indicating social status in a hierarchical system, also enable males to dominate rival males and play a decisive role in sexual selection (Volume 2, section 1.1.1). An adaptive diversification of signals and clever tactics as well as clever stratagems developed by particularly imaginative males.

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Bibliography: *Curr.Biol.,* 2012, **22**: 1440-1443 & DOI:10.1016/j.cub.2012.05.050, *J.Fish Biol.,* 2013, **83**: 343-354 & DOI:10.1111/jfb.12175, *Proc.Roy.Soc.B*, 2011, **278**, 1718: 2318-2324 & DOI:10.1098/rspb.2010.2483

### *Defensive mimicry*

Cheating a predator is an approach that seems completely honest. The predators generally use the eye of their potential prey as their focus of attack, their body position predicting their direction of flight. The prey, refusing to be mere expiatory victims, have developed antipredation devices. One of them is to have a false eye or ocellus in the form of a round colored spot surrounded by a contrasting concentric circle, generally of black color, which underlines its existence and perfectly mimics a classic visual organ. Its presence in various ichthyic species (butterfly fishes of the *Chaetodon*, hence their name of four-eyes, wrasses, gobies, damselfish, etc.) as well as in birds, insects (butterflies) or even mollusks, seems justified by the advantage that it gives to its owner. The effectiveness of a false eye is enhanced when the true eye is concealed in the center of a black transverse band. Hiding one's eye from the predator helps to create a diversion and effectively upset the attack. Its protective function is based on the diversion it creates by deceiving the assailant as to the target itself, its attention being focused on a part of the body less vital than the head and the direction of flight of the latter which is opposite to that expected by the predator during its attack, which greatly increases the prey's chances of survival. Such a directional error committed by a predator is experimentally demonstrated by equipping a three-spined stickleback *Gasterosteus aculeatus* with such an ocellus, which is then offered as artificial prey to a visual predator. Its diversionary function is thus confirmed, but its supposed intimidating function – a large ocellus resembling the eye of a large predator which may be a deterrent? – has not been demonstrated.

Adopting a disguise that makes you look like the predator you fear is a strategy to guard against their attack. The juveniles of the lamprologue cichlid *Neolamprologus furcifer* of Lake Tanganyika, unlike adults with a dark brown color, adopt a color pattern composed of white stripes which copies the color of their natural predators, the snails *Raymondia horei*, which seems to give them a protective value. In populations where snails are absent, these juveniles have a color comparable to that of their parents.

Even pelagic larvae of many species use mimicry as a survival strategy for their populations. These marine teleost larvae generally have a particularly high mortality rate, often greater than 99% during the early stages of their development – both eggs and larvae. Since larval survival is essential for the survival of populations, the larvae of different families have often elaborate characteristics which, if they offer

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little similarity to adult forms, mask their identity and their capacities for escape. It involves either long spines as in the groupers or an imitation of the characteristics of gelatinous plankton (hydromedusas, ctenophores, siphonophores, salps, etc.), which is poorly identifiable because of its transparency and unattractive to a predator because of its low metabolic value (high percentage of water), unpleasant taste and/or toxicity (rich in cnidocytes*). The leptocephalic larvae of anguillids and those of bothiid flatfish perfectly mimic this gelatinous zooplankton and adopt such a strategy which is decisive in the survival of their populations. The current climate change, favorable to the development of gelatinous plankton, can only be of great benefit to the larval survival of the species who use this subterfuge.

Bibliography: *Anim.Behav.,* 2016, **111**: 189-195 &
DOI:10.1016/j.anbehav.2015.10.028, 2017, **124**: 75-82 &
DOI:10.1016/j.anbehav.2016.12.001, *Mar.Ecol.Prog.Ser*, 2016, **551**: 1-12 &
DOI:103354/meps 11751, *Proc.Roy.Soc.B*, 2013, **280** &
DOI:10.1098/rspb.2013.01458

### *A dual strategy, both offensive and defensive*

A great flexibility of color change has been found in a pomacentrid of the Indo-Pacific, which, on the Great Barrier Reef of Australia, adopts various phenotypes: morphs which are colored brown, yellow, pink, orange or gray related to alternative development of the chromatophores – melanophores, xanthophores. It thus shows similarities with other harmless damselfish such as *Pomacentrus amboinensis*, *P. moluccensis* and *P. chrysurus*. Such chromatic mimicry is both offensive or aggressive, because it enables an approach to unsuspecting prey, which favors their capture, and defensive or cryptic*, because it ensures a certain camouflage in the reef environment, which reduces the risk of predation. This phenotypic plasticity has been tested during various translocations in reef habitats of various colors and generates deceptive signals for both prey and predators. A wolf in sheep's clothing.

Bibliography: *Currr.Biol*., 2015, **25**: 949-954 & DOI: 10.1016/j.cub.2015.02.12

### *Deceiving one's sex partner: the height of dishonesty?*

As females generally appreciate large males and the criterion of size is important for reproductive success (Volume 1, section 1.1.1), some males do not hesitate to bluff their partners by posing as larger than they are in fact. To do this, it suffices to channel some of their energy, not towards tissue growth – cutaneous, muscular, skeletal, etc. – which is expensive in energy, but to substitute for it a fallacious

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fact, economical to produce. Thus, the caudal ornament that is the sword of the male swordtail *Xiphophorus helleri* (Volume 2, section 1.1.2.6) which consists only of a lengthening of the rays of the caudal fin and is energetically inexpensive. It pleases the ladies, however, and is a clever and profitable subterfuge. These females are thus easily duped by males who skillfully manipulate their visual cues.

Females of the guppy *Pœcilia reticulata*, in their search for quality males, also direct their preferences towards those of large size (Volume 2, section 1.1.1). Hence, some males use subterfuge to be chosen, by increasing their apparent length thanks to the development of a large caudal fin. A large tail requires, for its growth, less energy and has a lower tissue cost than that of the vertebral muscle and skeletal tissues usually required during normal growth. Females thus duped, who believed that their quality mating would produce a good offspring, should be disillusioned because their offspring, numerically smaller, have smaller sizes and lower reproductive potential than those resulting from mating with males with small tails. At the most they could console themselves by thinking that their many sons with the same long tails, because this character is hereditary, and using the same stratagems as their fathers, will in turn experience great successes in reproduction. Long-tailed guppy males following caudal fin extension, though they can hope to gain mating success thanks to this trait which is attractive to females, pay for their deception by a decrease in their swimming performance, thus an additional cost in energy to keep up with the current and above all, because of this handicap, less ability to occupy certain habitats with fast water flow, with an increased risk of predation.

In many species of fish, females are the weaker sex, subject to the “wishes” of their male partners, who are the dominant sex. They sometimes develop coercive behavior and use trickery to unknowingly deceive the males who believed themselves naively to be the strongest. So, in the guppy *Poecilia reticulata*, females are victims of forced mating, copulations being stolen (Volume 2, section 1.2.1) by small males called sneakers* who, taking advantage of their small size and high mobility, manage to access the females without the knowledge of the dominant males who hunt them. They then proceed to thrusts of their gonopod* accompanied by ejaculations. If the paternity rates of these small males are not negligible at the end of these copulations, a high percentage of them are canceled because of the power that females have to eliminate or neutralize this sperm which does not please them. Small male sneakers* of the Mexican shortfin molly *Pœcilia mexicana* are little appreciated by females who prefer the large, dominant males who are distrustful of them, knowing they are capable of pilfering fertilizations. Therefore, to achieve their ends and make females less suspicious, they simulate homosexual behavior by frolicking among males and biting each other’s genital orifices (Volume 2, section 1.1.8), thus demonstrating sexual health, which may, in the end, interest females who are always in search of successful mating. Better to mate with small

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While males of the rosy bitterling *Rhodeus ocellatus* make great efforts in sperm production to ensure the fertilization of the multiple females they are courting, avoiding above all spermatic depletion and even a "dry fault" (Volume 2, section 1.1.9), some females simulate an act of spawning by introducing their ovipositor into the branchial chamber of a freshwater mussel, but this introduction is not followed by an emission of oocytes. Males who cannot check for the actual existence of oviposition ejaculate their precious sperm near the inhalant siphon of the mussel (Volume 1, section 3.4). This deception results in a waste of sperm.

Omission of spawning is not uncommon, with females stopping their ovarian development (sexual rest), interrupting their vitellogenesis (reabsorption of vitellus*) or dispensing with oviposition* (retention of mature oocytes). Saving energy to be more fertile during the following sexual cycle?

Bibliography: *Fish Fish.,* 2005, **6**: 50-72, *J.Fish Biol*., 2007, **71**: 1841-1846 & DOI:10.1111/j.1095-8649.2007.01624.x

### Fooling rivals

In the Mexican mountain swordtail *Xiphophorus nezuhualcoyotl*, some small males who are usually victims of inter-male competition, hunted by the big males, manage to fool them by posing as females by sporting a horizontal pigmented bar like that possessed by females as well as a false mark of pregnancy. Despite the possession of a sword that could reveal their deception, they are less often victims of aggression and manage to better approach the females. Subordinate males* of the dark-edged splitfin *Girardinichthys multiradiatus* use the same subterfuge: the possession of a black spot near the anus that makes them look like females, the dominant males do not use this female trap. Satellite males of the bluegill *Lepomis macrochirus* try, imitating the color pattern of females, to fool dominant males into spurious fertilizations. Their rate of *testosterone* is weaker and that of *estradiol* and *cortisol* higher than those of their rivals, but they tend to decrease with experience.

Bibliography: *Behav*., 2006, **143**: 1457-147, 2010, **147**: 1443-1460 & DOI:10.1163/000579510X519693, *Biol.Lett*., 2007, **3**: 628-631 & DOI:10.1098/rsbl.2007.0379, *Ethol.Ecol.Evol*., 2001, **13**: 331-339 & DOI:10.1080/08927014.2001.9522764

### Counter-adaptation to flush out cheaters

Some females among the poeciliids such as the guppy *Pœcilia reticulata* manage to develop a counter-adaptation to expose those who cheat on their size, by

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which depend on their actual size, or by manipulating their clutches in order to reduce their descendants and to hope for better success in future litters. In addition to the possibility of reducing the duration of copulation – *coitus interruptus* – these females can get rid of some of the inseminated semen that is stored in their gonoduct* by jerking of the body to reject some of the ejaculates, thus performing postcopulatory spermatic selection*. A form of contraception.

On the other hand, the risk of females inbreeding with family males – brothers with their mothers, sisters, etc., which generates offspring carrying deleterious recessive genes responsible for severe organic deficiency (Volume 2, section 1.1.5) – leads them to make corrections by manipulating the sperm. They prioritize fertilization with the sperm of non-family males.

How to check the quality of their multiple inseminations? By playing on the speed of movement of sperm and their fertilization success which are conditioned by the quality of the ovarian fluid inside which they seek to fertilize the oocytes. Given the spermatic competition, the best fertilization rates (+10%) following artificial inseminations of virgin females are obtained with the sperm of males whose genome is distant from that of the females. Such mechanisms of postcopulatory* selection demonstrate that it is the females who, as a last resort, are the managers of love games. They thus always have the "last word" by carrying out selective, hidden or cryptic fertilizations*, because they are limited to the framework of subtle cellular interactions of oocyte-spermatozoid genetic compatibility – chemotactic effects – that take place without the knowledge of their partners, and of which even they are not aware. Nature plays a subtle role in avoiding dangerous crosses and promotes good paternity with, ultimately, genetic quality for the offspring. Female cheating? Intersexual conflict? Or rather a fair rebalancing among the risks of widespread cheating?

Bibliography: *Proc.Roy.Soc.B,* 2011, **278**: 2495-2501 & DOI:10.1096/rspb.2010.2369

### *Fooling customers*

A very original form of deception consists of establishing privileged relationships of trust with a familiar partner as part of a form of mutualism, then taking advantage of their lack of mistrust to unknowingly take from them elements of corporeal tissues, becoming a real parasite. This is what happens between bluestreak cleaner wrasse *Labroides dimidiatus* and their customers – groupers, moray eels, snappers, etc. – carnivores who could make a mouthful of this little fish and who let themselves be peacefully de-parasitized by it, without understanding that this expected service is sometimes diverted from its purpose. Indeed, the cleaner

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may feed, not on copepods or parasitic isopods attached to their skin as is most often done, but rather on fragments of the skin, scales and mucus which cover them, elements that are possibly more nutritious than ectoparasites* and often stolen with impunity. However, it runs the risk of being punished by an unhappy customer after discovering that they were fooled. Thus, cleaners show a clear preference for the mucus of the daisy parrotfish *Chlorurus sordidus* even when it has many isopods full of blood that should make them happy. Quality parrotfish mucus, rich in *sugars carbohydrates* and in *lipids*, is then preferred to mucus of the snapper *Lutjanus fluviflamma*.

Personality differences (Volume 2, section 3.7) between cleaners have been observed on the Great Barrier Reef. Some individuals show a zeal for cleaning by actively feeding upon parasites without ever cheating, while others, more active and bolder against predators with more exploratory behavior, able to move up to 20 meters from their cleaning site, are inclined to also show deceit. Honest workers coexist, in the same population, with sharp villains. Deception, an exercise often practiced brilliantly by humans: an inheritance from fish?

Bibliography: *Ethol.*, 2014, **120**: 904-912 & DOI:10.1111/eth.12262

## 3.9. Having a very precise biological clock

### *The day–night "circadian" cycle*

Fish, like all living creatures, know how to synchronize their vital feeding, migratory, social, reproductive and other activities with the natural cyclical variations of their environment: seasonal variations of winter–summer alternation and diurnal fluctuations of day–night alternations or L/D cycle (*Light–Dark*). These seasonal biological rhythms – circannual with a period of a year, and circadian with a period of 24 hours – are not only immediate responses to variations experienced but also anticipations of these events so that a given activity occurs at the right moment – the right event in the right time – thanks to the implementation of endogenous factors corresponding to an internal biological clock or circadian clock inscribed in their genes. Such an anticipatory effect of seasonal changes and daily fluctuations constitutes one of the foundations of a perfectly successful adaptation to a given geographical environment. The spawning of the kelp bass *Paralabrax clathrus* of the California shorelines occurs in summer, during spawning aggregations between 32 minutes before and 120 minutes after sunset, or at the time when predation risk is least. That of the Cubera snapper *Lutjanus cyanopterus* of the Belize coastline occurs 40 minutes before and 10 minutes after dusk, without however reducing predation from the oophagic whale shark *Rhincodon typus*.

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A circadian rhythm* of activity is classically known in the African sharptooth catfish *Clarias gariepinus*, the stone loach *Barbatula barbatula*, etc., who display essentially nocturnal activity. Keeping them in continuous light has the effect of stressing them and making them aggressive. The wels catfish *Silurus glanis* is also considered a nocturnal fish. Radio telemetry* tracking in a Czech river confirms minimal activity during the day, the resumption of activity being at dusk and continuing for a part of the night. Seasonal variations are observable as well as fluctuations according to the level of the water, 24-hour continuous activity occurring during flooding*. An exceptional diurnal activity is known in the Tarn river (Volume 1, section 1.2.2).

The question of circadian rhythms raises the question of the possible interruption of activities of feeding, reproduction and anti-predator defense during a period of sleep. If its modalities, duration and *timing* are highly diversified according to zoological groups, researchers agree that the physiological data of its control have been remarkably preserved during evolution. Histological, histochemical and histoenzymological studies confirmed that various brain neuronal activities – *aminergic, cholinergic, GABAergic, serotonergic*, etc. – involved in sleep and which can be pharmacologically manipulated in the laboratory are common to zebrafish *Danio rerio*, used as a model of fish, and to the various birds and mammals tested. There are common molecular bases and structural and functional homologies.

Reproduction of fish in temperate regions is essentially seasonal under neuroendocrine regulation in relation to the natural photoperiodic cycle, and the timing of spawning is synchronized with the day–night circadian cycle, demonstrating the importance of light as a factor in testicular and ovarian sexual maturation and in oviposition and spermiation. This luminous factor strongly induces reproduction.

The equipment of ocular photoreceptors – retinal cells forming cones and rods – doubles that of non-retinal brain photoreceptors: the pinealocytes and parapinealocytes of the epithalamus* and the hypothalamus*, which specialize in the detection of light signals and in appreciation of the photoperiod. Small reef-dwelling, plankton-eating damselfish such as *Dascyllus marginatus* use a sunlight window of about 45 minutes at sunrise to emerge from their night shelters and feed on zooplankton before the risk of predation subsequently increases. This timing is well programmed to access food in an environment which is still secure.

Bibliography: *Anim.Behav.*, 2005, **70**: 133-144 &
DOI:10.1111/j.anbehav.2004.10.014, *Curr.Biol.*, 2016, **26**: R1073-R1087 &
DOI:10.1016/j.cub.2014.08.068, *J.Fish Biol.*, 2005, **67**: 83-101, 2006, **68**: 157-184,
*Mar.Ecol.Prog.Ser.*, 2001, **215**: 275-282.

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### *The lunar or semi-lunar cycle of tides or tidal rhythm**

The reproduction of many marine species is synchronized with great precision to the lunar calendar and the movements of masses of water related to rising or ebbing tides which regulate the movements of dispersion of the eggs, then the larvae.



**Figure 3.5.** *Grunions Leuresthes tenuis deposited on a Californian beach during high tides lay in the sand, the hatched larvae being taken again by the tides of the following tidal cycle*

The Japanese fugu *Takifugu niphobles* group together in large numbers (1,000 individuals) with a rising tide and spawning occurs 2 hours before high tide, this semi-lunar rhythm being endogenous and maintained for a long time in the aquarium. The spawning of the sole *Solea senegalensis* takes place in Portugal during the autumn, with a period of 29 days, in phase with the full and the new moon, starting after sunset to reach a peak between 21:00 and 22:00, synchronized with the nocturnal secretion of *melatonin* whose production is very sensitive to even a low light intensity of 0.3 lx* at the full moon. This endogenous rhythm is maintained in the laboratory under continuous illumination over 2 days, under the control of an internal pacemaker. Similarly, spawners of the grunion of California *Leuresthes tenuis* synchronize their clutches with the tidal cycle, eggs laid in the wet sand of the beaches being intended to hatch during the high tides of new moon and full moon so as to drive the larvae back to sea. The females of the tropical threespot

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maturation – peak GSI* – followed by ovulation and oviposition rigorously correlated with high tides. Endocrine conditioning of spawning – conversion of *testosterone T* into *17β-estradiol* or $E_2$ under the effect of a discharge of GTH – strictly respects very precise environmental temporal parameters corresponding to the cycle of full moon and new moon according to a well-regulated scenario.

The laying of most reef species belonging to the families of acanthurids, apogonids, blenniids, carangids, chætodontidae, labrids, lutjanids, scarids, siganids, sphyranids, sparids, siganids or serranids obeys endogenous semi-lunar and lunar rhythms controlled by the clock-genes that govern the tidal cycle – tidal rhythms* – and play a key role in the oceanic dissemination of larvae (Volume 2, section 2.2.3).

The mechanisms regulating behavior related to annual and daily photoperiod variations depend on a complex neuroendocrine system involving sensory organs (the eye) as well as areas of the brain (Volume 2, section 4.3) (epiphysis and hypothalamic–pituitary axis), via a molecule, melatonin, common to all vertebrates and even present in invertebrates. Comparisons between phyla make it possible to judge the preservation of these basic systems during evolution. All vertebrates possess this same capacity on the basis of their biological rhythms that regulate the timing of their feeding, breeding and migratory activities.

Bibliography: *Fish & Fish.,* 2004, **5**: 317-328, *Histol.Histopathol.,* 2004, **19**: 487-494, *J.Fish Biol*., 2005, **67**: 1029-1039 & DOI:101111/j.1095-8649.2005.00806.x, 2007, **71**: 101-114 & DOI:10.1111/j.1095-8649.2007.01471.x, 2009, **74**: 820-841 & DOI:10.1111/
j.1095-8649.2008.02163.x, **75**: 17-38 & DOI:10.1111/j.1095-8649.2009.02260.x, 61-74 & DOI:10.1111/j.1095-8649.2009.02263.x, 2010, **76**: 7-26 & DOI:10.1111/j.1095.8649.
2009.02481.x, 27-68 & DOI:10.1111/j.1095-8649.2009.02500.x, *J.Freshwat.Ecol.,* 2004, **19**: 77-85, *Zool.Sci*., 2008, **25**: 572-579 & DOI:10.2108/zsj.25.572, 2010, **27**: 555-5583.9.3. Melatonin, key molecule of timing

This hormone is secreted in fish at two major sites: the retina of the eye and the epiphysis or pineal organ of the brain (Volume 2, section 4.3). It targets hypothalamic and pituitary relays (the suprachiasmal neurons SCN of the hypothalamus*), so as to maintain an endogenous rhythm that can be out of synchronization with external events for a certain period of time, hence the role of time-keeper attributed to it. The brain of the minnow *Phoxinus phoxinus* contains, for example, in its dorsal (epithalamus*) and ventral (hypothalamus*) parts, photosensitive nerve cells: pinealocytes* and parapinealocytes, which are homologous to retinal photoreceptors and which, without any visual function, provide photoperiod-related information and are at the origin of biological rhythms. Its production is related to the dark phase of the day–night cycle, its concentration in

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duration and amplitude according to the season: low duration and high amplitude in summer and long duration and low amplitude in winter, with intermediates in spring and autumn.

Experiments with pinealectomy* and melatonin administration demonstrate the reality of these phenomena, the epiphysis playing a role of pacemaker and synchronizer of many activities. Thus, all daily movements of ascent and descent in the water column, horizontal movement, meeting with or dissociating from schools, foraging and prospecting for a sexual partner, etc. are controlled in such a way that all individuals in the same population respond together and synchronously to the astronomical events to which they are sensitive and which punctuate their daily way of life. As we have mentioned, the spawners of a given species – see the spawning of groupers (Volume 2, section 1.2.2) – are active at the same time, at the same breeding sites, with remarkable inter-annual consistency.

The lunar cycle of nocturnal reproduction of spinefeet *Siganus canaliculatus* and *S. guttatus* is under the control of the gene *Period2* which is expressed in the retina and the pineal gland* where it is stimulated by the lunar light of the full moon and under-regulated during the new moon period. This is molecular regulation of reproduction with clocks synchronized to the lunar cycle.

Bibliography: *Cybium*, 2011, **35**: 3-18, *Gen.Comp.Endocr*., 2008, **157**: 186-195, *J.Comp.Neurol,* 2010, DOI:10.1002/cne.22408, *J.Fish Biol.,* 1999, **55**: 1213-1222, *J.Pineal*., 2006, **40**: 236-241 & DOI:10.1111/j.1600-079X.2005.00306.x, 2008, **45**: 133-141 & DOI:10.1111/j.1600-079X.2008.00566.x, *J.Soc.Biol.,* 2007, DOI:10.1051/jbc.2007.003

The molecular mechanisms of biosynthesis and mode of action of *melatonin* on specific receptors are identical to only variations of distribution in all Craniata*, their diversification being particularly high in fish. Its role concerns in particular the circadian rhythms of feeding, reproductive and social communication activities, for example, the nocturnal vocalizations of the toadfish *Porichthys notatus* (Volume 1, section 3.1). This *melatonin* controls many hormonal secretions such as prolactin, *growth hormone* or *GH*, sex hormones like *LH** as well as neuromessengers like *dopamine DA* or *vasotocin VTC* according to basic mechanisms common to all, with all vertebrates endowed with the same basic mechanisms of time measurement.

*Melatonin* plays a significant role in the mechanisms of falling and remaining asleep (Volume 2, sections 3.9.2, 3.9.5 and 4.2).

Bibliography: *Curr.Biol.*, 2016, 26: R 882-R902 & DOI:10.1016/j.cub.2016.08.045

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### *Fish showing original qualities*

It is remarkable that a high degree of conservation in the vertebrate lineage has been accompanied by a plasticity of tissue as well as cellular diversification of the receptors, resulting in all cases in the pieces of the puzzle being put together in every species' complex of rhythmic activities.

The wealth of data relating to the chronobiology of fish that continues to surprise specialists in this discipline is based on common biomolecular mechanisms serving very different organisms with very diverse lifestyles in very distinct and very complex ecosystems. Such regulation of biological rhythms also concerns deep-sea species of –2,000 to –5,000 meters, such as grenadiers *Coryphænoides ornatus* of the Northeast Atlantic. The secretion of *melatonin* and the possession of an endogenous biological clock with maximum activity during the night seem here to act as a synchronizer with tidal currents that actually occur rhythmically in deep waters. Biological rhythms are therefore generalized to deep waters.

Some species show differences in diurnal rhythm of activity that can be seen as original "chronotypes", markers of their personality. So, the pearly razorfish *Xirichthys novecula* presents a diurnal rhythm of activity, remaining buried in sediment overnight to reduce the risk of predation. Individuals exhibit differential chronobiological circadian rhythms, variations in the duration of resting time depending on the time of awakening and resumption of feeding activity.

Fish are generally considered "good specialists" in the subtle field of chronobiology.

Bibliography: *Deep-Sea Res*., 2007, **54**: 1944-1956 & DOI:10.1016/j.dsr.2007.08.005, *Roy.Soc.Open Sci*., 2017, **4,** 2 & DOI:101098/rsos.160791

### *Additional role of melatonin in health and fitness*

A certain universality of *melatonin* has been recognized. This molecule is indeed present in a multitude of animal and plant taxa and many microorganisms. Its ubiquity seems linked to basic vital functions such as antioxidant defense, the fight against free radicals* in the same way as *vitamins C* and *E* and *glutathione*, hence its involvement in health, fitness*, senescence and life span. This involves a valuable immune function, melatonin being a ubiquitous and "miracle" molecule.

*Melatonin*, acting in concert with the melanocyte-stimulating hormone (MSH) *prolactin* (*PL*), conditions, inter alia, pigmentary development – *melanin, carotenoids* etc. – which determines the colors of nuptial color patterns (Volume 2,

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Thus, these various data show that the fish has a remarkable potential for measuring time which enables it to know *when* to rest, *when* to look for food with a high probability of meeting its favorite prey, *when* to protect itself from predators with a probability of fewer encounters with them, *when* to join its congeners with a probability of adopting the same social rhythms, *when* to undertake migratory movement considering the duration of the trip and the foreseeable date of reaching the goal and *when* to mate with a likelihood of encountering sexual partners with the same favorable dispositions to produce viable offspring with appropriate food during the larval and juvenile phases. For every appointment that it is imperative not to miss, there are requirements of calendar and *timing*, not only seasonal, but daily and hourly. Latecomers will sometimes have to wait until the following year, the next fortnight or the following day. It is imperative to have a good chronometer and not to miss some dates and some scheduled appointments that are vital to the longevity of the population.

Each fish will then mobilize all its neuroendocrine and neuromuscular systems in order to respond precisely, together with all its congeners to the temporal requirements characteristic of its species.

Bibliography: *Trends in Endocr.Metabol.Sci.Direct*, 2007, **18**, 2 & DOI:10.1018/j.tem.2007.01.002, *Biol.Rev.*, 2010, **85**: 607-623.

Fish are not content to demonstrate complex behaviors in the area of their vital and basic requirements of nutrition, protection and reproduction. They may also show astonishing behaviors in the use of tools, evaluation of quantities and even the demonstration of playing abilities and the expression of a certain esthetic sense of which we did not believe them capable, which seemed to be the prerogative of birds and especially mammals.

Some of these behaviors may seem somewhat “simplistic”, but must take into account the fact that fish are gifted with weak means of handling objects, because deprived of articulated limbs, such a handicap leading them to use their mouth as a tool for work and a means of expression out of which they manage to make the

Regardless of the behaviors observed, differences occur between the individuals tested, testifying to the expression of their personality, which runs counter to the misconception of a certain apparent standardization among populations.

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# 4

# Neurological and Neuroendocrine Conditioning Requirements

The explanations for the neurohormonal conditioning requirements of the behaviors mentioned in the preceding chapters provide proof that any behavior, whether innate or learned, is the result of precise and rigorous control enacted by the brain, which is the "conductor" of all neurosensory, neuromotor and neuroendocrine activities involved in all vital manifestations. It is therefore logical that we seek to explain these in the light of recent knowledge acquired in vertebrate neurobiology, particularly in the neurobiology of fish.

## 4.1. Experience of stress and suffering

The sensitivity of fish to stress has been acknowledged and demonstrated; however, the question of whether fish are sensitive to conscious pain has long been debated and is still the subject of speculative debate.

### *Sensitivity to stress*

Opportunities to test manifestations of stress in fish are numerous: parasitic infestation, capture, angling, hooking, confinement, high density, poor water quality, starvation, various manipulations, slaughter, etc.

The behaviors of rainbow trout *O. mykiss* in response to electric shocks or an experimental injection of *toxins* such as bee *venom* and *acetic acid* which cause agitation, tremors, shivering and movements of friction against the bottom tend to demonstrate the existence of stress and sensitivity to pain that can be mitigated

Fish Behavior 2: Ethophysiology,
First Edition. Jacques Bruslé and Jean-Pierre Quignard.
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by the application of *anesthetics* – *benzocaine* and *morphine*. Their sensitivity to pain is therefore well recognized.

Thus, sardines *Sardina pilchardus* which are kept in captivity in basins after capture by a purse seine* suffer from stress accompanied by scale loss and caudal fin erosion which induce bacterial infections. After a high mortality in the first day of captivity, a situation of returning to normal healthy blood parameters is observed after 2 weeks. Manipulation stress in the cod *Gadus morhua* is detectable by an acceleration of opercular beats followed by a fast return to normal frequency in 90 minutes. This is a relatively easy recovery.

Weather events such as floods accompanied by water turbidity are stressors sticklebacks *Gasterosteus aculeatus*; the turbidity disturbs their visual and olfactory abilities to detect prey. In addition, females infested by the cestode *Schistocephalus solidus* are under chronic stress that results in a decrease, in their brain – telencephalon – of the level of *monoamine neurotransmitters*: *5-hydroxytryptamine* (*5-HT*), *dopamine* (*DA*) and *norepinephrine* (*NE*), proving the existence of neuroendocrine alterations likely to induce behavioral modifications.

In preslaughter conditions, the European bass *Dicentrarchus labrax* in hatcheries demonstrates measurable stress responses measured by rates of *cortisol*, *glucose* and of plasma *lactate* and organic changes (muscle, mucus, digestive tract) following activation of the axis: chromaffin* cells → hypothalamus → pituitary → interrenal. Are these fish aware of what will happen to them?

Acute stressors such as exposure to air for 60 seconds or chronic stress such as confinement, experienced by the sea horse *Hippocampus abdominalis* and measurable by blood parameters, are followed by a quick return to normal in 6 hours.

In a situation of chronic stress – see its rate of *cortisol* – which has a higher impact during activity phases during the day than during rest phases at night, zebrafish *Danio rerio* loses its ability to learn to avoid an electric shock. Its cognitive skills are inhibited by stress. On the contrary, return to a certain post-stress well-being is favored by the social context in this gregarious species: participation in a group of familiar congeners reduces stress compared to isolated and solitary individuals, as evidenced by the rate of *cortisol* respectively released into the water. Social comfort seems to be provided by congeners.

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Differential responses to predator-induced stress are observable in guppies *Pœcilia reticulata*. Males are more sensitive to danger than females, who seem able to better control their fear, as evidenced by their comparative rates of *cortisol* released into the water. Males are more active and thus more exposed, and their risk-taking is often much appreciated by females (Volume 2, section 1.1.1).

The zebrafish *Danio rerio* currently serves as a model for comparative study of the serotonergic system (*serotonin* (*5-hydroxytryptamine* (*5-HT*)) in vertebrates. *Serotonin* is involved in stress, defense and aggression reactions.

Bibliography: *Anim.Behav.,* 2017, **132**: 189-199 & DOI: 10.1016/j.anbehav.2017.08.017*, Behav*., 2007, **144**: 1347-1360, **145**: 1267-1281, *J.Exp.Biol.,* 2014, **217**: 3919-3928 & DOI:10.1242/jeb.109736, *J.Fish Biol*., 2005, **67**: 384-391 & DOI:10.1111/j.1095-8649.2005.00745.x, 2007, **70**: 131-1316 & DOI:10.1111/j.1095.8649.2007.01507.x, 1447-1457 & DOI:10.1111/j.1095-8649.2007.01422.x, 2008, **72**: 103-120 & DOI:10.1111/j.1095-8649.2007.01660.x, 747-752 & DOI:10.1111/j.1095-8649.2007.01717.x, 2011, **79**: 256-279 & DOI:10.1111/j.1095-8649.2011.03013.x, *Proc.Roy.Soc.B*, 2001, **268**: 1411-1415, *Progr.Neuro-Psycho-Farm.biol.psychiatry*, 2014, **55**, 3: 50-66 & DOI.org/1016/ j.pnpbp.2014.03-008, *Rev.Fish.Sci*, 2012, **20**: 181-182 & DOI:101080/10641262. 2012.696898, *Roy.Soc.Open Sci*., 2018, **3** & DOI.10.1098/rsos.172268

### *Actual suffering?*

Humans generally show little empathy for fish who agonize and suffocate when they experience major respiratory stress related to leaving the water. The fact that they do not express their suffering through noisy demonstrations such as cries and groans or by facial expressions inducing any pity in their observers has long credited the idea that they were incapable of suffering. Are not the greatest pains mute?

Nevertheless, the presence in the skin of teleosts of nociceptors* comparable to those of higher vertebrates, including the human species, and which are known to be specialized receptors and pain inducers, has cast doubt on this denial, considering the existence of 22 of the 58 sensory receptors detected on the head of a trout which are classified as nociceptors*. Electrophysiological responses involving the trigeminal nerve* have been identified which argue for the pain mechanisms common to all vertebrates.

Bibliography: *Dis.Aquat.Org*., 2007, **75**: 131-138, *Fish Fish*., 2014, **15**: 97-133 & DOI:101111/faf.12010

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### *Neuropsychological data compared and a mental construct of pain in fish*

The very notion of suffering presupposes the existence of a capacity for awareness that relies on the possession of specialized encephalic nerve structures such as telencephalic* pain areas located in the cerebral neocortex and amygdala (Volume 2, section 4.3) which are well known in the human species in clinical neurology but seem to be lacking in fish. The latter are said to only have common homologous nerve structures such as a pallium* whose functional equivalence with that of the mammalian encephalon is sometimes questioned, hence the idea of a consciousness quite different from our own. Is there a danger of too much anthropocentrism?

The sensation of pain in humans has been related to specific structures of the cerebral cortex that are completely lacking in fish who do not have equivalent structures. It seems then established that the latter would be insensitive to the "emotions" related to pain with its psychic component that characterizes the human species, although their nociceptors have the ability to induce the physiological and neuroendocrine response characteristic of stress. Measures in favor of a certain welfare of fish, especially in aquaculture, are however recommended (Volume 2, section 4.1.4).

Bibliography: *J.appl.animal welfare Sci*, 2018 & DOI.org/10.1080/1088705.2018.15330596, *Rev.Fisheries Sci*, 2002, **10**:1-38 & DOI.org/101080/20026491051668

However, some researchers recognize that the lateral pallium* and medial pallium* regions of fish are perfectly homologous to the mammalian hippocampus and amygdala and that their respective functions may not be so distinct; therefore, fish have the neurological ability to experience some form of pain.

Elasmobranchs appear to have fewer sensitive nerve structures than teleosts, for example hammerheads sharks *Sphyrna* sp. who consume rays with dangerous venomous spines as prey. In addition, pike, black bass, trout and char, when they are caught by anglers with hooks on the tongue and/or jaws and released by *catch and release*, are able to bite again a few minutes later as if nothing had happened. A very large variability of size – a 20 g brain in the megamouth shark *Megachasma pelagios* of 1 ton, and 60 g in the hammerhead shark *Sphyrna* sp. whose body mass is 200 kg – and neural structures between these species makes some interpretations difficult. However, electrophysiological tests support the idea of a clear response of receptors to pain, but its emotional psychological dimension, so important in the human species, remains debated and is often strongly denied.

Bibliography: *Mar.Ecol.Prog.Ser*., 2017, **582**: 147-161 & DOI:10.3354/meps12334

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### *Safeguarding well-being*

The issue of animal welfare has been the focus of attention for some decades. The acquisition of a certain physical and mental equilibrium for animals in farms, laboratories, zoos and aquaria was recommended, and "positive standards" were established for mammals and birds, and then expanded more recently to fish. "Happiness" (?) in fish is very difficult to establish in the absence of facial expressions and vocalizations recognized as specific to a psychological state (delight, sadness, etc.).

Various behaviors such as counter-current swimming in the goldfish *Carassius auratus*, following a route through labyrinths to access partners in Mozambique tilapia *Oreochromis mossambicus*, and choosing variously colored substrates in the Nile tilapia *O. niloticus* have demonstrated the reality of the phenomenon of seeking "a full and complete life" (*sic*) according to the authors of these experiments. The benefits of such favorable environmental situations are shown in reduced stress (lower *cortisol* and *adrenaline*), improvement of the immune functions (less sensitivity to pathogens*), and an increasing capacity to explore new habitats among minnows *Phoxinus phoxinus*. These behaviors of exploration of new habitats following an increase in the curiosity of individuals seem to be the evidence of existence of "positive emotions" and a certain "sense of pleasure" in them, which results in an increase in the cerebral rates of *endorphins**, *serotonin*, *dopamine*, *oxytocin* *isotocin*. Some authors add, as criteria of expression of a certain well-being which remains difficult to analyze, an ability to develop behaviors of play (Volume 2, section 3.4).

This issue of the notion of consciousness of pain in fish is gaining importance as part of an animal welfare policy is advocated in the management of centers of fishing and fish farming. Such an ethic of avoiding unnecessary suffering in fish is justified in many areas where fish are used as targets for human activities: commercial and recreational fisheries, spearfishing, fish farming, aquariology (35–40 million ornamental fish marketed annually in the United States) and scientific research – laboratory fish such as zebrafish is seen as *mouse fish*.

Recommendations for the treatment of farmed fish, "Welfare in Farmed Fishes", were recently enacted (2019) in the form of a "FishEthoBase" project for 41 farmed species (out of a total of 362 "cultivated" species) at all stages (larvae, juveniles, adults, spawners) of their exploitation.

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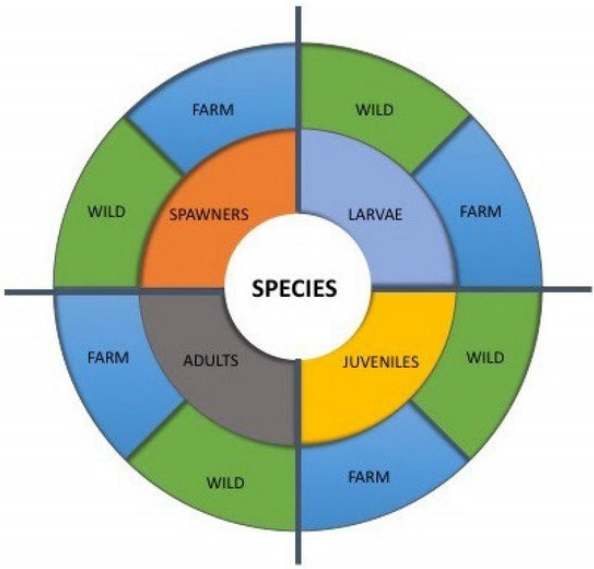



**Figure 4.1.** *Diagram of a "FishEthoBase" taking into account comparative data between wild and farmed fish at all stages of their development and exploitation (source: Saraiva et al., Fishes, 2019, 4, 2, 30, figure 1). For a color version of the figures in this book see www.iste.co.uk/bruslé/fish2.zip*

An optimum density in breeding ponds is sought in the case of Atlantic salmon *Salmo salar*. It is established at medium densities that rates of aggression between individuals are found in both low- and high-density basins.

However, if the *UK Cruelty Act* 1876 concerning cats, dogs and cattle as well as primates was extended to elephants, dolphins, pigs and chickens, fish are still waiting for such legislative gestures of protection. The American *Animal Welfare* does not mention them, and the *UK Aquatic Animal Health Regulations* 2009 are only a small step in this direction. In France, the civil code (article 515-14) recognizes, since January 2015, an animal, therefore a fish, as "a living being endowed with sensitivity", which marks the end of an archaic vision of animals. A long and regrettable lack of empathy! Only recreational fishing fans who practice *catch and release* are respectful of a true ethic.

Bibliography: *Anim.Behav*., 2015, **106**:147-153, *Can.J.Sci.Halieut. Aquat*., 2007, **64**: 336-344 & DOI:10.1139/f07-018, *Fishes*, 2019, **4**, 30 & DOI.org/10.3390/fishes4020030, **31** : 1-14, *Fish Fish.*, 2004, **5**: 281-295, *J.Fish Biol*., 2006, **68**: 332-372 & DOI:10.1111/j.1095-8649.2005.01046.x, *Rev.Fish Sci*, 2002, **10**: 1-38 & DOI:10.1080/20026491051668

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## 4.2. A question asked about their period of inactivity: are they able to sleep?

Various modalities of mono- or multi-phase sleep demonstrated by electroencephalogram in various vertebrates make it possible to limit the risks of behavioral *blackout* that can only benefit predators, a total immobilization allowing, most often, escape from visual identification by a potential predator (Volume 1, section 1.3.3).

### *Do fish really sleep?*

Animal sleep is generally considered to be a necessary physiological condition which, although variable in quality and intensity depending on the species, promotes energy saving and remodeling of neuronal synaptic* activities during a suspension of the state of consciousness, of sensory perception activities and of voluntary movements. Such a vital need for quiescence seems to be shared by all vertebrates, including fish. Moreover, an experimental deprivation of sleep for the blue zebrafish *Danio rerio*, by maintaining permanent conditions of light (24L/00D), exerts negative effects on their memory capabilities and impacts their cognitive potentialities in discrimination and recognition of objects or paths learned in mazes. A single night of disruption of its sleep-like rest phase is enough to induce memory disorders.

The question of whether fish actually sleep and experience periods of “real sleep” has often been raised and debated because, given their lack of eyelids, they never close their eyes. However, ethologists confirm the existence, in them, of periods of quiescence assimilated to sleep. Even sharks and large pelagics like tuna, who constantly swim, seem to sleep while swimming.

Sleep definition criteria, applicable to higher vertebrates such as *Rapid Eye Movement* (REM) or electroencephalograms that distinguish different types of sleep, including paradoxical sleep, are not found in fish. However, their variations in activity related to the nycthemeral* cycle show the existence of rest phases that can be assimilated to falling asleep, which does not fail to be high risk and can only be realized in a very secure environment. *Serotonin* (*5-hydroxytryptamine (5-HT)*) of hypothalamic origin has the function of promoting sleep in the absence of stress-generating stimulation (Volume 2, section 4.1.1).

Quiet sleep can involve large species that have few natural predators such as Pacific black sleeper shark *Somniosus pacificus*, whose large size greater than 7 m preserves it from enemy attacks and whose name is linked to benthic* and

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apparently lethargic behavior, although it is capable of catching fast prey such as salmon of the genus *Oncorhynchus*, tuna *Thunnus alalunga* and seals *Phoca* sp., by means of ambush hunting behavior rather than a chase.

Bibliography: *Anim.Behav*., 2005, **70**: 723-736 & DOI:10.1016/j.anbehav.2005.01.008, *Anim.Cogn*., 2017, **20**: 159-169 & DOI:10.10007/s10071-016-1034-x, *J.Fish Biol.,* 2006, **69**: 392-405 & DOI:10.1111/j.1095-8649.2006.01096.x, *Progr.Neuro-Psycho-Pharm.biol.psychiatry*, 2014, **55**, 3: 50-66 & DOI.org/10.1016/j.pnpbp.2014.03-008

### *Experimental sleep deprivation generating anomalies in cognitive performance*

The demonstration that sleep plays a key role in cognitive processes involving learning and memory in fish has been experimentally shown among zebrafish *Danio* : total deprivation of sleep induced by treatment with *ethanol* causes a disruption of activities (memory, learning) that obey diurnal circadian rhythms quite comparable to those of mammals. As in the latter, treatment with *melatonin* causes a recovery of these functions, demonstrating the experimental value of this small fish in terms of analysis of its cognitive potential.

Bibliography: *Behav.Proc.,* 2018, **157**: 656-663 & DOI:10.1016/j.beproc.2018.04.004

### *Insomniac populations*

Populations of the Mexican tetra *Astyanax maximus* are distributed between surface watercourses and dark underground caves in Latin America. The epigeal* forms exposed to sunlight are colorful and conspicuous while the hypogeal* forms are depigmented and blind. Comparative neurology studies show the existence of neural disparities between these two types of populations and the possession, by the cavefish, of “orexinergic” neurons, secretors of a neurotransmitter, *orexin*, which plays a vital role in the regulation of sleep. Located in the hypothalamus, these neurons rich in *hypocretin* maintain the organism in a state of permanent wakefulness, repression of sleep favoring the availability of foraging. Such mechanisms are of interest to specialists in the study of disorders of human insomnia who are able to pharmacologically block the action of this molecule and put cavernicolous tetras to sleep.

Bibliography: *eLife*, 2018 (6/02) & DOI:10.7554/eLife.32637

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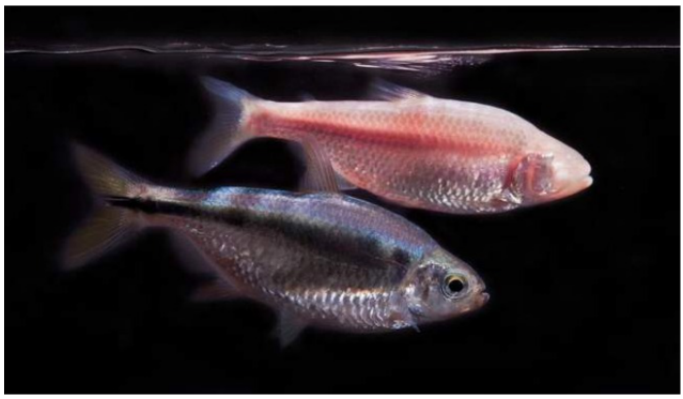


**Figure 4.2.** Tetras Astyanax mexicanus: *hypogeal (top) and epigeal (bottom) form (source: A. Keene, Florida Atlantic University)*

## 4.3. The complexity of their brains: their cognitive abilities

All the behaviors described in the preceding chapters are dependent on a decision-making center, a central power, a control tower that is the brain. The latter, using both endogenous information, originating from their genes and translating the genetic potential inherited from their parents, and exogenous information in the form of signals emitted by their physical (surroundings, habitat) and social (congeners, neighbors, predators) environments, exerts a neuroendocrine coordination. This enables rapid and appropriate neurosensory and neuromotor responses which promote their survival, both individual and collective, and respond best to vital adaptive needs. This is a remarkable coordination of the functioning of the decision-making centers.

### *A primitive brain in a lower vertebrate?*

The brains of fish differ from those of birds and mammals in their smaller volume and their weaker apparent structural organization, which initially led anatomists to consider that they were poorly equipped and weakly able to develop cognitive processes and memorization. Indeed, the multilaminar cerebral cortex that characterizes the evolved mammalian brain is lacking, and the pallium* or striated bodies of fish are structurally simpler. However, their telencephalon* has homologies with that of terrestrial vertebrates, testifying to a remarkable conservation of the basic nervous system architecture during the phylogenesis* of vertebrates.

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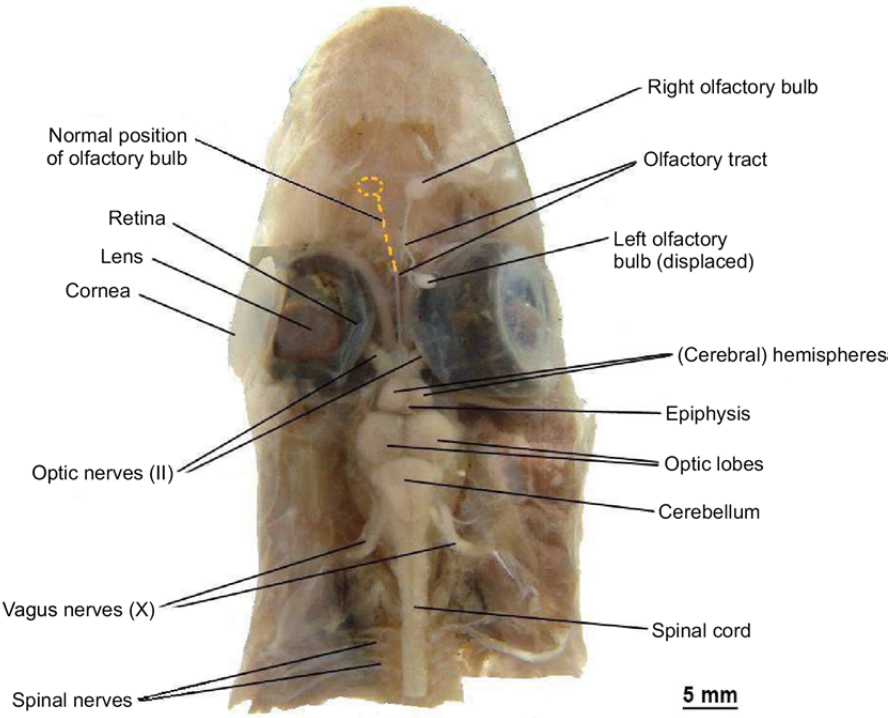



**Figure 4.3.** *Fish encephalon (roach* Rutilus rutilus*) in dorsal view*

Various recent studies, however, have led to the modulation of old and traditional judgments, the tempering of conclusions considered too negative, and the revision of somewhat minor concepts.

Understanding the cognitive mechanisms specific to fish is all the more interesting because this group, ancestor of vertebrates, is at the origin of the phylogenesis* of tetrapods. Indeed, recent technological progress enables us to visualize the functioning of neurons in the brains of fish. Transparency of the skull in larvae of the zebrafish *Danio rerio* now enables us to observe the neural activity of their brain in real time. Their neurons of the optical roof, linked to the retina through the optic nerve, respond to visual activity induced by prey in motion such as a paramecium, thanks to an influx of *calcium ions* $Ca^{++}$ which makes them fluorescent and visualizable by fluorescence microscopy. These neurons are no longer observable when the paramecium stops swimming and they are reactivated as soon as it resumes swimming. Such nerve mechanisms promote the capture of prey in these hunting larvae. The same method of observation makes it possible to

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demonstrate the role of habenula neurons in the neuromodulation of odor reception, *bile salts* acting according to the dose as attractants or repellents. A cartography of larval neuronal activities has thus been established with precision.




**Figure 4.4.** *Larvae of zebrafish* Danio rerio *(top) and neuronal activity rendered fluorescent and visualizable by fluorescence microscopy (bottom)*

Vision, a very developed sense in most open-water species – sensitivity to luminous radiation + sensory perception of images – is related to the development of a diencephalic optical roof* as confirmed by electrophysiological studies conducted in the Siamese fighting fish *Betta splendens*. Perception, under experimental conditions, of visual recognition of fish – trout, eel – by the cichlid *Pseudotropheus* sp. and by the whitetail damselfish *Dascyllus aruanus* involves not only still images but also moving images presented in the form of videos at different speeds. Animated digital images programmed by computer make it possible to present precise and varied visual images of the fish that are tested. Their visual ability, after a brief learning period consisting of presenting images more than twice, is comparable to that of higher vertebrates such as birds and mammals.

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The architecture of the pallium of lampreys such as the European river lamprey *Lampetra fluviatilis* is not unlike that of the cortical frontal lobe of mammals, the motor neurons of its optical roof* controlling movements of the eyes or the trunk in a manner quite comparable to that observed in mice. These nervous cortical projections may be common to all vertebrates.

Today, this pallium, which consists of three nerve layers, is considered as a basic structure that has been remarkably preserved in reptiles and is at the origin of the six layers of the mammalian neocortex following evolution which has lasted some 500 Myr. Thus, the oldest zoological group of anamniotes* was the precursor of reptilian brains, then mammalian brains. The concentration in these palliums of neurons rich in GABA* receptors is correlated with the possession of the *homeobox** genes *ANF/HESX1* which are recognized in all vertebrates. Fish are the ancestors of this conservative phylogenetic strain.

Bibliography: *Anim.Cogn.,* 2014, **17**: 359-371, 2015, **18**: 1077-1091, & DOI:101007/s10071-015-0976-y, **24**: R947-R950 & DOI:10.1016/j.cub.2014.08.043, *Biol.Lett*., 2009, **5**: 117-121 & DOI:10.1098/rsbl.2008.0397, *Curr.Biol*., 2014, **24**: 1167-1175 & DOI:10.1016/j.cub.2014.03.073, 2017, **27**, 3264-3277-e5 & DOI:10.1016/j.cub.2017.09.034, *Curr.Sci*., 2014, **24**: R1048-R1050 & DOI:10.1016/j.cub.2014.09.043, *Env.Biol.Fish.,* 2004, **70**: 285-291, *J.Exp.Biol*., 2013, **216** & DOI:10.1242/jeb.077867, *J.Fish Biol*., 2009, **75**: 738-746 & DOI:10.1111/j.1095-8649.2009.02347.x,

## *Physiological basis of stress common to all vertebrates*

The neuroendocrinology of the brain is common to all vertebrates under acute stress, and the biochemical mechanisms of increasing plasma rates of *catecholamines* (*adrenaline*, *noradrenaline*) and of *corticosteroids* (*cortisol*) are comparable. The stimulation of the hypothalamus → pituitary → adrenal axis in mammals matches its counterpart: cerebral chromaffin cells → hypothalamus → pituitary → interrenal in fish, etc. These neurological systems are considered equivalent and involve the same *neuropeptides*: *dopamine* (*DA*), *vasotocin* (*VTC*), *serotonin* (*5HT*), etc. The neurological bases of their spatial recognition in a representation of a map of their environment involving, in fish, the optical roof, the cerebellum and the amygdalan pallium are recognized as comparable and homologous to those of birds and mammals, confirming a remarkable unity of the world of vertebrates.

Bibliography: *Brain Res.Bull*., 2005, **66**: 277-281 & DOI:10.1016/j.brainresbull. 2005.03.021, *Fish*., 2003, **4**: 247-255, *J.Exp.Biol*., 2014, **216**: 4435-4442 & DOI:10.1242/jeb.091751, *J.Fish Biol*., 2014, **84**: 1748-1767 &

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### Memorization skills

Some writers have joked about the supposed "three-second duration of a goldfish's memory", suggesting that their memory skills are particularly limited. This is not the case, as has been demonstrated by various experiments of placing fish in often complex environments such as labyrinths in which they are supposed to find food or avoid predators. The duration of their learning varies by species, age and sex, but they still manage to keep accurately mapped images of their environment in memory. Recent sophisticated experiments on zebrafish *Danio rerio* have confirmed that they have a remarkable episodic memory, since they are able to remember *what objects* – colorful Lego figurines – *where, when* and in *what environmental context* they have previously undergone memory training. Such memory skills are quite comparable to those of pigeons and laboratory mice.

These abilities are significantly stimulated by physical activity, and the learning faculties of these zebrafish are faster (3 days in active individuals vs. 5 days in their congeners with reduced physical activity). The benefits of sport on mental health also affect fish. These zebrafish display such cognitive abilities that this fish was chosen for experimental studies in neurobiology, its genetic and physiological potential having strong homologies with mammals and justifying its choice as an experimental model.

Bibliography: *Anim.Cogn*, 2016, **19**: 1071-1079 & DOI:10.1007/s.1071-016-1014-1 *Behav.Proc.*, 2013, **100**: 44-47 & DOI:10,1016/j,beproc.2013.07.020, 2014, **106**: 1-4 & DOI:10.1016/j.beproc.2014.03.010, 2019, **158**: 200-210 & DOI:10.1016/j.beproc.2018.11.010

### Brain differences between the two sexes

Although the existence of a direct relationship between the volume and weight of the brain and actual cognitive abilities of the individuals tested has been questioned in mammals and in particular in humans, such a relationship has nevertheless been examined with some interest in fish.

An individual's possession of a "big brain" is *a priori* considered to offer an advantage because of the greater potential cognitive skills that it may confer, as has been demonstrated in the guppy *Pœcilia reticulata* comparing the performance of females with large brains and females with smaller brains, a difference in volume of about 10% in relation to their respective sizes, when tested on learning in experimental labyrinths in which they must teach themselves how to distinguish between two and four symbols – circles and black squares – to reach their food. The leaders among these have better abilities to recognize the symbols

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these complex habitats and to memorize the best routes to save their energy and collect the greatest benefits from them. This mental superiority of "big heads" with a larger optical roof* that would help store visual information is, however, balanced by lesser development of the digestive tract, which is shorter, and by lower fertility. The development of brain nerve tissues proves to be costly in energy; we witness a transfer of energy towards these at the expense of the digestive and gonadal tissues.

The size of the brain also conditions the respective behaviors of males and females of the guppy *Pœcilia reticulata* when exposed to a predator. Faced with the threat of a predator, the cichlid *Crenicichla alta*, guppies of the two sexes have different survival rates depending on the respective size of their brains: females with large brains have higher predation survival rates than females with small brains, as if they had superior cognitive skills enabling them to escape the risk of predation. These large-brained females carry out a longer inspection of the threat during a short-range approach, risky behavior that makes them bolder than females with small brains, and males who stay at a greater distance from this predator. Richer in colored pigments, these males are more vulnerable to predation, and their survival rate is lower than that of females with a duller color pattern and whose greater size and higher swimming speed are beneficial against predation. Such better-performing females better survive the risk of predation thanks to more developed optical lobes that promote better visual perception and a larger telencephalon* that increases their speed of decision-making. These females have superior cognitive abilities that enable them to better judge a dangerous situation while the males are more cautious, because they are exposed by their bright color patterns. Predatory pressure seems to favor brain evolution, following positive selection for females who are more gifted.

Other experiments, however, contradict this last interpretation concerning a supposed mental superiority of females. Orientation tests in complex labyrinths show males demonstrating an aptitude for correct orientation at the first attempt, while females are unable to do so after five attempts. Higher cognitive flexibility of males is common to vertebrates and related to the fact that they generally disperse more widely in spatially varied habitats, with higher abilities for environmental exploration than females. Can they however be qualified as "more gifted" and "cleverer" than females? We might often doubt it. Moreover, studies carried out by other researchers who test, on the same species, skills of learning to navigate in a labyrinth lead to a different conclusion: the females surpass the males, with 68% of correct answers on the first day and 80% on the fifth day, performances of which the males are not capable. This raises the question of different experimental conditions between the different teams of researchers.

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Females of the mosquitofish *Gambusia affinis* who undergo sexual harassment by males (Volume 2, section 1.2.3) develop a larger brain (+6% by weight) than their non-harassed counterparts, following some kind of development of a "social brain".

There have also been shown to be differential cell targets in the brain between males and females: neural receptors for *androgens* and *estrogen* are distinct in the ventral telencephalon and the pre-optic zone of each sex and respond differently to *sex hormones* produced by the gonads, respectively *testosterone* and *estradiol*, which would justify differential behavior controls between the sexes. Would differences between a male brain and a female brain be related to different motivations? Indeed, females are mostly concerned with food because of their production of oocytes rich in energy reserves that justify these trophic necessities. In males, these concerns are essentially sexual: the search for females.

Bibliography: *Anim.Behav.,* 2017, **123**: 53-60 & DOI:10.1016/j.anbehav.2016.10.026, **125**: 69-75 & DOI:101016/j.anbehav.2016.12.022, *Curr.Biol*., 2013, **23**: R63-R65 & DOI:10.1016/j.cub.2012.11.042, *Ecol.Lett*, 2015, **18**: 646-652 & DOI:10.1111/ele.2015.issue-7/issuetoc, *Proc.Roy.Soc.B*, 2012, **279**: 5014-5023 & DOI:10.1098/rspb.2012.2011, *The conversation,* 27-11-2016, 3p

### *Brain differences related to the physical and social environment*

The size and structure of the brain are strongly influenced by the complexity of the habitat, conditions of rearing, social status, etc., and such plasticity is appreciable between wild individuals and their counterparts originating in hatcheries. Therefore, among the *chinook salmon O. tsawytscha* in which two categories of males coexist, the dominant *hooknose** (Volume 2, section 1.2.1.3) possess a smaller brain relative to their body size than smaller *jacks** or *sneakers** whose brain size is proportionally multiplied by 2, as if there was a transfer of energy between somatic growth of the body and brain development, the latter being particularly energy-intensive. A bigger brain involving *a priori*, but not certainly, the possession of a larger number of neurons would assume, also *a priori*, superior cognitive abilities in *sneakers**. Should we see in this the behavioral differences related to access to mating, the small stealthy males that are the *jacks** having to be smarter to access females and be able to steal fertilizations (Volume 2, section 1.2.1) at the expense of the big, dominant *hooknose** males? It seems possible that reproductive behavior is correlated with the size of the brain.

Occasionally hatchery-reared individuals with rich and abundant food while living in the absence of predators have larger brains than their wild counterparts, who are sometimes subject to food scarcity and often face predation

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nurseries have an impact on brain development. Being well nourished and under-stressed during youth seems to constitute a factor favoring the development of a larger brain. The assertion that a large brain, with a difference of +9.3% in female guppies *Pœcilia reticulata*, may be correlated with greater cognitive skills has been demonstrated by some experiments, but has also sometimes been questioned. Indeed, captivity can be responsible for less brain development, –19% in the telencephalon* and –17% in the optical roof* of the guppy from the first generation maintained in laboratory breeding, compared with wild individuals. The telencephalon* is involved in spatial memory and the optical roof* in visual processes and sensory integration.

A similar phenomenon is known in domesticated mammals (such as sheep, cats, pigs and in farmed salmon) following neurogenesis, which is repressed by a particularly simplistic environment compared to the much more complex natural environments. The plasticity of the developing brain is correlated with the number of environmental stimuli, a highly structured living environment, rich in niches, promotes cognitive skills that are not provided by the unchallenging, bare and simple environment of captive breeding. Thus, transgenic* procedures applied to salmon *O. kisutch* lead to the development of individuals with high body growth who acquire maximum sizes much higher than those of natural individuals, but have less brain development than that of wild fish, with their optical roof* developed but their cerebellum smaller.

These data prove that brain morphology is correlated with environmental conditions, and the development of the brain, very plastic, is conditioned by the demands of the environment. The latter are far fewer in a nursery, which is much more barren than the more structured natural environment. Greater behavioral flexibility is also found in Atlantic salmon *Salmo salar* who are placed in a complex environment, compared to individuals located in a captive breeding environment. Their capacity for learning is greater, and their behavioral flexibility such as foraging, predator avoidance, grouping in schools, recovery from stress and social learning is considered superior when they develop in the natural environment. Captivity compromises the neural development expressed by a subexpression of the gene $NeuroD_1$ in the forebrain or pallium* of individuals grown in breeding conditions. Brain development is therefore conditioned by the importance of the richness of the environment in the early stages of smolt life, which induces neuronal complexity, particularly synaptic complexity, during early neurogenesis. An increase in the number of structures in breeding ponds is therefore recommended for fish destined for subsequent release into the wild in the context of restocking operations, in order to improve their learning and memorization abilities, which are demonstrable in a labyrinth and which are particularly useful for their survival.

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Certain toxic substances present in the environment, such as anthropogenic pollutants, have harmful effects on cerebral function, as in the case of *aluminum (Al)* which disrupts the cerebral plasticity of the Atlantic salmon *Salmo salar*, whose performance of movement through a labyrinth is lower than that achieved by healthy congeners.

Bibliography: *Anim.Behav.,* 2008, **76**: 911-922 & DOI:10.1016/j.anbehav.2008.02.017, 2013, **86**: e1-e3, e4-e6 & DOI:10.1016/j.anbehav.2013.07.011, *Canad.J.Fish.Aquat.Sci*, 2014, **71**: 1430-1436 & DOI:10.1139/cjfas-2013-0624, *Ethol.,* 2009, **115**: 122-133 & DOI:10.1111/j.1439-0310.2008.01585.x, *J.Exp.Biol*., 2013, **216**: 3148-3155 & DOI:101242/jeb.083550, 2014, **71**: 1430-1436 & DOI:10.1139/cjfas-2013-0624, *J.Fish Biol*., 2012, **81**: 987-1002 & DOI:10.1111/j.1065-8649.2012.03348.x, *Proc.Roy.Soc.B*, 2013, **280** & DOI:10.1098/rspb.2013.1331

### *Brain activity stimulated during the reproductive period*

The plasticity of the fish brain is demonstrated by seasonal variation in its weight, as in the round goby *Neogobius melanostomus* whose telencephalon* is heavier in the spring than in autumn and especially during the breeding season, as if love made them more intelligent.

Recall that the reproduction of fish is dependent on the neuroendocrine pituitary-gonad axis, with two cerebral *neuropeptides**, *gonadotropin-releasing hormone GnRH* and *arginine-vasotocin AVT* secreted by pituitary neurons* in the preoptic* area of the forebrain and involved in brain function controlling reproduction, via a cascade of endocrine events: *gonadotropins LH* and *FSH*, *sex hormones*.

The plasticity of sexual modalities is manifested in males who practice alternative sexual behaviors. If, in the molly *Pœcilia latipinna*, *sneaking** is correlated with an oversupply of small males (Volume 2, section 1.2.1), it is otherwise with the plainfin midshipman *Porichthys notatus*. In this species there co-exist large males who are courtiers and singers as well as builders of nests and guardians of clutches (type 1) and small male *sneakers** who do not sing, do not court and do not build a nest (type 2). The neurons of the former are larger and more active in the secretion of *neuropeptides** than males of the second type; in other words, there are two neuronal phenotypes which characterize two types of males with development benefitting the most creative among them.

These same brain *neuropeptides** also control sex changes (Volume 2, section 1.2.10). The regulation of the hypothalamus–pituitary–gonad axis via the action of neurons secreting *GnRH* is controlled by the brain genes *kiss1* and *kiss2* of

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*peptide* system* called *kisspeptin*, which is a key molecular system underlying mechanisms of reproduction, remembering that in both fish and humans, sexuality and reproduction occur first of all "in the head".

Bibliography: *J.Fish Biol.*, 2010, **76**: 161-182 & DOI:10.1111/j.1095-8649.2009.02496.x, 2014, **85**: 1785-1792 & DOI:10.1111/jfb.12507

### *Morpho-anatomo-physiological lateralization*

Laterality is defined as manifestation of the importance, right or left, given to the position, to the development of a morphological or anatomical structure and to the operation or preferential use of a limb, organ or part of an organ located to the right or left of the plane of symmetry. Such morphoanatomical laterality is well known in fish, also involving pigmentation, eye position, mouth shape, lateral line, development of paired fins, shape and position of nostrils as well as the shape, the situation and the development of internal organs or structures such as gonads, brain or otoliths. Flatfish like soles are undeniably the most characteristic in this field. Among the latter, two groups stand out: left-handed ones whose eyes are located on the left side of the head – Bothidae, Cynoglossidae, Scophthalmidae – and right-handed ones whose eyes are located on the right side of the head – Pleuronectidae, Soleidae. Within each species, some individuals may do not respect the specific and family type of laterality. Therefore, in the flounder *Platichthys flesus*, a typically right-handed pleuronectid, left-handed individuals are encountered. All studies of flatfish have shown that the otolith – the sagitta – on their upper ocular surface is less developed than that on the blind underside, for both right-handed and left-handed individuals, such asymmetry not exceeding 18% of the individuals examined. Differences also exist in the concentration of certain elements. For example, the right sagitta of the common sole *Solea solea* is richer in *lithium* (*Li*) and *strontium* (*Sr*) than the left in the north-west of the Mediterranean, and the functional significance of these differences remains unknown.

In round fish, the asymmetry is generally more discreet and mainly affects coastal and freshwater benthonectonic* species. An external asymmetry is well marked in the cichlids *Perissodus straeleni* and *Neolamprologus fasciatus* whose mouth is deviated to the right or to the left and in the largescale four-eyed fish *Anableps anableps* of Suriname whose penis, a modified part of the anal fin, is directed to the right or to the left, and the genital opening of the female is located on its right flank or on its left flank. This asymmetry must be taken into account during mating.

Scarification visible in females of the manta ray *Manta alfredi* is clearly lateralized, with 99% of cases involving the left pectoral fin as a result of bites

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dental dimorphism with a more developed cusp than females, and their teeth are functional only for copulatory purposes. It has been deduced that this perfectly stereotyped pre-copulation bite is intended to induce receptivity in the females.

Asymmetry in the number of pectoral fin radii varies according to strains of the rainbow trout *O. mykiss* and serves as a criterion for recognizing their origin. Fish in coral ecosystems are often affected by pectoral lateralization, which involves for example 78% of longfin mojarra *Pentaprion longimanus* from the Arabian Sea. From the anatomical point of view, mature gonads are often asymmetrical, as in grey mullets (Mugilidae) and *Aphanius* sp. (cyprinodontidae), and among silverside (Atherinidae) only one gonad develops, the right one, while in *Gambusia* sp., a single ovary results from the fusion of right and left ovaries. The shape of otoliths* is often used by fishers to discriminate stocks – populations – within a species for management. It would seem that non-lateralization of sagitta is the most frequent phenomenon, regardless of the systematic position or the ecological type of the fish. Right and left sagittas are similar in bluefin tuna, swordfish, barracuda, red mullet or golden sardinella, while lateralization has been highlighted in the herring *Clupea harengus* and the grey mullets *Liza ramada* and *Mugil curema* of both sexes. Local differences at sexual level were found in females of the annular seabream *Diplodus annularis* which exhibit otolith symmetry in the waters of Djerba and asymmetry in that of the Kerkennah Islands, while the males of the two Tunisian populations have asymmetrical sagittas.

Lateralization of the receptor organs of electrical sensitivity is observed in the Peters' elephantnose fish *Gnathonemus petersii,* which depends on their personality: "brave" individuals use their right hemisphere while the "shy" use their left hemisphere, unlike vision which is also lateralized, but invariably linked to the left hemisphere in all individuals.

We are still far from understanding the origin and the cost of such morpho-anatomical and functional lateralities that vary according to species, populations, individuals and sometimes even sex. Their genetic basis, the role of environmental factors and the composition of their diet are explored to better understand their likely impact on behavior.

Bibliography: *Biol. Letters*, 2009, **5**: 73, *Acta Icht. Piscat.*, 2015, **45**: 363-372, *Annales Hist. nat.,* 2011, **22**: 1-6, 2012, **22**: 83-88, *Aquat. Living Resour*., 2012, **25**: 27-39, *Cah. Biol. Mar*., 2014, **55**: 499-506, 2016, **57**: 214-227, *Can. J. Fish Aquat.Sci*., 1986, **43**: 1228-1234, 2015, **72**: 10-202016, **73** & DOI:10.1139/cjfas.2015-0332, *Cybium* 2015, **39**: 271-278, *Fish. Res*., 2013, **143**: 153-160, *Int. J. Mar. Sci*., 2016, **6** (37) :1-5, *Ital. J. Zool*. 2015, **82**: 446-453, *J.Fish Biol.*, 2015, **87**: 646-663 & DOI:10.1111/jfb.12746, 2016, DOI:10.111/jfb.131117, *Mar.Ecol. Prog.Ser*, 2016, **555**: 167-184, & DOI:10.3354/meps11784, *Vie et Milieu*,

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### *Lateralization of the brain*

Recent neurobiological studies have shown that fish have sensory and motor lateralization of the brain. In the zebrafish *Danio rerio*, left-right differences are identifiable at the level of the dorsal habenula*, which reflects differential abilities in processing visual and olfactory information that are very important functions in almost all fish. Activation of neural circuits and distinct neuronal targets in the brain would then condition some original behavioral programs. Several hundred neurons located in the right dorsal habenula* of this same fish may be visualized by fluorescence microscopy and their mapping has been established in 4D images. They are activated in response to olfactory stimuli – specific odors of *bile salts**. Individual differences in cerebral lateralization between males or females also result in a preference of optical involvement – left eye or right eye – and bodily positioning relative to a congener that is attacked during assaults, males having a tendency to favor the left eye and the left side. A partition of brain tasks between the two hemispheres of the brain has consequences for behavior and *fitness**, the most lateralized individuals having superior abilities over non-lateralized individuals in terms of learning skills, escaping predators and taking risks. This cerebral lateralization is clearly positive.

Cerebral lateralization, which is based on a partition of brain functions between the two hemispheres, is a ubiquitous function among vertebrates, and each hemisphere is specialized in the perception of sensory stimuli with a predominance of dominant perception by the right hemisphere – right habenula – of adverse stimuli. The right hemisphere specializes in negative stress-inducing emotions such as those related to predation threats. In fish who have eyes in lateral position, preference for specialized and asymmetrical observation of objects – prey, congeners, predators, etc. – is naturally strongly marked. It is dependent on local environmental conditions and the role of early experiences and is strongly influenced by the existence of predation threats induced by the secretion of *alarm substances* issued by congeners when attacked by a predator (Volume 1, section 3.2). Thus, the lateralized behavior of the convict cichlid *Amatitlania nigrofasciata* consists of a response to adverse stimuli favoring the nervous stimulation of its right hemisphere via visual perception by its left eye. Females have higher lateralized antipredation responses than males, possibly due to their sensitivity to lower concentrations of *alarm substances* and probably related to their dispensing of parental care (Volume 2, section 2.2.1). In addition to these inter-sexual differences in sensitivity, inter-individual differences – courage or fear – also exist: they are interpreted as differences of personality (Volume 2, section 3.7) which seem to be dependent on secretions of *dopamine* (*DA*) in the right lobe of the habenula. The responses of juvenile ambon damselfish *Pomacentrus amboinensis* when put in contact with a predator are strongly influenced by their degree of

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behaviors. Lateralization thus appears to confer an advantage in various situations, in particular knowledge of the environment and response to a risk of predation.

A natural solicitation of the left eye, therefore of the right hemisphere, which is reinforced by the presence of *alarm substances* has also been demonstrated in the *Pœcilia reticulata* and is seen as an effective way to increase vigilance and thus improve the chances of survival in a risky environment. However, when mosquitofish *Gambusia affinis* inspect a predator by approaching it, they prefer to observe it with their right eye, which supposes an inhibition of the natural reactions of fear and flight by the left hemisphere. Such superiority in anti-predator defense may be qualified by a lower capacity for intraspecific competition, as if there were a certain balance between the advantages and disadvantages of behaviors subject to different selection pressures.

Cerebral conditioning of the fear behavior of the larvae of zebrafish *Danio rerio* is dependent on a left-right asymmetry of the brain. Indeed, the nuclei of neurons located in the dorsal left side of the habenula attenuate immobilization reactions or freezing by stimulating the motor activity of swimming, and therefore flight, against a threat of predation. It is specialization of the left lobe of the habenula that determines the chances of larval survival by reducing by 2 seconds the duration of immobilization that occurs at the sight of a predator. Such cerebral asymmetry seems to be generalizable to all vertebrates, including humans.

In the guppy *Pœcilia reticulata* individuals who are raised from birth in the presence of chemical signals emitted by predators are more lateralized than those raised without these signals. Lateralization of the brain is therefore predictable in a risky environment. Does living dangerously also make one smarter?

However, there is a difference in brain size between the two sexes: in the presence of predators, the females have a larger brain, whereas the male brain is not affected by this predation pressure. Similarly, in the panamanian killifish *Brachyraphis episcopi*, neonates whose mothers were raised in high risk environments in the presence of predators have a more strongly lateralized brain with a strong tendency to turn left when encountering a new object, following stimulation of their right hemisphere, than those whose mothers lived in sites of low predation and who tend to turn right under the same circumstances. Such a particularly sensitive lateralization in males may seem derisory at the individual level, but may also have a vital value at the population level and lead to progress in the formation of well-coordinated and cohesive social groups that would have better tolerance for predation pressure than their counterparts with weak or no lateralization. This would be a hereditary advantage in *fitness** to both detect predators early and form anti-predation groups; a heritable lateralization, beneficial

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Visual laterality in the early stages of development plays a role in inducing lateralization of the brain of the guppy *Pœcilia reticulata*. Experiments performed on neonates who are confronted with asymmetric images stimulating either their right eye or their left eye determine their subsequent asymmetric behavior that depends on a cerebral counter-laterality – left eye-right brain and right eye-left brain – and generally promotes adaptation to local ecological conditions. Thus, a fish that lives in a river maintains its position and moves upstream or downstream by maintaining visual cues in relation to the banks along the stream, which enables it to save its swimming energy and to remain vigilant about the risks of predation, especially fish-eating birds. Most individuals naturally prefer to examine their congeners – social stimuli – with their right eye and predators with their left eye. On the contrary, following early stimulation of their left eye, they later use their right eye to examine predators. Such a distinction has important behavioral consequences for swimming in schools when they join their congeners, during mating when they examine their sexual partners and during their anti-predator defense. Correlations between visual lateralization and motor laterality are established during their early life and suppose the induction of an architectural organization of the brain. This demonstrates the plasticity of the brain.

Lateralization of the brain is manifested in scarlet soldierfish *Myripristis pralinia*, involving the unilateral visualization of congeners and their recognition during the early juvenile phases of development, involving their left telencephalon, as evidenced by a surgical removal of the latter which causes a loss of attraction towards congeners. This is a particularly useful skill during the recruitment phase (Volume 2, section 2.2.3).

Left-handed and right-handed individuals are both encountered among the cichlids *Perissodus straeleni* (Volume 1, section 1.2.2) and *Neolamprologus fasciatus* whose behaviors are strongly lateralized. The existence of variously lateralized morphs with respect to the position of the eyes in flatfish such as Pacific flounder *Platichthys stellatus*, with dextral forms with eyes positioned on the right side and senestral forms with eyes on the left side, involves sensory cerebral nervous controls – binocular vision – and different motors. Such asymmetry results in well-differentiated feeding behaviors and trophic strategies depending on the angle of attack of the prey. This polymorphism is not simply due to a mirror effect in these anatomical characteristics which have ecological incidences, the senestral characteristic increasing from 50% in California to 100% in Japan. The question of whether senestral forms are errors in the developmental program of a naturally dextrous species remains debated.

In the context of lateralized morphs, those affecting the genital tract are relatively frequent. In the big-scale sand smelt *Atherina boyeri,* only the right

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ovary is present and well developed. The same is true for certain populations of the toothcarp *Aphanius fasciatus*. In the Anablepsidae and Jenynsiidae, the gonopod and the genital opening of the females are directed to the right or to the left according to the individual. Another well-known lateralization is the opening of the mouth to the left or right in the cichlid *Perissodus microlepis* (Volume 1, section 1.2.1.7).

The natural lateralization of a species is likely to be modified by environmental factors and disturbed by anthropogenic changes. Therefore, the two-spotted goby *Gobiusculus flavescens* naturally adopts lateralized behaviors based on asymmetry in favor of the right, thus under control of the left brain. Such laterality is modified by exposure to high concentrations (1600 µatm) of $CO_2$ which causes a preferential inversion of certain movements to the left, thus under control of the right brain. Differential sensitivity to $CO_2$ occurs between males and females. It is not known whether this change in laterality is likely to affect, in the long term, the visual patterns of the species' anti-predator behavior.

This question of lateralization currently excites ichthyologists and justifies new research.

Bibliography: *Anim.Behav.,* 2007, **74**: 231-238 & DOI:10.1016/j.anbehav.2006.08.014, 2008, **75**: 2359-1366 & DOI:10.1016/j.anbehav.2007.09008, 2013, **86**: 617-622, 2016, **117**:3-8 & DOI:10.1016/j.anbehav.2016.04.011, 2017, **130**: 9-15 & DOI: 10.1016/j.anbebehav.2017.05.006, *Anim.Cogn*., 2016, **19**: 949-958 & DOI:10.10007/s10071-016-0995-0, 2017, **20**: 537-551 & DOI:10.10007/s10071-017-1081-y, *Curr.Biol.,* 2014, **24**: R285-R287, 2017, **27**: 2154-2162 & DOI:10.1016/j.cub.2017.06.017, *J.Fish Biol*., 2007, **71**: 737-748 & DOI:10.1111/1095-8649.2007.01531.x, *Proc.Roy.Soc.B*, 2015, **282**: 1132 & DOI:10.1098/rspb.2015.1132, *Roy.Soc.Open Sci*, 2018, **5**, 3 & DOI:10.1098/rsos.171550

### *Differences between selachians and teleosts*

Weight differences occur between the brains of teleosts and those of pelagic sharks*, yet their significance escapes us. What to think of the brain (1.42 g) of the striped marlin *Tetrapterus audax* compared to that (53.3 g) of the silky shark *Carcharhinus falciformis*, for body weights of 2.6 kg and 98 kg respectively? Encephalization quotients are found to range from 1.6–2.9 in selachians to 0.32–0.55 in teleosts. The pelagic selachian* brain (including sharks) is therefore more developed than the pelagic teleosts* (dolphinfish, tuna, marlin and sailfish): the telencephala and olfactory bulbs* are larger in the former, whereas the optical roof* prevails in the latter with significant individual variations. The strong migratory and predatory capacities of these large pelagics* have been linked to

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a great development of their telencephalon*. An "ecomorphology" of brains and different sensory strategies may thus be established.

Bibliography: *Anim.Cogn.,* 2015 **18**: 19-37 & DOI:10.1007/s10071-014-0762.x, *J.Fish Biol.,* 2006, **68**: 532-554 & DOI:10.1111/j.1095-8649.2006.00940.x

### 4.3.10. *Cerebral sexual dimorphism*

In the Uruguayan weakly electric fish *Brachypopomus gauderio*, breeding males exhibit a proliferation – a multiplication between 3 and 7 – of the brain nuclei involved in electrocommunication (Volume 1, section 3.1) which function as a pacemaker in inter-sexual communication and social signaling. Males thus have a boosted brain during the breeding season. A particularly complex system of specialized neurons in the peripheral organs of signal reception, then in the brain, would thus enable a certain decoding of the electrical messages received by these weakly electric fish.

Distinct cerebral lateralization between the sexes of the convict cichlid *Amatitlania nigrofasciata* (formerly *Archocentrus nigrofasciatus*) corresponds to negative stimuli (low trophic activity) in the right brain in males and positive feeding stimuli (higher activity) in the right brain in females. In the context of parental care (Volume 2, section 2.2.1), males prefer to be defenders and fighters, while females are more specialized in egg and larval care. A correlation was found between females' brain size and the quality of their parental care, as if looking after one's offspring required cognitive skills.

Bibliography: *Behav.Proc.*, 2009, **82**: 25-29 & DOI:10.1016/j.beproc.2009.03.005, *Biol. Lett.*, 2008, **4**: 338-340 & DOI:10.1098/rsbl.2008.0206, *J.Exp.Biol.*, 2011, **214**: 794-805 & DOI:10.1242/jeb.051037, *Proc.Roy.Soc.*, 2009, **76**: 161-167 & DOI:10.1098/rspb.2008.0979

### 4.3.11. *Forms of training*

Behavioral changes may result from interventions that have the value of training, such as during operations for tourism purposes of fish-feeding which have the aim, by feeding them, of attracting the fish to precise places where, stuffed with food, they lose their aggressiveness, like sharks transformed into "nice doggies". In a marine park in New Caledonia, spangled emperors *Lethrinus nebulosus* are thus faithful to appointments planned for the reception of tourists, from 11 am to 2 pm, in particular on public holidays and during the school holidays. This practice applies even to sharks. Such unnatural domestication is generally condemned by ethologists,

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In contrast, humans have increased, by selection of the most aggressive subpopulations*, the natural combativity of Siamese fighting fish *Betta splendens*. Some of these champions have become ruthless killers in deadly fights organized in the Far East. They have become circus beasts.

Bibliography: *Aquacult.*, 2007, **264**: 54-58*, Arch.Polish Fish.*, 2008, **16**: 453-457*, Can.J.Fish.Aquat.Sci,* 2015, **72**: 125-134, *J.Fish Biol.*, 2008, **72**: 1-26, 2014, **84**: 1527-1538, *J.Mar.Biol.Ass.UK*, 2008, **88**: 825-829, *Live Sci*.1/09/2005

### 4.3.12. *Really intelligent fish?*

The memory abilities of fish have been tested in various species such as zebrafish *Danio rerio* who respond to object recognition tests, especially involving geometric figures (squares, triangles, circles, crosses, etc.). Experiments with facilitating these skills involve the stimulation of their brain neuromediators *nicotine*. Inverse pharmacological effects were obtained with *scopolamine mecamylamine*.

Denial of the existence of real intelligence in fish is not only limited to the general public but also concerns a part of the scientific world, rooted in the very notion of evolution of vertebrates conceived as a linear progression from lower forms to higher forms, with the human species at its summit and fish inexorably located at the base of this system, and therefore unjustly considered primitive compared to so-called advanced forms. This rejection of the idea of cognitive differentiation among vertebrates follows strict respect for the notion of a relatively straight "evolutionary line", without taking into account the existence of various radiations rich in individual specializations. Everything happens as if the fish were locked in the "Linnaean system*".

Why stick to the idea that, because they are the oldest – the Devonian, 410 Myr* ago, being considered "the age of the fish" – they should remain confined to the bottom of the evolutionary ladder? Might we not also consider that this lapse of time of hundreds of millions of years, far from having frozen them forever in their primitiveness, has on the contrary given them more time to evolve and to adapt to the many ecological niches that they successfully occupy today? Moreover, the massive speciation* of African percomorphs dates back only 50 Myr* with a peak of diversity at 15 Myr*, which is almost at the scale of the evolution of primates and hominids.

The image of fish should not be limited to the idea that they are moved only by "instinct" and that their behaviors remain sadly limited by three seconds of memory, those attributed to the unfortunate goldfish. Rather, they should be viewed as

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some of which are even Machiavellian (Volume 2, section 3.8; section 3.9), combining an individual's potential for innovation with a certain respect for cultural traditions linked to social learning, which enables them to adapt often subtly. An intelligence that is both individual and collective or, perhaps, a particular form of intelligence is an "existential" intelligence.

In addition, the question asked about the cognitive abilities of teleosts can be extended to selachians (sharks, rays, torpedoes, etc.) and even to certain invertebrates (squid, octopus, bees, etc.) which, with nervous systems very dissimilar to each other, have sometimes very sophisticated cognitive potentialities. Thus, the ability to use tools (Volume 2, section 3.3), which is considered a mark of cognitive evolution, has been recognized in various families of teleosts (Labridae, Balistidae, etc.) as well as in elasmobranchs (freshwater rays), all endowed with a certain brain development. The debate about the existence of animal intelligence is still relevant.

A gap separates the popular perception of fish intelligence from scientific reality. Are not there 32,000 species inventoried today – and how many are still unknown? – a greater number than all other vertebrates combined, with a great diversity of occupation of ecological niches and an extreme variety of behaviors adapted to them?

Finally, it is now admitted that the brains of fish, although deprived of a neocortex, but which can nevertheless perform common functions, are much more comparable to ours than what has been commonly considered until now.

Jonathan Balcombe published in 2016 a book entitled *What a Fish Knows*, in which he says that some fish are cleverer than reptiles, birds and even large mammals. He thus evokes, as arguments, the case of gobies that display a topographical memory of the beaches on which they jump from pool to pool and find their habitat between tidal cycles, and especially that of wrasses of the genus *Chærodon* who, according to an observation of G. Bernardi in 2009 in the Pacific, carry clams with their mouth (over about 30 m) to break them by throwing them onto rocks. Tool use is an argument that seems convincing. A new compelling argument concerns a recently established comparison between a fish, the bluestreak cleaner wrasse *Labroides dimidiatus* and a primate, the capuchin monkey *Cebus (Sapajus) apella*, both subjected to comparative multiple-choice foraging tests based on visual cues relating to the shape, color and spatial arrangement of receptacles containing food. Performances in recognizing paths to success following training are at least identical between the two vertebrates tested, and it even happens that the fish discovers the food source more quickly than the primate.

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It is now clear that some fish provide evidence of individual intelligence well above the – weak! – credit that we usually give them.

Bibliography: *Anim.Behav.*, 2016, **119**: 189-199 &
DOI:10.1016/j.anbehav.2016.06.023, *Anim.Cogn.*, 2015, **18**: 1-17 &
DOI:10.1007/s10071-014-0761-0, *Fish.Fish*, 2003, **4**: 199-202,
*Progr.Neuro-Psycho-Pharm.biol.psychiatry*, 2014, **55**, 3: 80-86 &
DOI.org/10.1016/j.pnpbp.2014.03-010

### 4.3.13. *Remarkable cognitive skills in sharks*

Sharks have long suffered from a disastrous reputation, that of killing machines deprived of all sense and all mental capacity, reduced to the pejorative name *Jaws*. The discovery of the nervous system potential of both pelagic* and benthopelagic* species endowed with large brains, and the progress of knowledge related to their neuro-eco-ethology have led to the conclusion that *Jaws also has brains*. The gray bamboo shark *Chiloscyllium griseum* has been experimentally tested for its ability to move and orient in mazes as well as 2D geometric image recognition – squares, triangles, circles, rhomboids, etc. – as well as those of various objects and categories of objects and symbols. After a brief period of learning, three sessions are sufficient; it distinguishes between an image of a fish and that of a snail when presented in the form of black drawings on a white background, white on a black background, photographs or animations. Any image of a fish, regardless of the species represented, its shape, its size or its color, is perceived in the category "fish". Such mental categorization is comparable to the performance of humans, monkeys and birds, and these abilities are useful for the identification of prey, predators, congeners and heterospecific individuals. Its ability to perceive and prefer symmetrical objects is greater than that cichlids *Pseudotropheus* sp. tested. The recognition by these selachians of symbols and images constituting optical illusions is comparable to that of teleosts and mammals.

Neurobiological and neurophysiological comparisons between fish and mammals are sometimes difficult to establish, given the very large difference between the number of scientific studies conducted on each of them. The studies conducted on mammals are infinitely more numerous than those based on fish, because large sharks cannot easily be kept under laboratory conditions. small-spotted catshark *Scyliorhinus canicula*, which is easier to raise in the laboratory, has demonstrated an ability to distinguish electrical signals of anthropogenic origin from bioelectric signals emanating from prey, memorizing

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them for up to 3 weeks. Comparisons are also made concerning the question of the controversial notion of animal suffering (Volume 2, section 4.1).

Bibliography: *Anim.Cogn.*, 2014, **17**: 1187-1205, 2015, **18**: 463-471 & DOI.10.10007/s10071-014-0815-3, 497-507 & DOI:10.1007/s10071-014-0818-0, *Curr.Biol.*, 2014, **24**: R942-R956

### 4.3.14. *Fish as victims of optical illusions*

Fish trained to recognize geometric figures based on their length, their width or their diameter can be victims, as are birds (chickens, pigeons, etc.) and mammals (chimpanzees, horses and humans) who have been tested, of visual illusions related to distortions caused by contrasts surrounding the central image. Therefore, the tropical goodeid redtail splitfish *Xenotoca eiseni*, just like higher vertebrates subjected to the same tests, is a victim of *the Ebbinghaus illusion*, which consists of believing that a central disc surrounded by small discs appears larger than a disc of identical size surrounded by large discs. This same fish trained to discriminate two lines of different length is victim of the same optical illusion as humans when these lines are accompanied by the signs ⊩⊣, – > or – <. This so-called "*Müller-Lyer*" illusion supposes the existence of mental mechanisms of visual perception which integrate in a common way the signals of visual stimulation, in the same way as the geometrical *Ebbinghaus illusion.* These identical deceptions of fish and mammals involve comparable mechanisms of cerebral interpretation of visual images that provide a means of comparing visual systems and their cerebral organization in the evolutionary series of vertebrates.

Bibliography: *Anim.Cogn.*, 2015, **18**: 533-542 & DOI.10.10007/s10071-014-0821-5, 2016, **19**: 123-132 & DOI:10.1007/s10071-015-0917-6

### 4.3.15. *Recognition of human faces*

Some fish seem capable of amazing performances in their ability to recognize and memorize images. For example, a team from Oxford University recently revealed that the spotted archerfish *Toxotes chatareus*, in addition to its talents as a blowgun hunter (Volume 1, section 1.2.2) which demonstrate a keen sense of visual observation, are able to recognize human faces, and even up to 44 different faces that are presented to it by digital images above it aquarium, which gives rise to a reward for a correct answer. Discrimination between frontal views of human faces is all the more remarkable that it can be successfully performed after rotation of the images by more than 90°. Such skills are put at the service of its hunting strategy.

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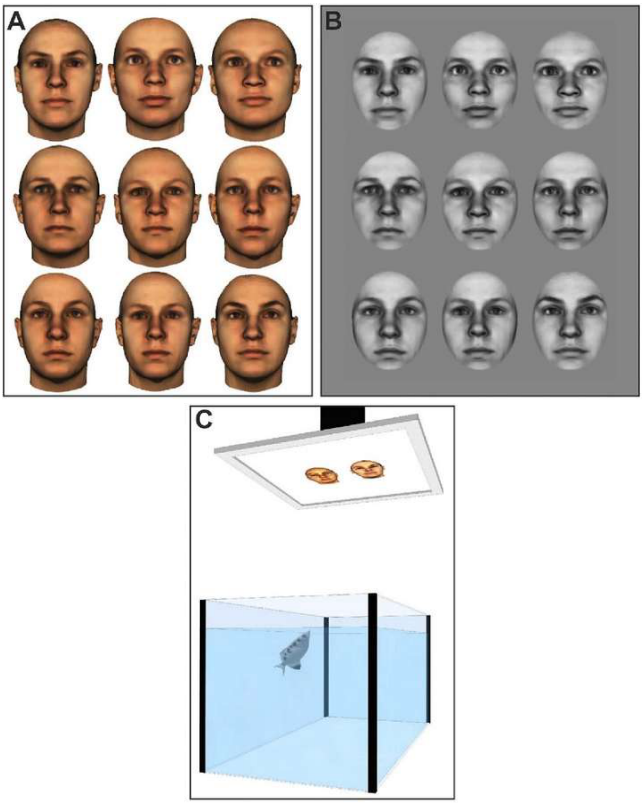



**Figure 4.5.** *Facial recognition test (top) in the spotted archerfish Toxotes sp. when projected above its aquarium (bottom) (source: Wasserman, Learn. Behav., 2016, p. 44,307)*

Such abilities, both visual and mental, involve neural mechanisms that may be common to a number of vertebrates and not specific to humans, in which they play an essential social role –an unsuspected performance as a physiognomist.

Mammals, hitherto tested to be capable of a similar performance – dogs, horses, cows, sheep, etc., who recognize their owner – have a neocortex, which may explain why a face whose image is particularly complex with two eyes, a nose, a mouth, etc., is correctly discriminated. It may seem surprising that fish that lack a neocortex can, however, perceive the same subtleties and are endowed with the same degree of sensory precision. When will archerfish detect professional cheats in casinos and potential terrorists at airports?

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### 4.3.16. *Sensitivity to music*

It has been amply demonstrated that making music and listening to music is a source of relaxation and enjoyment, following activation of reward circuits that generate *dopamine* (*DA*) secretion in the human species. The soothing effect of music has been applied to some animals, including cows, who increase milk production in barns with equipment for playing soft music, pigs and chickens, reducing the negative effects of farming stress.

Fish are also sensitive to listening to anthropogenic musical sounds. In intensive breeding of European sea bass *Dicentrarchus labrax,* of gilt-head *Sparus aurata* and of carp *Cyprinus carpio*, the diffusion of music in pools, lasting 30 minutes at 90 minute intervals, induces improvements in growth performance due to reduced stress – measured by rates of *dopamine*, *serotonin* *catecholamines* – responsible for energy losses caused by conflicts related to competition for space and food. Music soothes their social behavior. Some fish are also very eclectic, enjoying *Frère Jacques* as much as a Mozart symphony, *Eine kleine Nachtmusik.* More recently, researchers at the University of Tokyo have conducted tests that tend to prove that goldfish *Carassius auratus* are able to tell the difference between Bach's music (*Toccata in D minor*) and Stravinsky's *The Rite of Spring*). Organizations that can appreciate music can, of course, be anything but not stupid. Note, however, that the "musical sense" of the goldfish is limited to a simple discriminative value for obtaining a food reward during tests of choice, without implying a real artistic preference, because they clearly avoid all noisy stimuli.

It should also be remembered that fish are themselves sometimes musicians and singers who produce sounds by various mechanisms (Volume 1, section 3.1). These sounds are modulated according to their frequency, their intensity, duration and repetitiveness, and induce behavioral responses from receptive individuals, especially during courtship behavior (Volume 2, section 1.1.3). Thus, the female grass goby *Zosterisessor ophiocephalus* is charmed, and then attracted by the song of a male of her kind, but she is also sometimes frightened by him.

Bibliography: *Anim.Cogn*., 2014, **17**: 55-65, 2015, **18**: 19-37, 72 &
*Anim.Learning.Behav.*, 2001, **29**: 353, *Aquacult. Engineer*., 2007: 61-336
DOI:10.1016/j.aquaeng.2006.07.001, *Behav.Proc.*, 2013, **99**: 26-33 &
DOI.org/10.1016/j.beproc.2013.06.009, *J.Fish Biol*., 2008, **73**: 9801004 &
DOI:10.1111/j.1095-8649.2008.02001.x, *Scientif.Rep*., 2016, **6**: n°27523 &
DOI.10.1038/srep27523

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### 4.3.17. *Active embryonic and/or larval ontogenesis* or neurogenesis*

Neurologists are interested in cellular and morpho-anatomical processes during brain development. Therefore, in the green terror cichlid *Aequidens rivulatus,* immunocytochemical monitoring of early neural cells during larval life shows the existence of a cell strain called *neural stem–progenitor cells* (NSPCs) present telencephalon, the optical roof and the cerebellum. These cells have strong capacities for proliferation, then for differentiation into glial cells or astrocytes and neuroblasts which develop into neurons. A very active larval neurogenesis. One-week-old larvae of the zebrafish *Danio rerio* are already able to perform complex innate movements involving their visual system and cerebral connections, and their brains of less than 1 $mm^3$ volume already are rich with 100,000 neurons. The structural and functional organization of the oculomotor nervous circuits, built on a model common to vertebrates, is accessible in MRI imaging because of the absence of cranial box and pigmentation in a nacre mutant, which enables a fine mapping of the nervous networks of the optical roof stimulated during capture of prey or escape from a predator. It is a particularly interesting model and evidence of early and already successful neurogenesis. Fish that never cease to amaze us. Fluorescent scanned images of vestibular neural networks stimulated during the swimming activity of larvae of the zebrafish provide direct evidence of early neuronal activity. Precious imagery of brain scanning.

Bibliography: *Curr.Biol*., 2016, **26**: R377-R385 & DOI:10.1016/j.cub.2016.03.054, 2018, **28**: 23: 3711-3722 & DOI:10.1016/j.cub;2018.09.060, *J.Fish Biol*., 2017, **90**: 205-221 & DOI:10.1111/jfb.13170

### 4.3.18. *The certain existence of collective intelligence*

If the notion of individual intelligence is still debated in fish, as we have just mentioned, that of a collective intelligence is widely recognized among them. The advantages conferred by grouping into schools have been treated previously (Volume 1, section 3.3).

Groups of fish are more capable of solving cognitive tasks than isolated individuals, and the solutions, in terms of food detection (“many eyes”) or protection against predators (greater vigilance), are directly correlated with the number of individuals participating in a shoal the more numerous the constituents of a community, the faster the information flows between them, the richer the network of centralized social interactions, the better the collective response and the cognitive performance of the community.

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Such a form of *swarm intelligence* is well known in various zoological groups: insects such as ants, bees, wasps, and also birds such as crows and mammals such as rodents. It has been demonstrated experimentally in the laboratory, for example in green damselfish *Chromis viridis*, the mosquito fish *Gambusia affinis* or the *Pœcilia reticulata*, and has highlighted the benefits of integrating sensory information (vision, olfaction, hearing, mechanoreception, etc.) from multiple individuals which circulates between them to solve behavioral problems. This collection of social information is based on "reciprocal altruism" and a "pool" of collective skills.

Bibliography: *Behav.Proc.*, 2017, **141**: 141-151 & OI10.1016/j.beproc.2016.10.005

Recent neurological evidence indicates the relative organic proximity of all vertebrates, in which neuroendocrine and nervous mechanisms are fairly common and basic because of their close phylogenetic links.

Fish, far from being the "poor relatives" of the world of vertebrates in the behavioral domain, occupy an interesting place which, instead of being the last, far behind birds and mammals, also deserves to be considered as "the first" in terms of seniority, precocity and anteriority. Have fish finally been rehabilitated?

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# Conclusion

The review of the various and numerous behaviors presented in this book can only convince us of the remarkable "adaptive abilities" of fish who have been able, over successive generations and regardless of the climatic changes and the tectonic upsets occurring in the times they have lived through, to find morphological, anatomical, physiological and behavioral "solutions" in order to survive and make the most of the potential offered by their environment.

We also have evidence of their contemporary adaptability as in the case of a small cyprinid, the bullhead minnow *Pimephales vigilax*, which successfully responded to selection pressures imposed by the construction of a hydroelectric dam on an American watercourse, with organic and swimming behavioral changes resulting from the disappearance of a hydraulic current that was present for the first 15–20 generations. Recent "innovative" behaviors have been described in tiger *Hydrocynus vittatus* in a lake in South Africa, who hunt swallow (Volume 1, section 1.1.2), and wels catfish *Silurus glanis* who, at Albi, became, in a few years, adept at hunting pigeons in the Tarn River (Volume 1, section 1.1.2).

Fish, besides being able as our "distant ancestors" to offer us "life lessons" related to their seniority and their experiences acquired and perpetuated since their appearance 500 Myr ago, can contribute significantly to better situating ourselves in the dynamic scale of the evolution of animal species. They can also help us solve some biotechnological problems if we know how to draw on their "know-how", such as when developing procedures for palpation by robots similar to the operation of the pectoral fins of the bluegill *Lepomis macrochirus*, or during the manufacture of swimsuits copying the modalities of hydraulic friction in contact with a liquid element, based on the model of sharks' skins. In addition, some common biomolecular and cellular mechanisms that we share may inspire therapeutic research. For example, the emission–reception mechanisms of the electrical

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functions: those controlling the composition of intestinal flora (microbiota*) whose dysfunctions or dysbiosis cause serious disorders, those related to neurogenesis and brain interpretation of visual images (scanned images, optical illusions) and finally those involved in carcinogenesis and in various human pathologies.

Today, the danio or zebrafish *Danio rerio* is used as a universal laboratory animal (*mouse fish*). It constitutes an ideal model for understanding certain cellular mechanisms involved in embryonic development, particularly neurogenesis and the establishment of laterality. It has played a role in the understanding of certain immune mechanisms (B and T lymphocytes), and the latter are active in leukemia, in carcinogenesis and in the analysis of responses to drug treatments for cancer control. It has given rise to a vast medical scientific literature: more than 30,000 articles from 1995 to 2017.



**Figure C.1.** *Zebrafish or* Danio rerio*, a laboratory model. For a color version of the figures in this book see www.iste.co.uk/bruslé/fish2.zip*

Multiple biomedical abilities have been detected in this fish, such as the ability to repair spinal cord lesions from glial cells that have seven genes coding for a *protein CGTF* that regenerates tissue. As humans share 90% of their genes with this zebrafish which has 26,000, it is hoped that a research program may lead to the repair of certain lesions of the cerebrospinal axis in humans. It has revealed other interesting abilities, such as the possession of glial cells in its retina, called Müller cells, which can differentiate into nerve cells (rods and cones) subsequent to an eye injury. Could such regenerative potential be scalable to the treatment of human degenerative eye disease (AMD, retinitis)? It also serves as a very good model for the study of certain psychiatric disorders (depression, autism, schizophrenia, etc.).

More anecdotal was the production, in Singapore in 1999, of the first transgenic fish from the zebrafish, the *Glofish*, fluorescent under UV light, following

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the incorporation into its genome of the EGFP gene from a green fluorescent jellyfish. This "*Frankenstein fish*" was a hit with aquarists all over the world. More original is the quite surprising discovery of "zombie genes", 548 genes which are activated at the death of the fish for 4 days *post-mortem*, which is interpreted as a desperate attempt of the organism to survive following a lack of *oxygen* and energy.

The zebrafish may undoubtedly be considered the champion of "cellular and molecular ethophysiology".

Finally, it should be noted that the relationships between humans and fish have, since their natural cohabitation in the Quaternary period, been clearly conflictual, and fish are victims of our fishing operations – and even *overfishing* – as well as the anthropogenic degradation of their natural environments and poisoning by pollutants, not to mention the introduction of new and "invasive" species which are sometimes formidable and decimate the "native" populations. Humanity has often appeared as an enemy of nature and a dangerous opponent of fish, to the point that some have wondered about their possible coexistence.

However, we do not always behave like predators, destroyers of their habitats and disturbers of their ecological balances: we also happen to be, more or less, their benefactors, etc. Cases where humanity can be cited for our interventions in favor of fish are not so rare: access to new seas such as the Lessepsian* migrations into the Mediterranean linked to the opening of the Suez Canal, the protective effect of marine reserves such as that enjoyed by the dusky grouper *Epinephelus marginatus* on the French coasts of the Mediterranean, the artificial creation of new microhabitats resulting from various coastal developments – harbors, artificial reefs – which benefit, for example, four species of sars *Diplodus* sp.

Maybe humanity is not so bad as our ugly reputation suggests? And what about the application of various genomic techniques – choice of strains, interspecific and intergeneric crosses, selection, monosexage, transgenesis*, etc. – to farmed fish in order to improve their survival, growth and reproduction performances, with some projects even proposing "to adapt fish to a changing world" (*sic*)? And what about the generosity from the human species, or treacherous games of "sorcerer's apprentices", particularly Machiavellian and maleficent for both fish and humanity?

Fish behavior studies have focused on more than 600 species. It should be noted, however, that experimental laboratory studies have involved only a small number of species: zebrafish *Danio rerio*, the "famous" guppy *Pœcilia reticulata* (referring to Dr. Guppy, its "discoverer" in Trinidad in 1866) and other small poeciliids such as the mosquitofish *Gambusia affinis*, because of their ease of breeding in

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The results of some of these studies are diverse and sometimes even contradictory depending on the species and strains chosen, the age and sex of the individuals tested, the conditions of the experiment conducted (season, temperature, lighting, diet, etc.), without forgetting the existence of possible subjectivity among the experimenters.

The authors of this book have endeavored to report, as closely as possible, the data collected in the international scientific literature without prejudging possible errors made by some of the scientists who authored these publications.

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# Glossary

**µA:** microampere.

**µm:** micrometer.

wavelength.

**m:** ohm-meter.

**Abduction–adduction:** abduction is a movement that moves a structure (a member) away from the midline of the organism, while adduction: is the opposing movement that moves a part of the body closer to the midline.

**Adipocytes:** are connective tissue cells specializing in storing fats.

**Allele:** is one of the possible forms of a gene. There may be several alleles that have the same position (locus) on homologous chromosomes. All alleles have the same function but their modes of expression are different.

**Allochthonous:** species originate from a place other than where they have been found (not indigenous).

**Allometry:** is a phenomenon in which the general shape of an individual changes according to their size during their growth, or the relative proportion of certain parts of the body changes according to size or age.

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**Allopatry, allopatric:** refers to two populations of the same species that occupy different geographical areas and between which there is no (or very little) exchange of individuals (opposite: sympatry).

**Amino acid:** is the constituent element of proteins. It is an organic molecule that contains at least one carboxylic group and one primary amino group (e.g. leucine, lysine).

**Amphidromous:** refers to an organism with the ability to live in two different environments.

**Amphihaline:** refers to a living being that is able to occupy waters with differences in salinity (moving from fresh water to marine water and vice versa).

**Anadromous:** indicates a migratory marine fish that swims across rivers to reach its freshwater spawning area.

**Anadromy:** is the act of going up a watercourse to reach one's spawning area.

**Anaerobic:** refers to an organism that grows in an oxygen-free environment. It is also used to refer to a non-oxygenated environment.

**Anamniotes:** are vertebrates characterized by the absence of an amnio duringembryonic stage (amnion: the innermost of the embryonic membrane of reptiles, birds and mammals).

**Androgenesis:** is the development of an egg solely from the male pronucleus (synonym: male parthenogenesis).

**Android:** indicates what is in human form; etymologically means "resembles a

**Aneuploidy:** describes a species having a chromosome number in a cell, that is not an exact multiple of the usual haploid number (haploid is the condition of a cell having one set of chromosomes, diploid having two sets of chromosomes).

**Anisogamy:** is a means of fertilization involving two gametes of different sizes.

**Anophthalmos:** is the absence of one or both eyes.

**Anosmic (synonym: anosmatic):** refers to organisms without a sense of smell.

**Anoxic:** condition of an environment where there is no molecular oxygen (O2).

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**Anthropogenic:** results from human action.

**Antibody:** is the serum immunoglobulin synthesized by plasma cells that are immune cells.

**Antigen:** is any substance capable of triggering an immune reaction (secretion of specific antibodies).

**Aphotic:** refers to an environment that is not illuminated.

**ATP:** adenosine triphosphate, the "energy fuel" of the cell produced by mitochondria.

**Atretic, atresia:** refers to degenerating cells, such as oocytes in an ovary.

**Audiogram:** refers to a graph that makes it possible to visualize the hearing ability of a subject.

**Automixis:** is the fusion of two haploid nuclei derived from the same cell. This is observed in the case of the fusion of a sex cell with one of its polar bodies.

**AVT:** arginine vasotocin hormone.

**Azoic:** refers to the deprivation of all animal life.

**Bathybenthic:** species live on the bottom in the bathyal zone (from a depth of 1,000 to 4,000 m)

**Bathymetry:** is the science of measuring depth.

**Bathypelagic:** refers to organisms in open water occupying a deep zone known as the "bathyal" zone. The marine area is located between –600 and –2,000 meters.

**Benthic:** refers to an organism that lives on or near the bottom.

**Benthonectonic:** species live on the bottom and swim near the bottom.

**Benthopelagic:** species move between the surface and bottom of the sea, lakes or rivers.

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**Benthophagous:** species feed on organic matters living on the bottom (algae, animals, etc.).

**Bile salts:** are also known as bile acids, which are formed by cholesterol derivatives and acid steroids secreted by the liver and are present in the bile.

**Bioconcentration or bioaccumulation:** is a process in which a substance in an environment is absorbed and stored in a living organism, with the quantity of stores potentially increasing along a food chain.

**Bioluminescence:** is the process of producing biological light; some living beings produce the so-called biological light.

**Biomagnification:** is the process of toxins, which have entered waterways, moving up the food chain in increasing concentration for species higher up in the food chain.

**BL:** body length.

**Bloom:** refers to plankton proliferation.

**Branchiospine:** refers to the gill spine at the base of the gill arch and part of the "gill filter", which is particularly developed in plankton-feeder species.

**Canopy:** is a roof like covering or anything that seems to cover.

**Carotenoids:** are any terpene fat-soluble pigments (including carotenes, xanthophylls and vitamin A).

**Catadromy:** refers to the behavior of catadromous organisms, i.e. animals (fish) living in fresh water and migrating (outmigrating) to reproduce at sea.

**Cercaria:** is the larval form of parasites of digenous trematode worms.

**CGPM:** CGPM = GFCM: Commission générale des pêches pour la Méditerranée = General Fisheries Commission for the Mediterranean.

**Chorion:** is the outer envelope of the oocyte with an opening or micropyle through which the sperm enters.

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**Chromaffin tissue:** is the tissue composed of chromaffin cells located in the sympathetic lymph nodes and in the center of the adrenal glands. Within the adrenal medulla zone, chromaffin cells store hormones (adrenaline, dopamine and noradrenaline) that are released during stress, pain, etc.

**Chromatophore:** is a cell containing a colored pigment (chroma): melanin, guanine, carotenoids, etc.

**Circadian rhythm:** is a natural, internal process regulating the sleep-wake cycle, repeating it roughly every 24 hours.

**Clone:** is a group of individuals with the same genetic characteristics.

**Cnidocytes:** are explosive cells containig one secretary organelle (toxin) fiondin Cnidaria ( anemones, jellyfish, etc.).

**Collagen:** are fibrous glycoproteins synthesized by connective tissue cells.

**Colloids:** are colloid gelatinous or mucinous substances, with particules of 1 to 1,000 millimicrons dispersed within a continous medium.

**Commensalism:** is a type of relationship between two living organisms in which one organism benefits from the other without harming it.

**Cone:** is a photoreceptor cell of the retina with a conical outer segment. Cones are responsible for color vision and operate in bright conditions.

**Craniata:** describes species with a cranium.

**Cryogeny, cryogenics:** is the production of low temperatures (below –150°C or 120 K) in order to keep tissues or organisms alive.

**Cryopreservation:** is a technique of preservation at very low temperatures (freezing).

**Crypt (ovarian):** is the invagination of the ovarian cavity that allows the storage of sperm in species practicing internal fertilization.

**Cryptic:** means “hidden”, which refers to a behavior of dissimulation in holes and crevices of the habitat.

**Cuspid:** is a projection, point on the teeth or the scales.

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**dB:** decibel, which is a unit of magnitude that reflects the sound level of an environment.

**Demersal:** refers to a species living near the bottom of the sea.

**Dendrite:** is the cytoplasmic branching of a neuron that receives nerve impulses and guides it to the cellular body.

**Desmosome:** is an intercellular protein structure whose role is to hold two neighboring cells together mechanically.

**Detritivore:** describes the diet of organisms that feed on non-living organic matter or that refers to organisms that consume detritus or debris from dead organisms.

**Diadromous:** animals migrate between fresh and salt water.

**Diandria:** refers to the presence of two male categories in a population.

**Dichromatism:** indicates the vision of colors where only two types of colored receptors exist.

**Diploidy:** is the condition of a cell or organism that has two sets of chromosomes.

**DNA:** deoxyribonucleic acid.

**Dopamine:** is a catecholamine, which functions as a neurotransmitter and precursor of norepinephrine and adrenaline.

**Echolocation:** is the system of tracking by reception or perception of waves emitted or reflected by obstacles (prey, opponents, etc.).

**Ecomorph:** is a variety of species whose appearance is determined by their ecological environment.

**Ecosystem:** describes a community of living organisms interacting with the nonliving components environment.

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**Ecotype:** describes a subspecies or a population with inherited characteristics resulting from adaptation to a particular habitat (limnetic, benthic, etc.).

**Ectoparasite:** is a parasite that develops on the outer surface of its host's body.

**Ectotherm:** refers to an animal that does not maintain a constant temperature and whose value reflects that of the environment.

**Endemic:** refers to a species that occurs only in a well-defined area.

**Endotherm:** refers to an animal that maintains a constant temperature despite variations in the temperature of its environment.

**Enzyme:** is a protein substance that accelerates (catalyzes) biochemical reactions.

**EOD (Electric Organ Discharge):** is the discharge from the electric organs of electric fish (electric rays, mormyridae, etc.).

**Epibenthic:** refers to an organism living on the surface of a soft or rocky substrate at the bottom of an aquatic biotope.

**Epibiont:** is an organism that lives on the surface of another living organism.

**Epifauna:** is an aggregate of animals that live on the surface of the bottom of the sea, lake, river or on other organisms.

**Epigated:** refers to a living being that lives on the surface of the ground.

**Epigenetics:** refers to the development conditioned by environmental factors (temperature, salinity, light, habitat, etc.) that purely dominate genetic factors.

**Epilithic:** is an organism growing upon stone or stonelike material.

**Epipelagic:** refers to a species that occupy the upper edge of a body of water.

**Epiphyseal:** is the end of a long bone that is originally separated from the main bone by a layer of cartilage.

**Epiphyte:** is an organism that grows (fixed or not) on plants.

**Epithalamus:** is the dorsal part of the diencephalon, as opposed to the ventral hypothalamus.

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**Euryphagous:** refers to an organism with a broad diet. Species with omnivorous or polyphagous regimes are euryphagous.

**Eutrophication:** is the enrichment of waters with nutritive mineral salts (nitrates, phosphates, etc.), causing the proliferation of algae and higher aquatic

**Exophthalmos:** is the anterior extrusion of the eye out of the eye socket.

**Exundation:** is an overflow.

**Eyespot:** is a circular-shaped spot.

**Fatty acid:** is an organic acid with a hydrocarbon chain that consists of an even number of saturated or unsaturated hydrophobic carbons.

**Fishery:** is an occupation or place devoted to catching aquatic animals.

**Fitness:** refers to the successful adaptation of a population to a given environment in terms of survival, growth and reproductive potential.

**Flooding:** is the act of leaving the water by withdrawing or evaporating from a flooded area.

**Free radicals:** are unstable chemical molecules produced in small quantities by the body. They are mainly synthesized in the cell during reactions with oxygen. They are considered one of the causes of tissue aging.

**GABA:** Gamma-Amino-Butyric-Acid, acts as an inhibitory neurotransmitter.

**Globule:** is a cell of the blood (white, red globule) or a small haploid cell resulting from meiosis of an oocyte (polar body).

**Glycolysis:** is the enzymatic degradation of glucose.

**Glycoprotein:** is a compound that results from the combination of a protein and a carbohydrate group.

**GnRH (Gonadotropin-Releasing Hormone or gonadoliberin):** is a hormone secreted by the hypothalamus that stimulates the synthesis of gonadostimulin

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**Gonoduct:** is a duct from a gonad (oviduct or spermiduct).

**Gonopod:** in males, the external genital appendix is involved in copulation for the transfer of sperm into the female's genital tract.

**Gonopore:** refers to the genital orifice.

**Granulocyte:** is a white blood cell, also called a polynuclear cell (because it was thought to have several nuclei).

**GSI:** gonadosomatic index (see GSR).

**GSR:** gonadosomatic ratio (ratio of gonad weight to body weight), also called GSI (gonadosomatic index).

**Guanine:** is the nitrogenous base contained not only in nucleotides (base units of the DNA and RNA molecules) but also, among other things, in guano.

**Gynogenesis:** is the process of uniparental reproduction (form of parthenogenesis) from a single oocyte activated by a spermatozoon whose role is limited to the supply of sperm, with its chromosomes not forming part of the egg's chromosomal lining.

**Habenula:** is a tiny region in the epithalamus of a brain known for its role in the anti-reward system.

**Hair cell:** is a sensory receptor, cell with many cilia that protrude from the apical surface.

**Haline:** water describes water that contains dissolved salts (syn. salinity).

**Haploid:** a cell is haploid when it contains a single copy of chromosomes (N chromosomes) and diploid if it has duplicate chromosomes (2N chromosomes).

**Helper:** can refer to a non-breeding fish participating with parents (same species) in the breeding of their offspring.

**Hematocrit:** is the volume occupied by red blood cells in relation to the quantity of whole blood (red blood cells + plasma).

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**Hermaphrodite:** refers to an organism that possesses, simultaneously or successively, the attributes (gonads) of both sexes.

**Heterosis:** refers to the increase in the capacity and/or strength of a hybrid compared to pure lines resulting from selection.

**Heterozygous:** refers to the genetic situation of an individual with different alleles for a given gene on each of their homologous chromosomes, as opposed to a homozygous who has two identical alleles on the same locus of both chromosomes.

**Histocompatibility:** refers to the rate of compatibility between two organs or tissues, which allows a transplant (of an organ or cell) not to be rejected. The "major histocompatibility complex" (MHC) is, in immunology, a system for recognizing the self present in most vertebrates.

**Holobiotic:** species spend all their lives in the same environment.

**Homeobox:** is a short DNA sequence contained within all genes that code for a specicific amino acid sequence that binds DNA and regulated transcription.

**Homeostasis:** is the stable internal environment maintained by an organism, which is suitable for sustaining life.

**Home range:** refers to the habitat territory of a species.

**Homing:** is the migratory behavior on return to the original spawning site.

**Homochromy:** is a type of camouflage using mimicry that involves resembling the environment through colors.

**Homomorphic:** refers to the identity of structure, shape and size between two individuals or species.

**Homozygous:** see heterozygous.

**Hooknose:** is the term used to refer to a mature male salmon whose lower jaw has curved into a kind of hook at the time of reproduction.

**Humic acid:** humic substances are polymerized, amorphous organic matter that results from the decomposition of plant and animal matter and which gives water a characteristic yellow-brown color.

**Hybridization:** is the natural or artificial crossing of two individuals (plants or

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**Hyperbaric:** refers to the above atmospheric pressure.

**Hypogeal or hypogeous:** refers to an organism that lives and develops below the surface of the ground, in the ground, caves or groundwater.

**Hypothalamus:** refers to the structure of the central nervous system, located on the ventral surface of the brain. Through its connections with the pituitary gland, the hypothalamus is responsible for several metabolic processes and other activities of the autonomic nervous system.

**Hypoxia:** is the decrease in the amount of oxygen dissolved in the blood or in a body of water (river, lake, etc.).

**Hz (hertz):** is the unit of measurement of the frequency of an acoustic phenomenon.

**Immunoglobulins:** are proteins that play an essential role in the body's defense against attack.

**Imprinting:** is rapid learning that occurs during a brief receptive period typically soon after birth or hatching and establishes a long-lasting behavioral response to a specific individual or object, such as attachment to parets, etc.

**Intertidal:** refers to the part of the coastline between the extreme limits of the highest and lowest tides. It also refers to an organism that occupies this area.

**Introgression:** refers to a situation of "genetic pollution" in which genes of a different species are incorporated, during hybridization, into the genome of a given species.

**Invasive:** refers to the characteristic of a species with strong potential for colonization of new habitats.

**Invertivore:** refers to an animal that eats invertebrates (insects, crustaceans,

**Isotopes:** are different types of atoms of the same element that are distinguished only by their number of neutrons.

**Iteroparity:** refers to species whose reproductive capacities are distributed over

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"semelparous" species, which invest all their energy in a single egg-laying period and then die.

**Jack:** is a small salmon that returns early from sea to fresh water.

**Kairomone:** is a semiochemical substance released by a living being, triggering a behavioral response in another species and having a negative effect on the emitting species.

**Karst:** a karstic relief is a form of landscape caused by water infiltrating the subsoil of certain regions and modeling galleries and cavities temporarily or permanently occupied by water.

**Kelp:** is very large brown seaweed (order Laminariales).

**Kelt:** refers to a salmon or sea trout after spawning and before returning to sea.

**kJ:** kilojoule.

**Lateral line:** is the "line" generally visible on the sides of the body, consisting of scales pierced by pores and communicating with sensory cells (neuromasts) capable of detecting changes in the pressure of the environment.

**Lecithotrophy:** is the mechanism for feeding embryos and larvae from the yolk (or "lecithin") of maternal origin stored in the oocyte and then the egg.

**Lek:** refers to a particular territory where male spawners (exceptionally females) of certain species meet at the time of breeding.

**Lentic:** refers to still water biotopes with slow renewal (lakes, ponds, etc.).

**Lessepsian:** refers to faunal movements between the Red Sea and the Mediterranean Sea through the Suez Canal (dug by Ferdinand de Lesseps).

**Leukocytes:** are colorless blood cells.

**LH:** luteinizing hormone, is a gonadotropine of the anterior pituary gland.

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**Limnetics:** relates to stagnant fresh water.

**Linnaean:** refers to the Swedish naturalist scientist Linnaeus.

**Lithophilous:** refers to organisms that are dependent on stony bottoms and spawn on a substrate composed of stones, pebbles, rocks, etc.

**Locus:** is the location of a gene on a chromosome.

**Lotic:** refers to a hydrographic system that corresponds to running fresh water, as opposed to "lentic" that corresponds to stagnant water.

**Lx:** is the symbol for "lux", the unit of measurement for illuminance. It characterizes the luminous flux received per unit area.

**Lymphocyte:** is a leukocyte (white blood cell) involved in the immune response (secretion of antibodies) and lacking the capacity for phagocytosis.

**Magnetite:** is a ferromagnetic mineral. This iron oxide can be naturally found as crystals in eruptive rocks as well as in some animal tissues (biomagnetite). Its main characteristic is that it is a natural magnet.

**Mangrove:** is a marine marsh ecosystem that includes a grouping of specific woody plants (mangroves) that develop only in the tidal balancing zone of the low coasts of tropical regions.

**Marsupium:** is an abdominal pocket present in various animal classes, including seahorses and pipefish.

**Maternotrophy:** syn. maternal nutrition, the female nourishes the embryo.

**Meiosis:** is a cellular chromatic reduction mechanism responsible for obtaining haploid gametes (N) from a diploid sex mother cell (2N).

**Melanoma:** is a malignant tumor of the skin cells that produce melanin.

**Melanophore:** is a pigment cell or chromatophore containing a black melanin pigment.

**Melanosome:** is an organelle found in animal cells and is the site for synthesis,

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**Mesencephalon:** is the lower part of the brain, also called the middle brain, which is located at the back of the diencephalon.

**Mesopelagic:** is the oceanic area between – 150 and – 1,000 meters deep. It also describes the organisms living in this area.

**Metabolite:** is a compound resulting from the biochemical transformation of an initial molecule by metabolism.

**Metacercaria:** is the quiescent stage in the life cycle of a parasite in its intermediate host that allows it to survive until it can infest its definitive host.

**Methylation:** is a chemical modification consisting of the addition of a methyl group ($CH_3$) to a substrate. DNA can be methylated in cytosines as well as in the surrounding proteins and histones.

**MHC:** major histocompatibility complex.

**Microbiota:** are ecological communities of commensal, symbiotic and sometimes pathogenic micro-organisms (bacteria, protists, fungi, etc.), for instance, intestinal microbiota.

**Microsatellite:** is part of a chromosome, the telomere, whose short DNA sequences are repetitive and non-coding and are used as the genetic markers of an organism.

**Mimicry:** is the falsification of physical, chemical, behavioral or social signals, i.e. counterfeiting.

**Mitochondria:** is a eukaryotic cellular organelle. As the location of the Krebs cycle, it is an essential element in the production of the energy (ATP) required for the operation of the cell.

**Monandria:** is the reproduction mode of a monogamous female.

**Monoamines:** are neurotransmitters derived from amino acids containing an ethylamine group ($NH_2$ amine linked by a $C_2H_5$ bridge) linked to an aromatic ring (catecholamine, tryptamines, serotonin, etc.).

**Monochromatism:** is the state of being monochromatic. Monochromatic light is a light whose color is formed only by a wavelength frequency $\lambda$.

**Monogamy:** is defined as having only one sexual partner.

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**Morph:** is synonymous with “form”.

**Morphometry:** is the study of the geometry of objects or organs. This is a part of biometrics that focuses on shapes.

**mRNA:** messenger RNA

**ms:** millisecond.

**mtDNA:** mitochondrial deoxyribonucleic acid.

**Mucin:** is a large glycosylated protein that makes up the mucus.

**Mutualism:** is interaction between organisms of two different species which benefits each organism.

**Myoglobin:** is a protein similar to hemoglobin whose role is to transport oxygen to the muscles.

**Myr:** million years.

**Nectobenthic:** refers to organisms that swim in open water near the bottom of a sea or lake.

**Nectonic:** refers to marine and freshwater organisms that can swim freely in open water.

**Nectopelagic:** refers to organisms which actively swim in a body of water, from the surface to a great depth but remaining relatively far from the bottom.

**Nematocyte:** is a specialized cell containing a nematocyst use by cnidarians – anemone, coral, etc.) to defend them against predators or capture their prey.

**Neoteny:** is the retention of some larval or immature characters in adulthood.

**Neuromast:** is a group of mechanoreceptor sensory cells arranged in the lateral line of fish, making it possible to perceive acoustic vibrations.

**Neurons:** are specialized, impulse-conducting cells that are the functional unit of the nervous system.

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**Neuropeptide:** is a peptide (amino acid chain) secreted by a neuron and having a largely neuromodulatory function.

**Neurotoxin:** is a toxin acting on the nervous system.

**Nociceptor:** is a sensory neuron that responds to damaging stimuly by sending a possible threat signal to the brain (pain receptor).

**Nuclear:** has two meanings: 1) related to the nucleus of the atom and the energy produced from it, as well as to the techniques that use this energy; 2) belonging to or related to the nucleus of the cell.

**Nucleic acid:** is an unbranched polymer of nucleotides linked together by a 3.5 phosphodiester bond. There are two types of nucleic acids: DNA and RNA.

**Nutrient:** is a compound that can be directly absorbed by the intestinal mucosa (glucose, vitamins, amino acids, etc.).

**Nycthemeral:** is the diel or circadian rhythm.

**Ocytocin:** is a neuropeptide secreted by the hypothalamus and posterior pituitary gland known for its role in childbirth, breastfeeding, mother–child attachment and social bonding; it is known as a "love hormone".

**Offshore:** is a location in the sea away from the shore.

**Olfactory bulb:** is the distal bulge of the olfactory tract located at the level of the nasal cavities that communicate with the outside through the nostrils.

**Oligotrophic:** refers to water characterized by a low concentration of dissolved nutrient salts.

**Omphaloplacenta:** is the placenta whose "chorionic" villi are irrigated by yolk blood vessels from the yolk sac of the embryo.

**Oncogenic:** refers to genes that control the synthesis of oncoproteins, proteins that stimulate cell division (healing) or inhibit programmed cell death (apoptosis), which triggers disorderly cell proliferation. The term oncogenic can also refer to viruses that cause cancer.

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**Ontogenesis:** is the development of an organism from the formation of the egg to the adult stage.

**Oophagus:** means egg eater.

**Opsin:** is a photosensitive pigment of retinal cells.

**Optical roof:** *tectum opticum*, also called "optical lobes", represents the major integration center of the brain's nerve activities. It is a function performed in the most evolved vertebrates by the cerebral hemispheres.

**Osmoregulation:** refers to all homeostatic processes involved in regulating the concentration of dissolved salts in the internal fluids of a living being.

**Osteology:** is the science that studies the structure of bones and, more generally, of the skeleton.

**Ostracophile:** refers to someone with a special relationship with living or dead mollusks, mainly their shells.

**Otolith:** is a mineralized piece of limestone (aragonite) located in the inner ear (three pairs of otoliths: asteriscus, lapillus and sagitta).

**Overfishing:** refers to excessive fishing.

**Oviparity:** is a mode of reproduction of a female whose eggs develop outside the maternal organism.

**Oviposition:** is synonymous with egg-laying.

**Ovotestis:** is a genital gland in hermaphrodites that is both male and female.

**Ovoviviparity:** is a mode of reproduction of a female whose eggs hatch inside the maternal organism.

**Ovuliparity:** is a mode of reproduction of a female whose oocytes are fertilized outside the maternal organism.

**Paedogenesis:** is the presence of juvenile traits in an adult.

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**Paedomorphosis:** is the early sexual maturity of larvae and juveniles that have not reached the adult morphological stage.

**Palatability:** describes how much pleasure foods or fluids provide.

**Pallium:** is the primitive form of the cerebral cortex.

**Panmixia:** is a principle in population genetics that considers that individuals are distributed homogeneously within the population and that all participate, in reproductive terms, in the formation of the next generation.

**Parapatry:** is a combination of a geographical sympathy and an ecological allopatry.

**Parr:** refers to young salmon living in rivers.

**Parthenogenesis:** is the reproduction without involvement of male sex.

**Parturition:** is the action of giving birth to live organisms.

**Pathogen:** is an infectious agent that causes disease.

**Pelagic:** relates to organisms living in water away from the land or living near the surface.

**Pelagoplanktonic:** refers to plankton living away from the land.

**Pellet:** is the food used in aquaculture.

**Peptide:** is a molecule consisting of two or more amino-acids.

**Percolation:** is the passage of a fluid through a more or less permeable medium.

**pH:** is the measurement of the chemical activity of hydrogen ions ($H^+$, also hydrogen potential) in solution. This determines whether an aqueous solution is acidic or alkaline.

**Phagocytosis:** is a cellular process by which certain cells can ingest solid foreign particles of micrometric scale.

**Phenotype:** is a set of morphological and anatomical characteristics resulting from the expression of the genotype that are modulated by environmental conditions.

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**Pheromone:** is a chemical message produced by an organism and captured by the olfactory system of its congeners.

**Philopathy:** is the tendency of individuals to stay in or return to their country of origin.

**Photophore:** is a light-producing organ.

**Photopic:** denotes vision provided largely by the cones of the retina of the eye.

**Phylogenesis:** is the study of kinship relationships between living beings.

**Pinealectomy:** is the surgical removal of the pineal gland.

**Pineal gland:** is a small endocrine gland in the posterior forebrain, which secretes malatonin.

**Pinealocyte:** is an exocrine glandular cell of the pineal complex secreting melatonin.

**Planktonic:** refers to small organisms that float or drift in the bodies of water.

**Polyandry:** refers to the reproductive capacities of females that mate with several males.

**Polychromatism:** is the state of a body whose parts have different colors.

**Polygamy:** is the situation in which an animal breeds with several partners of the opposite sex. When a female breeds with several males, it is termed polyandry; when a male breeds with several females, it is termed polygyny.

**Polygyny:** refers to the reproductive capacities of males that mate with several females.

**Postpartum:** refers to the period immediately following parturition.

**Preoptic:** is a region of the brain situated infront of the optic part below the anterior commissure that plays a role in staying awake.

**Pre/postcopulatory:** refers to before/after copulation (selection).

**Pre/post-zygotic:** refers to before/after the fertilization of an oocyte or egg.

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**Protandry:** is the sequential hermaphroditism where the individual is first male and then becomes female.

**Proterogyny:** is the sequential hermaphroditism where the individual is first female and then becomes male.

**Protogyny:** see Proterogyny.

**Protrusion:** or hernia is an action that pushes forward an organ or an anatomical structure.

**Psammophilous:** refers to a plant or animal organism that lives on and/or in sandy substrates.

**Pterygopod:** is the sex organ of male selachians, which is derived from pelvic

**Purse seine:** is a large net whose bottom can be closed, which is designed to be set by two boats around a school of fish.

**Ranching, sea ranching:** is an aquaculture method that consists of producing juveniles in hatcheries and releasing them into the sea or lagoons.

**Recruitment:** is the term applied to fish, which involves the arrival, in a given biotope, of fish of a size or age capable of settling there (it can be either an immigration of young individuals from nurseries or that of adult individuals producing egg-laying eggs). In fishing, it is the arrival in the fishery of fish of a size that can be caught.

**Resilience:** is the ability to return to health, strength, etc., after something bad happens.

**Rheophilia:** refers to the movement of orientation or displacement (+ or –) in relation to the current.

**Rheotaxis:** describes the oriented movement of a organism in reponse to a current of fluid (water).

**RNA:** ribonucleic acid.

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**Rod cell (retinal):** is a photoreceptor cell in the retina with an external segment shaped like a rod; these cells are adapted to twilight vision.

**Sagitta:** refers to one of the otoliths (asteriscus, lapillus and sagitta) of the fish's inner ear.

**Satellite (fish):** refers to a dominated fish whose presence is accepted in the vicinity of a dominant fish of the same species and sex, without being attacked by the dominant.

**Scotopic:** relates to the field of photometry for which the observed surfaces have luminous luminances less than 1 millicandela per square meter. The term "scotopic vision" refers to vision in the dark or in total darkness.

**Semelparity:** see iteroparity.

**Seminal vesicles:** are structures related to the reproductive system of males with a spermiduct.

**Sex ratio:** is the proportion, in a population, of males and females, expressed as a ratio or percentage.

**Sigmoid:** refers to something in the form of an "S".

**Silvering:** refers to the silvering of sub-adult eels before they begin their reproductive migration to the Sargasso Sea.

**Smolt:** is a young salmon that runs down a river to reach the fattening areas at

**Smoltification:** is a series of physiological changes where juvenile salmonid fish adapt from living in fresh water to living in sea water.

**Sneaker:** see sneaking.

**Sneaking:** refers to the behavior of small subordinate males, or sneakers, who seek to steal fertilizations, in order to parasitize the fertilizations of dominant males.

**Speciation:** refers to all the behavioral and genetic mechanisms leading to the differentiation of new species.

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**Spent:** refers to a fish that has finished laying ("post-laying" situation).

**Spermatic selection:** is a form of sexual selection, where after copulation the female can eliminate the sperm when there is not a free choice of the mating partner.

**Spermatogenesis:** is the process of spermatozoid production.

**Spermatophore:** is a pocket secreted by the male apparatus and containing spermatozoa intended for the insemination of females or a simple cluster of spermatozoa agglutinated in mucilaginous secretions.

**Spermatozeugmas:** are small "packets" of spermatozoons that the male transfers to the female during copulation.

**Spermiduct:** is a channel that allows sperm to escape from the testicles and be released outside the body.

**Spiggin:** is a sticky substance produced by the kidneys of the male stickleback that helps to cement fragments of aquatic plants to build its nest.

**Steroidogenic:** relates to the process of producing steroids, such as by the adrenal glands.

**Stridulation:** is the emission of a strident and high-pitched sound, often obtained by rubbing certain organs against each other.

**Subpopulation:** is a population that is part of a larger population.

**Superfetation:** is the simultaneous development in the ovary of several successive generations of embryos in some cyprinodonts.

**Symbiotics, symbiosis:** is the association of two or more organisms with mutual benefits.

**Sympatric:** refers to species sharing the same geographical distribution area (unlike allopatric species).

**Synaptic:** is related to a synapse, which is a functional contact zone between two neurons or between one neuron and another cell.

**Systematic:** is the scientific discipline that allows the classification of taxa in relation to each other. It is based on the implementation of logical methods for counting, describing and organizing living groups.

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**Tacon:** is the name given to young Atlantic salmon (*Salmo salar*) during the first two or three years of their lives before their first marine migration.

**Tagging:** is the action of attaching a label to something such as an organism or a fish for monitoring purposes.

**Taxonomy:** is the science of classification that aims to describe living organisms and group them into entities called "taxa", in order to identify, name and classify them according to the binominal system generalized by Linnaeus. The scientific name of a species is the combination of two Latin words or words considered to be

**Telemetry:** is a technical method for measuring the distance from an object using optical, acoustic or radio elements.

**Telencephalon:** is the anterior brain made up of striated bodies or cerebral hemispheres (cerebral cortex, white matter and subcortical structures) and associated structures.

**Tetraploidy:** refers to the possession of a chromosomal heritage equal to four complete batches of chromosomes (4N), with diploidy (2N) being the most common chromosomal lining.

**Teutophagous:** refers to organism that eat cephalopods (octopus, cuttlefish,

**Thermocline:** is a zone of rapid thermal transition between surface waters (generally warmer and oxygenated) and deep waters (generally colder and less oxygenated).

**Tidal cycle:** describes the periodic rise and fall of the ocean.

**Tidal rhythm:** is displayed by seashore organisms living in the inter-tidal zone, their lifestyle has tidal rhythms.

**Tracking:** refers to all the technical means implemented to track the movements of an organism.

**Transgenesis:** is the implantation of one or more genes in a living organism, which can be expressed in the transformed organism.

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**Trigeminal nerve:** is the fifth cranial nerve responsable for sensation in the face and motor function, such as biting.

**Triglycerides:** are part of the class of lipids that constitute a very important energy reserve (e.g. cholesterol). Glycerol and acid compounds are mainly derived from the metabolization of sugars, alcohol and fats.

**Triploidy:** is a chromosomal abnormality of cells with three batches of chromosomes (3N) instead of two normal batches (2N).

**Upwelling:** is the rise of deep oceanic waters that occurs when strong sea winds push surface waters.

**UV:** ultraviolet.

**Vagile, vagility:** refers to a benthic organism capable of moving on the bottom (walking, creeping, jumping, etc.), unlike a fixed organism qualified as sessile.

**Veganism:** is a movement that advocates meals based on foods of plant origin

**Vitellus:** are reserve substances accumulated in the oocyte and then in the egg and intended for use by the embryo during its development.

**Viviparity:** is a mode of reproduction of a female in which the embryos develop completely in her genital tract where they can receive a nutritious supply from her and which, as a result, gives birth to live young (parturition).

**Vortex:** is a hollow swirling that originates, under certain conditions, in a flowing fluid.

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# Species Index

## A, B, C


*Abramis brama*, 55
*Abudefduf*
  *sexfasciatus*, 102
  *vaigiensis*, 30, 54
*Acanthochromi*
  *polyacanthus*, 107
*Acanthochromis*
  *polyacanthus*, 107
*Acanthurus triostegus*, 115
*Acipenser*
  *ruthenus*, 69

  *sturio*, 55
*Aequidens rivulata*, 187
*Amatitlania nigrofasciata*, 21, 98, 113, 176, 180
*Amphiprion*
  *clarkii*, 64
  *ocellaris*, 63, 107
  *polymnus*, 108
*Anableps*, 174
*Anguilla*
  *anguilla*, 3, 117, 122
*Aphia minuta*, 38, 118
*Arapaima gigas*, 78, 122
*Archocentrus*
*Aspidontus tæniatus*, 142, 143
*Astatotilapia*
  *burtoni*, 42, 144
*Astyanax*
  *mexicanus*, 165
*Atherina boyeri*, 3, 74, 123, 178
*Barbatula barbatula*, 151
*Barbus*
  *carpathicus*, 53
*Betta splendens*, 35, 57, 83, 138, 167, 181
*Blennius ocellaris*, 16, 102
*Blicca bjoerkna*, 55
*Brachypopomus gauderi*, 180
*Brachyraphis episcopi*, 26, 139, 177
*Carassius*
  *auratus*, 161, 186
  *gibelio*, 2, 38, 67, 69
*Carcharhinus*
  *albimarginatus*, 92
  *amblyrhynchos*, 31
  *falciformis*, 179
  leucas, 52
  *limbatus*, 68, 91
  *plumbeus*, 33, 52
*Carcharodon carcharias*, 126
*Centropristis striatus*, 64
*Centropyge ferrugata*, 66
*Cheilinus undulatus*, 30



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*Chiloscyllium*
*griseum*, 183
*punctatum*, 71
*Chlorurus*
*sordidus*, 150
*Chœrodon schoenleinii*, 125
*Chondrostoma nasus*, 55
*Chromis*
*chromis*, 59
*viridis*, 115, 188
*Clarias*
*gariepinus*, 151
*Clupea*
*harengus*, 175
*Cobitis taenia*, 50

, 8
, 125
*Coregonus*
*albula*, 54
*palaea*, 111
*Coris julis*, 63
Corynopoma risei, 16
*Coryphaenoides*
*ornatus*, 155
*Coryphopterus kuna*, 118

*kneri*, 75
*Crenicichla alta*, 170
*Ctenochromis horei*, 87, 111
*Cymatogaster aggregata*, 33
*Cyprinus carpio*, 3, 138, 186

## D, E, G

*rerio*, 12, 42, 112, 135, 139, 140, 151, 158, 159, 163, 164, 166, 167, 169, 176, 177, 181, 187, 190, 191
*Dascyllus*
*aruanus*, 167
*marginatus*, 151
*Dicentrarchus labrax*, 158, 186
*Diplectrum formosum*, 60
*Diplodus*
*annularis*, 123, 175
*Enneapterygius sp*, 42
*Epinephelus*
*fuscoguttatus*, 29
*lanceolatus*, 72
*marginatus*, 19, 56, 61, 191
*merra*, 64
*striatus*, 2
*Eretmodus cyanostictus*, 88
*Esox lucius*, 1, 140
*Etheostoma*
*olmstedi*, 102
*Eviota sigillata*, 118
*Gadus morhua*, 30, 45, 54, 89, 114, 123, 158
*Gambusia*
*affinis*, 47, 53, 65, 131, 134, 171, 177, 188, 191
*Gasterosteus aculeatus*, 7, 10, 12, 17, 19, 21, 24, 25, 35, 43, 57, 80, 81, 101, 104, 105, 110, 112, 125, 130, 133, 134, 136, 139, 145, 158
*Gnathonemus petersi*, 175
*Gobius*
*niger*, 41
*Gobiusculus flavescens*, 179
*Gymnocephalus cernuus*, 2, 109

## H, I, J

*Halichoeres*
*margaritaceus*, 10
*melanurus*, 65
*trimaculatus*, 42, 152
*Halobatrachus didactylus*, 102
*Heliconus dactylopterus*, 71
*Hemitilapia oxyrhynchus*, 84
*Heterandria formosa*, 54, 91, 111
*Heterodontis portusjacksoni*, 135

Downloaded From Vet-eBooks.com

*Hippocampus*
*abdominalis*, 94, 158
*hippocampus*, 31
, 3, 22
*Hoplosternum littorale*, 83
*Hydrocynus vittatus*, 189
*Iriatherina werneri*, 17
*Isurus oxyrinchus*, 52
*Jordanella floridae*, 104, 106
*Julidochromis*
*marlieri*, 98
*ornatus*, 99
*transcriptus*, 32

## K, L, M

*Knipowitschia panizzae*, 11
*Labroides*
*dimidiatus*, 66, 129, 137, 143, 149, 182
*viridis*, 61
*Lampetra fluviatilis*, 168
*Lamprologus*
*callipterus*, 36, 80, 128
*Lepidosiren paradoxa*, 104
*Lepomis*
*gibbosus*, 42, 101
*macrochirus*, 10, 58, 137, 148, 189
*megalotis*, 16
*Lethrinus*
*miniatus*, 121
*nebulosus*, 180
*Leuciscus*
, 69
*Leuresthes tenuis*, 152
*ramada*, 175
*Lutjanus*
*analis*, 29
*campechanus*, 108
*cyanopterus*, 150
*griseus*, 115
*Lythrypnus dalli*, 66
*Macropodus opercularis*, 83
*Manta alfredi*, 52, 92, 174
*Masterpiscis attenboroughi*, 95
*Microbrachius dicki*, 96
*Micropterus*
*dolomieu*, 101
*salmoides*, 89
*Mola mola*, 1
*Mycteroperca*
*acutirostris*, 142
*microlepis*, 63
*venenosa*, 17, 29

## N, O, P

*Neogobius melanostomus*, 19, 103, 173
*Neolamprologus*
*furcifer*, 145
*pulcher*, 32, 97, 141
*Nimbochromis livingstoni*, 142
*Nocomis*
*sp*, 125
*Notolabrus tetricus*, 10
*Oblada melanura*, 114
*Ophthalmotilapia ventralis*, 44
*Oreochromis*
*aureus*, 110
*niloticus*, 76, 78, 88
*Oryzias latipes*, 36, 65
*Pagellus bogaraveo*, 124
*Pagrus auratus*, 30
*Parachromis friedrichsthalii*, 142, 143
*Paralabrax clathratus*, 11
*Parapercis cylindrica*, 66, 140
*Pelvicachromis*
*taeniatus*, 100
*Pentaprion longimanus*, 175
*Perca*
*fluviatilis*, 135
*Perissodus*
*microlepis*, 179

Downloaded From Vet-eBooks.com

*Petromyzon marinus*, 22, 78
*Petroscirtes breviceps*, 23
*Phalloceros harpagos*, 111
*Phallostethus cuulong*, 49, 50
*Phoxinus*
*eos-neogaeus*, 37
*phoxinus*, 6, 17, 35, 153, 161
*Phreatichthys andruzzi*, 131
*Pimephales*
*promelas*, 131
*vigilax*, 189
*Plagioscion sp*, 122
*Plectropomus*
*leopardus*, 28, 109, 115
*Pleuronectes platessa*, 117
*Poecilia*
*formosa*, 67, 68
*latipinna*, 21, 35, 41, 46, 139, 173
*mexicana*, 34, 48, 57, 147
*reticulata*, 7, 9, 12, 16, 18, 20, 25, 26, 32, 33, 39, 46, 47, 50, 57, 70, 109, 128, 130, 132, 133, 136, 138, 140, 141, 147, 148, 159, 169, 170, 172, 177, 178, 191
*Pomacentrus*
*amboinensis*, 116, 146, 176
*bankanensis*, 136
*Pomatoschistus*
*canestrinii*, 19
*microps*, 1, 41
*minutus*, 3, 44, 58, 79, 101, 103
*Porichthys notatus*, 59, 154, 173
*Potamotrygon*
*castexi*, 120
*Prionace glauca*, 52
*Psetta maxima*, 117
*Pseudomugil signifer*, 16
*Pseudotropheus*
, 167, 183
*Pundamilia*
*pundamilia*, 106

## R, S, T

*Retropinna semoni*, 122
*Rhabdoblennius ellipes*, 75
*Rhadinocentrus ornatus*, 9
*Rhincodon typus*, 150
*Rhinecanthus aculeatus*, 115
*Rhinogobius brunneus*, 16
*Rhodeus*
*amarus*, 8, 12, 35
*Rutilus rutilus*, 55, 122
*Salaria*
*pavo*, 16, 23, 30, 36, 45, 82, 102
*Salmo*
*marmoratus*, 53
*salar*, 112, 137, 140, 162, 172, 173, 215
*trutta*, 3, 4, 15, 25, 78, 96, 137, 141
*Salvelinus*
*alpinus*, 10, 15, 42, 109
*fontinalis*, 77
*namaycush*, 76
*sp*, 121
*Sander*
*vitreum*, 108
*Sardina pilchardus*, 2, 29, 158
*Scardinius erythrophthalmus*, 55
*Schindleria praematura*, 37, 118
*Scyliorhinus canicula*, 28, 183
*Serranus*
*scriba*, 2, 61
*Serrasalmus brandtii*, 82
*Silurus glanis*, 151, 189
*Simochromis pleurospilus*, 85, 97, 110
*Skiffia bilineata*, 26, 47
*Solea*, 174
*Solea solea*, 117
*Somniosus pacificus*, 163
*Sparus aurata*, 2, 61, 63, 72, 186
*Sphyrna*
*lewini*, 52, 91
*sp*, 160

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*Squalius alburnoides*, 38, 69
*Squatina dumerili*, 52, 91
*Stegastes*
  *leucostictus*, 21, 102, 104
  *partitus*, 20
  *planifrons*, 103
*Symphodus*
  *ocellatus*, 43, 104
*Symphysodon discus*, 100
*Syngnathus*
  *abaster*, 89
  *scovelli*, 11
  *typhle*, 22, 95

*Telmatochromis temporalis*, 44
*Tetrapterus audax*, 179
*Thalassoma*
  *hardwicke*, 125
*Thynnus thynnus*, 2
*Toxotes chatareus*, 119, 184
*Triaenodon obesus*, 51, 68
*Tropheus*
  *duboisi*, 126
  *moori*, 86
*Xenotoca eiseni*, 184
*Xiphias*
  *gladius*, 123
*Xiphophorus*
  *birchmanni*, 17, 26
  *cortezi*, 46
  *helleri*, 16, 128, 147
  *multilineatus*, 18, 109, 130
*Xirichthys novecula*, 155

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# Summary of Volume 1


**Preface**

**Introduction**

**Chapter 1. Habitats: Occupation, Protection and Exploitation**

1.1. Diverse and unusual habitats
- 1.1.1. Psammophilous* habitats
- 1.1.2. Reef cavity habitats
- 1.1.3. Rocky habitats
- 1.1.4. Plant habitats
- 1.1.5. Zoohabitats
- 1.1.6. Intertidal* habitats
- 1.1.7. Karst* habitats
- 1.1.8. Intermittent habitats
- 1.1.9. Habitats modified by other animals
- 1.1.10. Manmade habitats
- 1.1.11. Ecological niches not frequented by other species
- 1.1.12. Seemingly unlimited pelagic habitats
- 1.1.13. Temporal fluctuations in habitat occupancy
- 1.1.14. Ontogenic and/or physiological fluctuations
- 1.1.15. An amphibious existence
- 1.1.16. An underground life
- 1.1.17. Living in the abyss

1.2. Food: the use of trophic habitats
- 1.2.1. Choose more or less energy-giving foods
- 1.2.2. Adopt original hunting methods
- 1.2.3. Use of cannibalism
- 1.2.4. Practice grazing



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1.3. Individual and collective protective habitats
1.3.1. Protecting oneself from environmental factors
1.3.2. Protecting oneself from congeners and competing species
1.3.3. Protecting oneself from predators
1.3.4. Practicing the art of camouflage
1.3.5. A safe resting phase
1.3.6. Owning and defending a territory
1.4. Breeding habitats

**Chapter 2. Strategies and Tactics for the Occupation of Available Territories**

2.1. Faithfulness to habitat and birth site
2.1.1. Remaining faithful to one's habitat
2.1.2. Loyalty to one's birth site
2.2. Habitat changes
2.2.1. The great migrators
2.2.2. Navigators
2.2.3. Great travelers
2.2.4. Divers
2.2.5. Illegal migrants
2.2.6. Adapting to ambient hydrodynamics
2.2.7. Overcoming an obstacle
2.3. The colonization of new territories
2.3.1. Invaders
2.3.2. Western colonizers
2.3.3. Eastern colonizers
2.3.4. Invasions of tropical species
2.3.5. Parasitic invasions
2.3.6. A most unfortunate introduction
2.3.7. Marine "aliens"
2.3.8. Recent tropical peril
2.3.9. Marine reserves and fish farms:
habitats that facilitate migration?
2.3.10. Other colonization related to aquaculture
2.3.11. Unexplained presence

**Chapter 3. Communication and Social Life: Behaviors Related to Social Interrelations between Congeners, Parasites and Predators**

3.1. Communication between partners
3.1.1. Accurate information signals

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3.1.2. Fast and efficient visual signals
3.1.3. Useful and precise olfactory signals
3.1.4. Substitution phenomena between sensory signals
3.1.5. Highly informative auditory signals
3.1.6. Remarkably discriminating electrical signals
3.1.7. Champions of neuroethology
3.2. Neighborly warning
3.2.1. Beneficial altruism between congeners
3.2.2. Acoustic solidarity for defensive purposes
3.2.3. A chemical alert for olfactory purposes
3.2.4. A survival benefit linked to competition between predators
3.2.5. Anxiety disorders triggered by alarm substances
3.3. Groups, shoals, swarms and masses
3.3.1. A simple convergence of interests
3.3.2. Artificial groupings of anthropogenic origin
3.3.3. Unity is strength
3.3.4. Choice of association
3.3.5. Coordinated swimming under light conditions
3.3.6. A defense: reducing vulnerability to predation
3.3.7. Learning to be careful in social relationships
3.3.8. Less need for security
3.3.9. Different motivations
3.3.10. Protection against parasites
3.3.11. Unique protection for females: reducing sexual harassment
3.3.12. Forming unisex communities
3.3.13. An energy goal: reducing the costs of movement
3.3.14. The advantage of a collective memory
3.3.15. Another objective: increasing opportunities for food
3.3.16. Who is the leader?
3.3.17. A colonization strategy
3.3.18. The role of collective education
3.3.19. A social life under cerebral neuroendocrine control
3.4. Mutualists and parasites
3.4.1. A model of association
3.4.2. Ectoparasites
3.4.3. Endoparasites
3.4.4. Accommodation of eggs by hosts
3.4.5. Zoophile fish
3.5. Cleaners
3.5.1. Removing parasites for “good customers”
3.5.2. Unsustainable early skills
3.5.3. Flexibility under neurohormonal control

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3.5.4. A sometimes dishonest job
3.5.5. A clownfish that acts as a cleaner… or a cleaner-turned clownfish?
3.6. Helpers
3.6.1. Social cooperation in parental care
3.6.2. Helpers able to escape their servitude
3.6.3. Behavioral gender differences
3.7. Selection of sexual partners
3.7.1. A major concern for any progenitor:
choosing a partner
3.7.2. Social learning
3.7.3. Most importantly, avoid choosing the wrong partner
3.7.4. How can the best partners be identified?
3.7.5. Initial choices
3.7.6. Varying preferences
3.7.7. Copying others
3.7.8. The desire for novelty
3.7.9. Females who refuse
3.7.10. Reconstituted couples
3.7.11. No choice
3.8. Sexual conflicts
3.8.1. Conflicting interactions between sexes
3.8.2. Intrasexual conflicts
3.8.3. Incompatibility between ecotypes
3.8.4. Who will win this conflict?
3.8.5. A conflict that ends in divorce
3.9. Joint provision of parental care
3.10. Competitors
3.10.1. Be a good observer
3.10.2. A competition for space
3.10.3. Competition for food
3.10.4. Sexual competition
3.10.5. Competition for nest building
3.10.6. Sperm competition
3.10.7. Females intervening to their advantage in sperm competition
3.10.8. Cases of social deprivation
3.10.9. Love or war or love and war
3.10.10. Females in competition using physical arguments
3.10.11. Chemical weapons
3.10.12. Dominance expressed through fecal olfactory signals
3.10.13. A peaceful solution for escaping competition
3.10.14. Cases of non-aggression

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3.11. Sense of family and recognition of familiar congeners
3.11.1. The value of recognizing “blood ties”
3.11.2. Interfamilial crossbreeding in spite of genetic barriers
3.11.3. Known congeners

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