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## Reproductive Behavior: Spawners

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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.

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 hermaphroditism as in the painted comber *Serranus scriba* or successive hermaphroditism, 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](#) *Gymnocephalus cernuus*), burying them in a sandy and gravelly mineral substrate

(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 cavitory 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\*<sup>1</sup>), 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

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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 genus *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 [shad](#) *Alosa* sp. and the [eels](#) *Anguilla* sp. whose populational movements, precise in

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**

### **1.1.1. 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.

### **1.1.2. 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 them.

### 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  *$\beta$ -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, and *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  *$\alpha$ -melanocyte-stimulating hormone ( $\alpha$ -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 ovata*, 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 than to the intensity of the color itself. Male guppies who possess a large colored

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 spermatid 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.*, 2010, **116**: 895-903 & DOI:10.1111/j.1439-0210.2010.01802.x, 2013, **119**: 605-613

& 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 expressed by the carotenoid pigments\*, but has the indicator value of social status,

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 *carotenoids*\*, 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 the [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.Freshwat.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

#### 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 in the **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.



**Figure 1.1.** The copulatory organ or gonopod of the male guppy *Poecilia reticulata*. For a color version of the figures in this book, see [www.iste.co.uk/bruslé/fish2.zip](http://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 hydrodynamic drag, which increases the risk of predation. Thus, laboratory analysis

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 of *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.

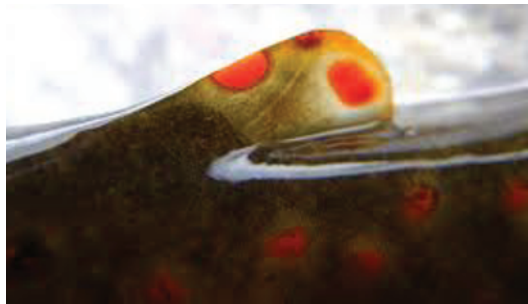
The development of the sword among the swordtails is genetically determined, under the control of several genes, principally *MSX*, which is common to all poeciliids and associated with the secretion of the androgenic hormone testosterone. In fact, juveniles do not possess swords; the expression of the gene is under-regulated during this juvenile phase by a deficit in the androgenic hormone. If most

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.



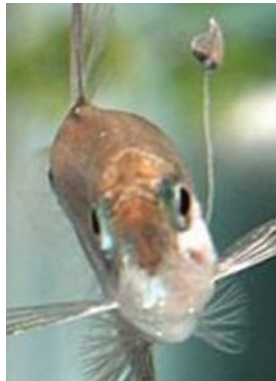
**Figure 1.3.** Adipose fin of a salmonid *Salmo trutta fario*

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 period, and seek all means to attract their attention so as to positively guide the

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 riisei*

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 swimming capacity. In contrast, the possession of long filiform expansions of the

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:10.1016/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).

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.

### 1.1.3. *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

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 rates 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 17β-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 courtship swimming behavior strongly stimulates couplings and is quite specific; the

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/jfb.12733, *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.

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 their reproductive success (Volume 2, section 1.2.7).

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

#### 1.1.4. *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

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<sub>2</sub>*; an interruption of this courtship occurs after ovariectomy. In addition, *prostaglandins (PGF<sub>2</sub>α)* 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  $\alpha$ , in intrasexual competition, interrupt the courtship solicitations of females of lower rank  $\beta$ . As for males, they restrict themselves to the accomplishment of their domestic task, namely parental care (Volume 2, section 2.2.1).

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

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:10.1111/1095-8649.2006.01086.x

### 1.1.5. *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

### 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 trout** *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

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** *Brachyrhaphis 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/j.1439-0310.2006.01225.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 accompanied by a high mortality of hybrids who suffer from lesser *fitness*\* and

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 postcopulatory 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.

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

#### 1.1.6. *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

### 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<sup>2</sup>, 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<sup>3</sup>. 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

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 10♀/1♂. 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 nest.

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, **518**: 239-254 & DOI:10.3354/meps11060

### 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 polyphkadion*, 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

### 1.1.7. *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* and *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

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 large *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  $\alpha$  males and small  $\beta$  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.

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:10.1098/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

### 1.1.8. *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 are larger than themselves and whose colorings are unknown to them. Heterosexual

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.

### 1.1.9. *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

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  $\lambda^* = 550\text{--}625$  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 eyes.

Females of the **Siamese fighting fish** *Betta splendens* reject males contaminated by chemicals such as *17 $\alpha$ -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 ejaculations (up to 20 per hour) with successive females see their density of sperm

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.

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 fish *Schindleria praematura* of the Red Sea is among the smallest vertebrates, where

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/j.fbi.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

## 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.

### 1.2.1. *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 low quality who, with only a low power of attraction in the eyes of females,

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 spermatocyst 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 gathered in the absence of females. They therefore produce sperm ready for use in

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 the **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, **301A**: 177-185 & DOI:10.1002/jez.a.20019, *J.Fish.Biol.*, 2000, **56**: 1381-1368, 2007, **71**: 1864-1872, *J.Evol.Biol.*, 2006, **19**: 1641-1650, *J.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

### 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 reproduction. They do not give up so much as play the role of spawner later, since

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 the *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

combative males and small *sneaker*\* males, characterize the reproductive behavior of the **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 non-colored males, who have invested all their energy in intense spermatogenic

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

### 1.2.2. *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 case of the **coelacanth**), phallic coitus (viviparous *Poecilia*, oviparous and viviparous

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 capable of shortening it and shaking herself to eliminate semen from a partner whom

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

### 1.2.3. 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.

In *western mosquitofish* *Gambusia affinis*, sexual intercourse is also often conflictual: males of all sizes, and especially small *sneaker*\* males (Volume 2,

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 mosquitofish** *Gambusia holbrooki* tend to group together and join groups of other

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.

### 1.2.4. *Violent couplings*

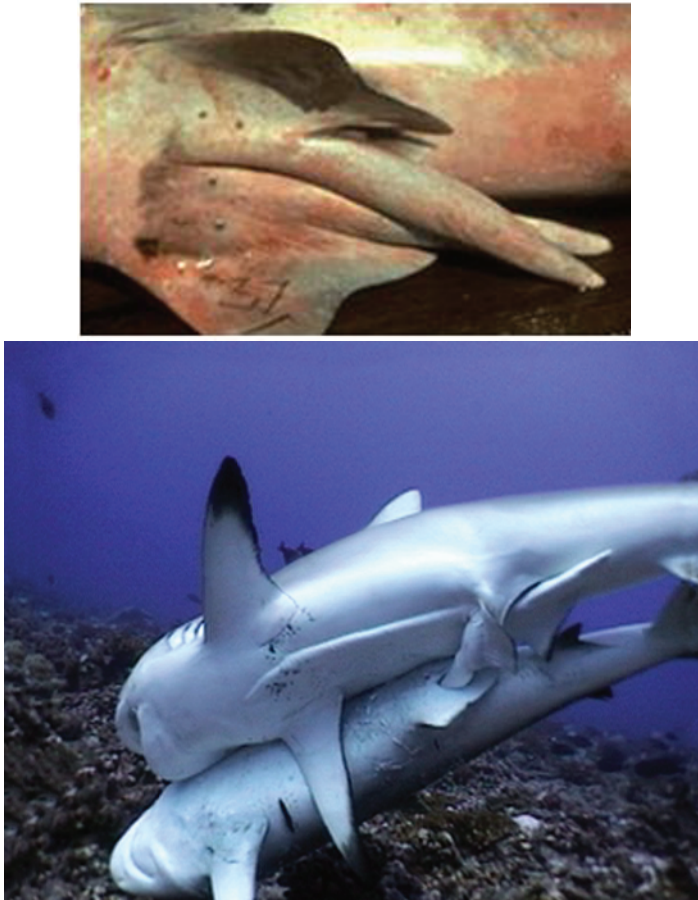
The male of the **priapus** or **penis head fish** *Phallostethus cuulong* – Priapus, the Greek god of fertility – is a small Vietnamese freshwater fish in the delta of the Mekong River. Its anatomical particularity lies in possessing its testes in a very forward position, under its mouth. This oddity 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.



**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 taenia*. 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.



**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

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:10.1139/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

### 1.2.5. 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* and *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.

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.

Crossings occur, in Canada, between males of **Chinook salmon** *O. tshawytscha* 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, the **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-ovulatory females, conspecific as well as heterospecific, which proves an interspecific identity of endocrine signals and reveals a strong ability for cross-fertilization.

Bibliography: *Cybum*, 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 ecomorphs\* with a spectacular polymorphism of colors, which have been the source

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

### 1.2.6. *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.

### 1.2.7. 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 the **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<sub>2</sub>S).

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

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

### 1.2.8. 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 nests are, however, able to distinguish, from olfactory signatures, their own

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,

## 1.2.9. 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 spermatozooids 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 theirs, guaranteeing complementary and compatible heterozygous\* crosses and thus

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.

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 hermaphroditism and successive or sequential hermaphroditism, 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 hermaphroditism.

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 and a functional ventral testis, which reflects successive hermaphroditism.

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 viridis*, 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 spermatozooids mature within seminiferous cysts. Such sexual inversion concerns a successive differentiation of the various categories of sexual cells inside the gonad, under hormonal induction.

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 hermaphroditism 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 ( $\text{♀} \rightarrow \text{♂}$ ) 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\* ( $\text{♂} \rightarrow \text{♀}$ ) 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.

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 ( $\text{♀} \rightarrow \text{♂}$ ), 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. Rational and intelligent management of living resources entails the balanced

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 even **wrasses** of the genus *Labrus*, as well as among the protandrous\* species such as the **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<sub>2</sub>* 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\*)* and *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 17β-estradiol (E<sub>2</sub>)* 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<sub>2</sub>*. The *androgenic hormone 11-KT*, catalyzed by a steroidogenic\* enzyme, the *cytochrome 11β-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<sub>2</sub>)*. Conversely, primary males undergoing an experimental implantation of *E<sub>2</sub>* develop

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 17 $\beta$ -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:10.1007/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 harem, protogynous\* **dwarf hawkfish** *Cirrhichthys 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.

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 harem 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 –  $\alpha$  and  $\beta$  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

### 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 carp** *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.

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 male

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 tiburo* 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

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 ruthenus*. 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

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** *Cephaloscyllium ventriosum*, the **white-spotted bamboo shark** *Chiloscyllum 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 sex.

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 disappearance.

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 “intropermatozoid” or introperm, 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.

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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  $-196^{\circ}\text{C}$ , 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 300  $\mu\text{m/s}$ , in comparison with respective values of 95% and 350  $\mu\text{m/s}$  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.

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