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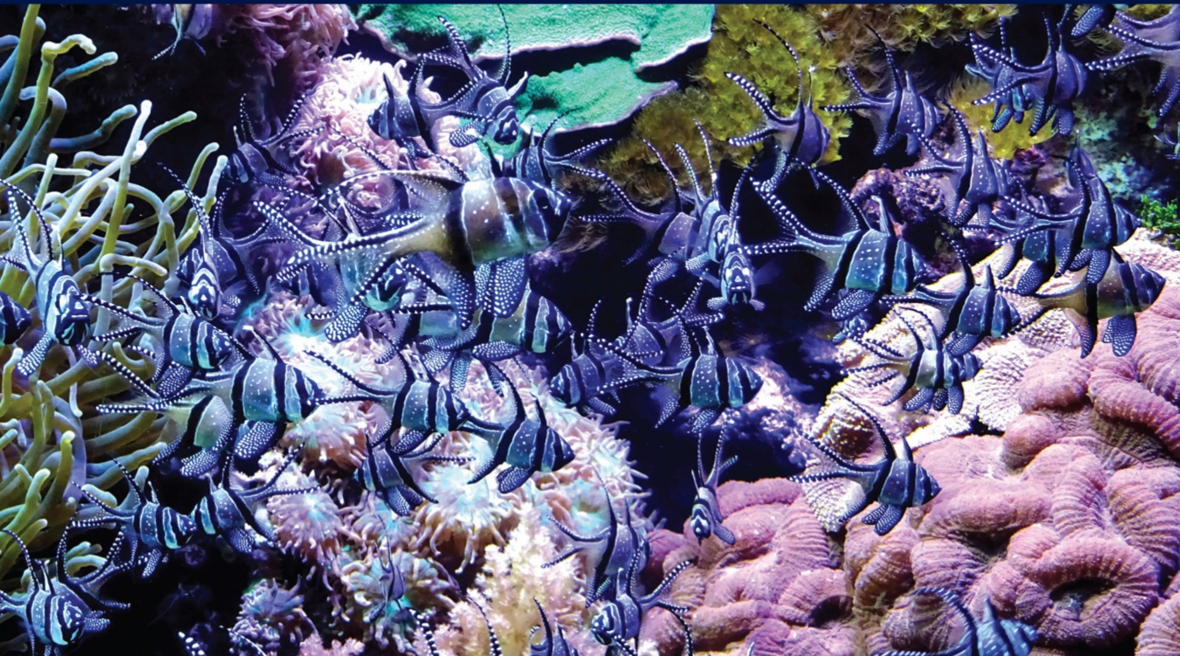
Fish Behavior 2

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

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

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

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

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 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

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.

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.

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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.

Fish Behavior 2: Ethophysiology,
First Edition. Jacques Truslé and Jean-Pierre Quignard.

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 *Cirrhitichthys 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 (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.

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 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

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.

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 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.,*

& 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 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 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