1

Habitats: Occupation, Protection and Exploitation

1.1. Diverse and unusual habitats

A species can occupy the same habitat throughout its life, from the larval stage to adulthood (pelagic fish), but most species, after a planktonic larval stage (open water habitat), change habitat to live either near the seabed (benthonectonic and demersal species*[1]) or in contact with the substrate or even buried in it (benthic species*). In addition, many species, depending on their life stages, choose temporary ecological niches that can be used for protection, feeding and reproduction and where intra- and interspecies competition may be less. Such a choice is often decisive in the survival of individuals and populations.

All aquatic ecosystems, and even some land-based habitats, have been used by fish populations, with few ecological niches deprived of their presence, as evidenced by the examples of fish colonizing many different types of habitats.

1.1.1. *Psammophilous* habitats*

The catfish *Pygidianops amphioxus* has the distinction of living constantly buried in the sandy substrate of the bed of Amazonian rivers since it has never been seen swimming in open water. More dependent on sediment than flatfish – sole, plaice, etc. – or than weevers, which are rather at the interface between sand and water and move above the seabed, feeding on the prey in this familiar environment: specifically, benthic insect larvae such as chironomids, as well as copepods that they absorb by suction through sedimentary particles. Its feeding activity is essentially

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

nocturnal, like that of other catfish. But how does it reproduce? Is this way of life safe, as though burrowing predators were not able to detect its presence and capture it by digging it up?

Flatfish prefer sandy or gravel substrates of a specifically determined granular size* that provide them with camouflage sites in which to develop their mimicry skills (Volume 1, section 1.3.4). In addition, some species, such as American plaice *Pseudopleuronectes americanus,* use burial in the sediment (3, 6 or 9 cm deep) for the thermal regulation of their body: their internal temperature is higher than that of ambient water in winter and, conversely, lower in summer, with the sediment providing natural air conditioning.

Other nectobenthic species, although less dependent on sandy environments, have an imperative need to use such an environment, either to feed like the red mullet *Mullus* sp., or to reproduce like the Californian grunion *Leurestes tenuis*, or the Japanese fugu *Takifugu* sp.

Bibliography: *Env.Biol.Fishes*, 2014, **97**: 59-68 & DOI:10.1007/s10641-013-0123-9, *Mar.Ecol.Prog.Ser.,* 2019, **609**: 179-186 & DOI.org/10.3354/meps123354

1.1.2. *Reef cavity habitats*

Reef corals create complex mineralized structures with an extreme diversity of habitats used by small fish whose size and morphology are perfectly adapted to the geometric structures created. The great diversity of coral structures, constituting a multitude of highly specialized microhabitats, makes it possible to shelter many small fish with highly diverse body shapes that use the structures as anti-predator refuges, food resources and egg spawning sites. On the Australian Great Barrier Reef, blennies such as the *Salaria*, *Glyptoparus* and others, all small fish particularly vulnerable to predators, must find safe havens, as species including snappers, groupers and morays are permanent threats. All cavities – holes, crevasses, drop-offs, caves – among *Porites* corals are therefore sought and occupied according to their diameter, depth and habitability, to within a few millimeters or a few centimeters, and affect all species in accordance with their own morphology, with precise interspecies differences reflecting a very specific division of habitats that promotes their coexistence. Competition for the occupation of the best shelters is generally fierce, and all species sometimes need to defend their personal habitat.

The gobies, *Gobiodon histrio*, live in close association with the coral reefs of the Red Sea, using microhabitats created by host corals according to the distance between *Acropora* branches and their own body morphology, in particular, their width, which allows them to creep into interbranchial spaces. Goby species with compressed bodies, laterally flattened, are favored in this interspecies competition and remain particularly faithful to their individual habitat. Described as cryptic*, they shelter in *Acropora* branches in accordance with their length and the interbranchial space of each branch, with lateral compression of the body and a small size ensuring a certain interspecies segregation. They jointly exploit coral architecture by adapting perfectly to its geometric constraints, with their maneuverability conditioning their protection and movement, and therefore their survival, and justifying their movement from branch to branch as they grow in order to continuously occupy "tailor-made" habitats.

The distribution of various species of damselfish, such as *Dascyllus aruanus* or *Chromis viridis* in Red Sea coral reefs, follows well-defined habitat rules reflecting the type of reef, continuous or sparse, and, especially, the specific morphology – size, volume, gill density – of the linked coral species, i.e. seven *Acropora* species. Similarly, *Chrysiptera parasema* prefers to use *Acropora* corals as a habitat-refuge, with 97% of juveniles associated with those corals. The density of its populations is closely correlated with that of the branchy corals of this species, which is particularly favorable to protection against predators. Reefs with wide coral cover support dense populations of these small fish, which are subject to very strong intraspecies competition for the occupation of secure habitats that provide valuable refuges and avoid overly exposed reef areas.

The distribution of butterfly fish, *Chætodon* sp., in New Caledonia, meets similar requirements for the availability of microhabitats in the coral ecosystem. This kind of individual selection of micro-habitats ensures that each resident is provided with food and, above all, security. The reduction in the coral coverage of more than 90% in some areas of the Great Barrier Reef, following coral bleaching, is seriously affecting populations of the various species of butterfly fish.

Naturally occupying the highly structured coral reef habitats, squirrel fish, *Sargocentron microstoma,* given their size and morphology and like many reef species, suffer severely from their deterioration and are the first victims of widespread degradation of reef ecosystems, whether caused by climatic phenomena, biological interventions of corallivorous species (starfish, fish) or destruction and pollution of human origin responsible for the loss of irreplaceable refuge habitats.

In contrast, an invasive alien species native to Australia, the serpulid *Ficopomatus enigmaticus*, a worm that builds serpulid reefs, is currently providing new anti-predatory and egg-laying shelters for the peacock blenny, *Salaria pavo*, which is encouraging its expansion in Mediterranean lagoons.

Figure 1.1. *Protected habitat of a squirrel fish, Sargocentron* microstoma*, with the branches of the Acropora coral adapted to its size and morphology. For a color version of the figures in this book see www.iste.co.uk/bruslé/fish1.zip*

Bibliography: *Anim.Behav.,* 2017, **125**: 93-100 & DOI:101016/j.anbehav.2017.01.003, *Env.Biol.Fish,* 2014, **97**: 1265-1277 & DOI:10.1007/s10641-013-0212-9, *J.Fish Biol.,* 2003, **66**: 966-982 & DOI:10.1111/j.1095-8649.2002.00652.x, 2006, **69**: 1269-1280 & DOI:1095-8649.2006.01161.x, *Mar.Biol.*, 2013, 1**60**: 2405-2411 & DOI:10.1007/s00227-013-2235-3, 2014, **161**: 521-530 & DOI:10.1007/s00227-013-2354-x, *Mar.Ecol.Prog.Ser.*, 2007, **333**: 243-248, 2014, **500**: 203-214 & DOI:10.3354/meps10689

1.1.3. *Rocky habitats*

Interspecies differences in orientation behavior and site memorization are seen between Australian gobies – species not mentioned – in intertidal zones*, with those occupying complex rocky habitats having better capacities for memorizing shelters in case of threat of predation than those of homogeneous sandy habitats, and the learning capacities to locate a shelter in an experimental labyrinth of the former being greater than those of the latter, in relation to many well located landmarks in complex habitats that lack monotonous habitats. Greater spatial information, in a complex familiar environment, results in a sharper neurosensory development that relies, for the marine gobies of rocky habitats, on the memorization of visual topographic cues and the creation of an accurate geometric spatial map of holes, crevices and rock cracks that provide them with stable shelters. The situation is different for sandy habitat gobies, where the location of refuges is more uncertain and unpredictable in the absence of visual physical cues and the physical instability of the substrate due to tidal movements. Their orientation is then based more on extraterrestrial signals such as sunlight – the sun's position – and UV radiation, and terrestrial signals such as geomagnetism and underwater sounds. Their survival depends mainly on rapid swimming in a zigzag motion and rapid burial in sediment.

Bibliography: *Anim.Behav*, 2005, **70**: 601-607

1.1.4. *Plant habitats*

The tropical seahorse, *Hippocampus*, comes from the Pacific, particularly vulnerable to predation because of its low vagility*, seeks protective habitats by successively using, during its growth, macroalgae beds – sargasses – and coral reefs that offer a diversity of protective microhabitats – tree sponges, branchy corals – depending on its size and camouflage capacities: homochromy* and homomorphy*.

Although some adult wrasses, such as *Symphodus rostratus*, generally occupy rocky habitats on the Mediterranean coast, the juveniles tend to favor underwater meadows of brown algae, *Cystoseira* sp., rather than other algal habitats and especially bare floors, which provide them, in their three-dimensional canopy*, with shelter from predators and food in the form of epibenthic prey*. These valuable nurseries are often currently in the process of degradation and are sometimes even threatened with extinction, which could seriously affect the recruitment of such labrid populations.

Tree trunks and branches are used as water shelters (Volume 1, section 1.3.1) and pest control refuges in streams in forest regions. A policy to restore some of them is being implemented in Canada and the United States, by depositing tree trunks in the beds of salmon rivers, *Onchorhynchus kisutch*, with the results proving controversial. On the other hand, an overly high plant density of macrophytes, *Eichhornia* sp., in Brazilian lakes is not favorable to occupation by various small species that prefer more sparse habitats.

Rhizophora sp. mangroves also provide highly structured complex habitats that form shaded areas rich in shelters that, like those of the Florida Keys, are densely populated with juveniles of many species, including those of the giant grouper, *Epinephelus itajara*. The hollow trunks of mangrove trees provide habitats for some species (10–20 individuals per trunk) such as the mangrove killfish, *Kryptolebias marmoratus*.

Bibliography: *Can.J.Fish.Aquat.Res*., 2014, **71**: 1498-1507 & DOI:10.1139/cjfas-2014-0020, *Endang.Species Res*., 2006, **2**: 1-6, *J.Fish Biol.,* 2007, **71**: 701-724 & DOI:10.1111/j.1095-8649.2007.01535.x, 2015, DOI:10.1111/s10641-015-0394-4

1.1.5. *Zoohabitats*

While coral or tube-worm reefs are remarkable sub-rocky complex habitats for many fish, non-calcified isolated organisms can also harbor fish, protect them from predators, feed them or facilitate their feeding and allow them to lay eggs under good conditions. This is the case with some jellyfish, such as *Rhyzostoma pulmo* and *Rhopilema nomadica*, which, as welcoming and benevolent hosts, protect, under their umbrella, the juveniles of many pelagic fish, many sea anemones that live in symbiosis* with clownfish of the genus *Amphiprion* and some holothurians *Holothuria tubulosa* and *Parastichopus regalis* that shelter a commensal, the thermometer fish, *Carapus acus*. Similarly, some ascidians are temporarily occupied to a greater or lesser extent by gobies that lay their eggs in their gill cavity. The snail fish, *Coreproctus* sp., a liparid from the coast of Georgia, USA, lays its eggs in the peribranchial cavity of the king crab, *Lithodes æquispinnis*; such commensalism* joins the cases of parasitism as the presence of these eggs affects the respiratory organs of the crustacean.

Ethologists now consider that certain large fish, such as sharks and tuna, constitute, alone and individually, and because of the hydrodynamic and trophic environment they create, a real habitat from which the suction cup fish, *Echeneis remora*, *Remora* sp., and pilot fish, *Naucrates doctor*, benefit. This is therefore a modern extension of the concept of an ecosystem as the shark alone constitutes a real ecosystem*.

Bibliography: *J. Mar. Biol. Ass. UK*, 2000, **80**: 379-380

1.1.6. *Intertidal* habitats*

On the coast, in the tidal swing zone exposed to strong water agitation from currents and waves, mechanical erosion forces small fish with limited swimming ability to either take refuge in crevasses to protect themselves, cling to the bedrock or bury themselves in loose sediment if it exists. Gobiids and gobiesocids, such as *Gobiesox maeandricus*, achieve such anchorage through a ventral suction cup producing a suction force. They cling to all kinds of substrates of varying roughness, with the rocks rarely bare and generally covered with a slippery mat – a bacterial and algal biofilm that acts as a lubricant – that modifies the conditions of fixation, thereby reducing the friction forces between the suction cup and the rock and making it difficult for this small fish (1.5–15 g) to adhere to it mechanically and to attach to a support. Tests on substrates of various sizes show that it is more difficult for it to stick to smooth surfaces than to rough surfaces. Small discs of 13 mm in diameter cannot adhere to substrates with a grain size greater than 270 µm, while larger discs of 34 mm in diameter attach firmly to coarser supports with a grain size of 2–4 mm. Choosing suitable granularity from the substrate and having a lot of tenacity allow the fish to stay well attached.

Juvenile Australian gobies, *Bathygobius cocosensis*, living in pools of intertidal water have differential cognitive skills depending on the type of habitat they have frequented during their ontogeny: those in structured habitats (rocks, oyster substrates) have a greater ability to adapt to new habitats than those from simple habitats (sand, gravel), demonstrating the importance of early development in complex habitats.

Bibliography: *Animal.Cogn.,* 2019, **22** : 89-98, *J.Exp.Biol.*, 2014, **217**: 2431-2432 & DOI:10.1242/jeb.110361, 2458-2554 & DOI:10.1242/jeb.100149

1.1.7. *Karst* habitats*

In order to cope with the periods of low surface water levels, some species inhabiting karst* systems, such as the cyprinid *Delminichthys adspersus* of the limestone mountains of Croatia and Bosnia, find refuge during the summer in groundwater where they spend several months migrating to deep locations in accordance with the hydraulic inputs from the various temporary sources feeding the complex networks of karst. The result is a fragmentation of populations and a high dispersion of sub-populations concerned with ensuring their survival during a very difficult period. The so-called cave populations (Volume 1, section 1.1.16.2), which temporarily or permanently occupy hypogeous environments*, such as caves, underground rivers and phreatic waters, are very interesting models that illustrate the phenotypic plasticity of fish able to “adapt to anything”.

The world’s greatest biodiversity of cavern fish is found in the western Balkans with about 400 described species. A new species of loche of the *Barbatula* genus has recently been discovered in southern Germany, in the 250 km^2 karst system of the Danube–Aach system. It is clearly distinguished from the epigeal* Danube species by small eyes, more developed barbels, a shorter lateral line and pale body coloring, characteristics considered adaptations to underground life. Its microsatellite genetic characteristics* confirm its recent genetic isolation from surface populations and its low genetic diversity – lower heterozygosity*, higher inbreeding coefficient – characteristics that have been linked to recent glaciations from –20,000 to –16,000 years and the retreat of alpine glaciers, proof of a relatively recent conquest of certain habitats.

Bibliography: *Curr.Biol.*, 2017, **27**: R243-R258 & DOI:10.1016/j.cub.2017.02.048, *Mol.Ecol.,* 2012, **21**: 1658-1671 & DOI:10.1111/j.1365-294X.2012.05507.x

1.1.8. *Intermittent habitats*

Species living in the African savannah are subject to strong hydrological variations characterized by a period of pond desiccation during the dry season. The survival of species depends on physiological resistance in response to the intermittent nature of the availability of water in their environment. Adult killifish, *Notobranchus furzeri*, have a short life of a few months during the wet season and early sexual maturation: females are sexually mature at 18 days of age. They die at the beginning of the dry season after several egg-laying cycles, and their eggs only survive at the bottom of the dried ponds, with their embryonic development being physiologically stopped during a period of dormancy or diapause lasting a few months. The resumption of embryo development is chronologically programmed and anticipates the return of rainfall, so as to allow rapid hatching as soon as the ponds return to water, with their life cycle properly programmed according to seasonal cyclical variations.

Bibliography: *Curr.Biol.*, 2015, **25**: R741-R742

1.1.9. *Habitats modified by other animals*

In some rivers in the United States, the small cyprinidae, *Lepidomeda copei*, benefit from the structured and complex habitats resulting from beaver activity, particularly through the creation of deeper pools and warmer, macrophyte-rich waters upstream of dams built by these rodents. The recent ecological reintroduction of beavers is proving beneficial for fish.

Bibliography: *Ecol.Freshwat.Fish,* 2018, **27**: 606-616 & DOI:10.1111/eff.12374

1.1.10. *Manmade habitats*

Many marine fish have benefited greatly from the development of oil and gas platforms, with more than 7,500 of these metal structures worldwide, located in the coastal zone or on the high seas offshore, making them ideal habitats. The submerged structures of derricks constitute complex habitats that serve both as shelters and food storage, taking into account the development of an algal flora and a fixed fauna made up of sponges, corals – epibionts and vagile forms* – worms, mollusks and crustaceans. A number of fish with platforms located at depths of –85 to –175 m and aged 16–22 years have been studied in Queensland, Australia, using submarines. The ichthyic populations, i.e. 31 species belonging to 14 families, are made up of both in transit pelagic* – yellowtail, *Seriola dumerili*, jacks, *Caranx melanpygus*, whale sharks, *Rhincodon typus* – and large sedentary predators – snappers, *Lutjanus argentimaculatus* and groupers, *Epinephelus multinotatus*. This case is an example of ecological conversion and an interesting example of sustainable development. However, such structures, when obsolete, can become dangerous vectors for the spread of their fauna and associated flora over long distances. For example, platforms towed by sea from the Gulf of Mexico to the Adriatic Sea have introduced fish from that Gulf.

Other marine developments are accompanied by an increase in the structural complexity of the environment, which is favorable to the artificial creation of new microhabitats such as shellfish beds, floating and/or submerged fish cages, marinas, artificial reefs, groynes and dikes protecting beaches from erosion.

Aquaculture farm cages, artificial reefs and FAD (Fish Aggregating Devices) (Volume 1, section 2.3) play an identical role as artificial habitats. The Marennes–Oleron intertidal zone, exploited by the shellfish industry, is subject to significant biodeposition (600 t/km^2/d) made of lamellibranch mollusk feces and a diatomaceous biofilm, with these *ex-polysaccharides* organized in *colloids**. Inside, soles, *Solea solea,* often have to withstand the hypoxic conditions of this muddy substrate.

Artificial reefs offer cavities and alveolar structures of various sizes from which fish can benefit. Wrecks of warships and commercial vessels are also rich habitats that have been successfully colonized by morays, conger eels, groupers and many sparids. It has been shown that marinas in north-western Italy and along the rocky coasts of France are favorable to sparid juveniles, such as the four species of sars, *Diplodus* sp., which find protective shelters in areas sheltered by boulders and artificial wavebreakers, thereby increasing their recruitment success*.

Bibliography: *J.Fish Biol*., 2005, **66**: 865-870, 2008, **73**: 186-195 & DOI:10.1111/j.1095-48649.2008.01924.x, *J.Mar.Biol.Ass.UK*, 2006, **86**: 847-852, *Mar.Ecol.Prog.Ser*., 2007, **331**: 219-231, 2016, **547**: 193-209 & DOI:10.3354/meps11641, *Scientia.Mar.,* 2014, **78**: 505-510

1.1.11. *Ecological niches not frequented by other species*

Being assured of a lack of interspecies competition may mean occupying sites that are not frequented by others. Some species do not mind occupying extreme habitats, even if they are considered dangerous owing to their toxicity. Some populations succeed in colonizing them, following remarkable adaptive resistance. As a result, sources rich in *hydrogen sulfide,* H_2S, a gas toxic to most animals, which results from the decomposition of organic matter, are inhabited in Mexico by small endemic livebearers, *Poecilia sulphuraria* and *Gambusia eurystoma* which have developed physiological resistance mechanisms in these microhabitats particularly low in *oxygen* and rich in *hydrogen sulfide*, H_2S, which is detoxified into *thiosulfate* by their liver mitochondria*. Species subject to anthropogenic pollution from tanneries, pulp mills and other sources, and especially those whose natural habitats are deep hydrothermal springs (Volume 1, section 1.1.17.2), have homeostasis* saving mechanisms that make them "extremophilic" fish.

Bibliography: *Ecol.Lett.,* 2014, **17**: 65-71 & DOI:10.1111/ele.12209, *J.Fish Biol.,* 2008, **72**: 523-533 & DOI:10.1111/j.1095-8649.2007.01716.x

1.1.12. *Seemingly unlimited pelagic habitats*

Open water species such as tuna and whale sharks apparently have no physical limits to their mobility, except for gradients in temperature (*thermocline*), salinity (*halocline*) and *oxygen* concentration (*oxycline*), which constitute hydrological and ecological barriers that can only be crossed with thermal, halin, respiratory and osmoregulation stress, which are always costly in terms of energy. In addition, current dynamics can lead to the creation of sanctuaries or corridors with a certain autonomy and hydrological originality that affect their frequency. Their freedom to maneuver, within the masses of oceanic or lacustrine waters, is therefore not as considerable as could be imagined, with some ocean courses sometimes presenting constraining limits.

1.1.13. *Temporal fluctuations in habitat occupancy*

The occupation of space by a species varies over time in accordance not only with the local hydrological fluctuations in its habitat during floods, low water levels, etc., but also the presence or absence of predators. Consequently, in an English river, during the winter, *Thymallus thymallus* graylings show large variations in distribution in their home range*. This increases 5–20 times in relation to the higher density of avian predators, such as *Phalacrocorax carbo* cormorants. A greater activity would correspond to behaviors to avoid predators rather than to the search for refuge habitats that other salmonid species, such as trout, preferentially exhibit.

1.1.14. *Ontogenic and/or physiological fluctuations*

A distribution of species according to depth – bathymetry* – concerns the different stages of development by an optimal occupation of the water layers according to their own hydrological characteristics, as well as their richness in planktonic prey. Separate ecological distributions can also result from parasitic infestation, such as in *Gadus morhua* cod on the Norwegian coast where individuals infested with the parasitic trematode *Cryptocotyle lingua* are found at a greater depth than healthy fish. Is this so as not to transmit their black spot disease to their fellow fish?

Habitat changes occur episodically in migratory species (Volume 1, section 2.2.1), between their feeding and breeding habitats and vice versa, and more randomly, but generally caused by thermal preferences and food requirements in nomadic species and, in particular, frequent travelers (Volume 1, section 2.2.3).

1.1.15. *An amphibious existence*

1.1.15.1. *Freeing oneself from the aquatic environment, a climax for a fish to achieve*

A successful transition from the aquatic to the terrestrial environment is an important step in the evolution of vertebrates, with an exit from the water followed by a gradual conquest of continental habitats. The physical conditions in the aquatic environment and those in the terrestrial environment are quite different, with the former containing only 3% of *oxygen,* O_2*,* compared to 78% in the latter. Such a continental "conquest" is considered advantageous because it is accompanied by the possibility to exploit new energy resources.

1.1.15.2. *A new way of breathing*

Such a change of environment can only be successfully achieved if the fish has the ability to capture atmospheric *oxygen*, with an aquatic respiration mode based on the gills through which normal respiratory gas exchanges occur, an almost universal mode of aquatic respiration.

About 450 fish species do not use only dissolved *oxygen* in the water, as most of the other 30,000 fish species do. Why do they have such a physiological peculiarity? It is a response to difficult periodic environmental conditions: water loss (low water levels in rivers, seasonal drying of lakes and lagoons, low tide, etc.) or to a drastic decrease in the concentration of *oxygen* (hypoxia*). These aerial fish generally have a double respiratory system, namely, gills and a complementary system that promotes gaseous exchanges between their blood and the atmosphere: either their skin, or oral, pharyngeal or intestinal diverticulae consisting of cavities irrigated by networks of blood vessels, with the transport of *oxygen,* O_2*,* ensured by the *hemoglobin* contained in red blood cells (erythrocytes) and the elimination of CO_2 ensured by the skin or gills.

This use of respiration is necessary for marine species (more than 70 intertidal species* belonging to 12 families) that are subjected to alternating periods of flooding* and immersion in relation to the rhythm of the tides, high and low.

In the pantodon, *Pantodon buchholzi*, which has to breathe air, the respiratory organ is its very large and vascularized swim bladder. It is related to the anterior part of the digestive tract through the pneumatic channel, which allows this African freshwater fish to breathe air at the surface and out in the water during the gliding flights that earned it the name “butterfly fish”. It swallows air every 2 or 3 minutes at rest if the water concentration is 5 mg O_2/l. Its air swallowing activity increases or decreases with the saturation rate of the water, but the breathing of air always dominates breathing through the gills. The Japanese bluespotted mudhopper, *Boleophthalmus pectinirostris*, which digs a burrow in the coastal mudflat area and remains partially confined within it, has a unique air storage method: when its burrow is submerged, it continues to breathe the air stored in it (up to more than 400 ml) and which provides it with the additional *oxygen* necessary for its survival in this confined environment.

Other species optionally breathe atmospheric air by “swallowing” it at the surface. This breathing pattern is a useful adaptation to ensure the survival of these fish in swamps where hypoxic conditions* often prevail, following an increase in temperature or fermentation phenomena (decomposition of organic matter). This is the case of the endemic *Brevimyrus niger* mormyrid in African tropical fresh waters, which breathes on the surface when it reaches 26°C, generating a deficit in dissolved *oxygen*. Similarly, some African anabantid animals, such as *Ctenopoma muirei* from Lake Victoria, are able to use alternately aquatic gill breathing and air breathing depending on the level of dissolved *oxygen* in the water. Airborne breathing, made possible by a vascularized suprabranchial chamber, supplements a risk of hypoxia* in the lacustrine aquatic environment (0.49 mg of O_2/l in the morning), as fish come to the surface to absorb atmospheric air.

Bibliography: *J.Fish Biol.,* 2005, **67**: 292-298 & DOI:10.1111/j.1095-8649.2005.00725.x, 2007, **71**: 279-283 & DOI:10.1111/j.1095-8649.2007.01473.x, 2014, **84**: 577-602 & DOI:10.1111/jfb.12270, 774-793 & DOI:10.1111/jfb.12324, *Zeit. für vergl. Physiol.*, 1969, 65: 324-339

1.1.15.3. *Mangrove visitors*

The Florida mangrove cyprinodont, *Kryptolebias* (ex *Rivulus*) *marmoratus*, has developed the ability to emerge from the water and travel on land in order to feed (capture insects such as termites and locusts), although it does not have morphological adaptations that favor land movement. Its movements on wet ground were analyzed from videos that show body oscillations consisting of the body swaying, “snake-like” ripples (lateral curvature of the vertebral spine), “rolling” movements and jumps (pectoral fin thrust). Would such "non-tetrapod terrestrial" vertebrate behavior constitute an evolutionary step towards a historic exit from water for these fish? Irrespective, it does not move away from its natural environment and the prey it captures in the air is immediately taken and consumed underwater. However, it is likely to live long enough out of the water (more than 30 days on wet leaves) due to its ability to breathe through the skin. This is proof that fish can exploit terrestrial habitats and consume aerial prey by leaving their natural environment in a more or less sustainable way. This fish lives most often in holes dug by crabs, which are a poor *oxygen* environment that it willingly leaves during periods of emergence. Its ability to remain out of water for a long time is related to the development of a rich vascularization (angiogenesis) of its skin, mouth and bucco-opercular chamber which are permanently moistened and to the activation of *oxygen* transport through an increase in the number and density (hematocrit*) of red blood cells and an increase in the affinity of its *hemoglobin, Hb*, for *oxygen* (HbO_2). It regularly swallows air, with its ventilation rate being approximately one "breath of air" every 12 minutes. Such a successful adaptation to aerial life would be similar to the one likely to have been experienced by the primitive tetrapods who left to conquer the Permian and Carboniferous continents. The removal of water from this mangrove killfish would also allow it to cool down on land by causing the moisture from its body surface to evaporate when the temperature of the mangrove water reaches high temperatures (sometimes as high as 38°C).

In tropical coastal areas, when leaving the water at low tide, periophthalms, *Periophthalmus argentilineatus*, also use the abundant food resources (copepods, amphipods, polychaeta worms, crabs, etc.) of mangroves that are not accessible to most marine species. Some marine blennies do the same.

Bibliography: *J.Exp.Biol*., 2013, **216**: 3988-3995 & DOI:10.1242/jeb.089961, 2014, **217**: 3988-3995 & DOI:10.1242/jeb.110601

1.1.15.4. *Fish in the trees*

Are fish unable to "get up high"? Didn't Albert Einstein once write: "if you judge a fish by its ability to climb a tree, it will live its whole life believing that it is stupid". Yet, this great thinker did not know that other fish species, quite different from goldfish, were actually able to climb trees. Indeed, climbing perch of the *Anabas* and *Ctenopoma* genera are anabantidae from Southeast Asia that are able to leave their lacustrine and marshy living environment to crawl on the ground, from hole to hole, and thereby reach the low branches of trees. *Anabas testudineus* is the best known of these perches. Originally from China and India, it tends to colonize Indonesian and Australian waters and is even considered invasive in Australia. Equipped with the capacity to breathe air (possession of a suprabranchial cavity) that renders it able to spend 6 hours of its life out of the water and an ability to crawl on the ground using its pectoral fins used as crutches, it hides in the foliage of trees where it captures flying insects (flies, wasps), which even act as food. Its feeding strategy is unique as it does not swallow the ingested prey but stores this material in its mouth. Its consumption of prey therefore takes place at a site other than that of their capture. Such *climbing fish* would have astonished Albert Einstein.

Figure 1.2. *Anabantid climbing perch, Anabas sp., able to leave the water and climb trees*

Bibliography: *J. Fish Biol.,* 2008, **73**: 1053-1057 & DOI:10.1111/d.1095-8649, 2008.01987.x

1.1.15.5. *Surviving the dry season*

Lungfish, which are the best known of the "aerial respirators", are becoming more sustainable in the aquatic environment. The Australian lungfish, *Neoceratodus forsteri*, is able to survive, in dry season and in a subtropical climate, a total flooding, enclosed in a cocoon of soil and mucus buried in the soil of the dried Australian marshes. However, it cannot escape the aquatic environment during reproduction, which occurs in the wet season (August–December) by depositing its eggs in inert waters in shallow (<20–40 cm) flooded areas on the banks of rivers, which are covered with submerged or aquatic terrestrial plants (macrophytes) (*Eichhornia* water hyacinths). This spawning is threatened by extreme thermal variations (approximately 20°C, with maximum values of 32°C), a decline in *oxygen* concentration (<1–2 mg O_2/l), changes in water level, poisoning due to the decomposition of plant material, the development of filamentous algae and desiccation when water levels fall. For these reasons, the long duration of egg incubation (23–30 days) and larval development (21 days) compromises the survival of embryos and larvae. Such mortality risks, combined with low fertility (maximum 500 eggs), explain why this fish is considered an endangered species. *Protopterus* *dolloi*, which also grazes during the dry season (5–6 months) in a mucus cocoon that protects it from water loss, has a significant reduction in its metabolic activities, which allows it to avoid weight loss, energy decline or the melting of its muscle *proteins*, with its muscle and liver *glycogen* reserves preserved following low enzymatic glycolysis* activity. On the other hand, its production of *ammonia*, NH_3, a very toxic waste, is replaced by an increase in the synthesis and accumulation of *urea* in its tissues, linked to an activity of the liver *enzymes** of the "*ornithine urea cycle*". Such metabolic progress in waste disposal is quite comparable to that of mammals. The neighboring species *Protopterus annectens* moves on the ground using its pelvic fins, with a "walk" (claudicant) involving only two muscles (a retractor and a protractor) whose morphology is simple compared to that of the muscles that rotate the pelvic joints of the tetrapods, which can be considered a first "historic" attempt to "walk on the Earth".

Such respiratory capacity to use atmospheric *oxygen*, sometimes surprising in the case of air breathing through the vascularized digestive tract, as in several species of catfish, such as loricariidae such as *Hypostomus pardalis* and *Pterygoplichthys* sp., which can live up to 30 days out of the water, callichthydae such as *Coridoras* sp. and the weatherfish, *Misgurnus fossilis*, is interesting to consider in an attempt to explain the anatomo-physiological evolution of vertebrates during their conquest of the terrestrial world.

Bibliography: *J.Exp.Biol.*, 2014, **217**: 3474-3482 & DOI:10.1242/jeb.105262, *J.Fish Biol*, 2008, **73**: 608-622 & DOI:10.1111/j.1095-8649.2008.01955.x, 2014, **84**: 163-177 & DOI:10.1111/jfb.12264, 547-553 & DOI:10.1111/jfb.12349, 554-576 & DOI:10.1111/jfb.12323, 603-638 & DOI:10.1111/jfb.12279

1.1.15.6. *Ground and air spawning*

Australian species such as *Galaxias truttaceus*, a small galaxid in the southern hemisphere, lay their eggs upstream of estuaries or in streams along seasonally submerged forests, in shoreline vegetation, among plant roots. Eggs develop out of water, but in a humid atmosphere, with their hatching dependent on a seasonal rise in water levels in the floodplain. This spawn may not be submerged when the embryos have exhausted their energy reserves, but, generally, the arrival of high water in the wet season not only promotes their hatching (after some mechanical agitation), but also ensures the downstream transport of larvae to the sea and their dispersion, with the high turbidity of the water reducing the risk of predation. These "aerophilic" spawners are waiting for the water to rise to save their lives.

This is also the case for the California grunion, *Leuresthes tenuis*, which lays eggs at low tide in wet beach sediments and whose eggs hatch only when they are covered with water during the high tides of the next tidal cycle*. Similarly, the eggs of the splash tetra, *Copella arnoldi*, develop in the open air, glued to the underside of the leaves of plants on the banks of the Amazon, with their humidification ensured by water projections (tailbeats) made by the male.

Bibliography: *Fish Fish*. 2006; **7**: 153-164

1.1.16. *An underground life*

1.1.16.1. *Living in burrows*

Some fish have an affinity for life underground, at least during a phase of their life cycle, such as the goby-lote *Zosterisessor ophiocephalus*, which digs burrows to lay eggs, as well as to pass the winter. Some other gobies also live in burrows, along with shrimp that have dug them. *Typhlogobius californiensis*, a blind and depigmented fish at the adult stage, lives in pairs at the bottom of a vast burrow dug by a pair of *Callianassa affinis* shrimp. Another goby, *Cryptocentris* sp. (*Vanderorschia* sp.), a fish with good eyesight, lives at the entrance of the burrow dug by the shrimp *Alpheus djiboutensis*, which has poor eyesight. Such cases of "shrimp-fish" associations within a burrow occur often in warm seas and are examples of "mutualism*" (Volume 1, section 3.4).

1.1.16.2. *Living in caves*

Other species complete their entire life cycle in caves. Living conditions "underground", in the absence of light, are necessarily more difficult than those in light environments and require specific adaptations to cope with them. Fish living in light environments use their vision to orient themselves in space and navigate within their habitats. But what is it that forms living in underground environments, known as "troglomorphs" or "troglobies", do in total darkness in a difficult environment, poor in *nutrients*,* and when they have undergone a reduction in eye size, or even an evolutionary regression of their visual functions, a situation comparable to that of life in the deep?

The underground populations of the Mexican tetra, *Astyanax mexicanus*, are blind. The question arose about their use of geometric spatial landmarks. In the absence of light signals that are picked up in conspicuous epigenetic* surface shapes, these hypogenetic shapes use hydrostatic pressure measurement signals, both with their gas bladder (pressure along a vertical axis, which varies with depth) and with the neuromasts* of their lateral line* (horizontal axis). They are able, thanks to their mechano-receptors, the hair-cells of their lateral line, to perceive the slightest change in their immediate environment, to detect obstacles encountered as a function of the distortion of water flows at their level and to obtain a "three-dimensional map" of their environment.

A sensory system such as the lateral line is present in all fish, but it is hyper-developed here to meet the ecological needs for adaptation to life in dark caves and in groundwater, in the manner of a "supplemental radar". Their superficial neuromasts* are more numerous than those of their counterparts living in light environments. In the absence of visual signals, these sensory cells, particularly those in the orbit and in the suborbital position, which are twice the size of those of surface fish, receive messages produced by hydraulic flows generated by fish swimming and reflected by obstacles, as well as by prey, allowing them to feed "blind".

The study of their swimming trajectories was carried out during tests in labyrinths integrating various horizontal and vertical components, with this fish showing its ability to use all spatial information, memorize it and adapt to the cognitive data characterizing its environment. It detects the position of stationary obstacles thanks to signals produced by the hydraulic movements of its own swimming, with its lateral line* capturing the disturbances of fluids generated (reflected waves) by the presence of obstacles whose distance it can measure. It therefore navigates using a combination of signals that constitute a system reminiscent of bat echolocation*. Memorizing certain spatial landmarks and the topography of the site (a GPS-type geometric map!) then facilitates its movement in a familiar environment in accordance with a precise geometric representation of its spatial environment.

The production of oral suction movements also generates a hydrodynamic flow that varies according to pressure gradients according to the distance of the obstacles, which facilitates the detection of obstacles through the lateral line using an echolocation method. It thereby manages to find its way with its mouth.

Their need to group together in schools for anti-predatory purposes is less than in enlightened environments due to the absence or rarity of predators, and populations of cave species tend to live in a more dispersed manner, with reduced social cohesion. They seem to lead a quiet life, far from the frenzied world of light environments.

Amblyopsis spelæa is also a blind and depigmented cavern fish. It was discovered by biospeleologists in a Kentucky cave in 2002. Its characteristics, in particular, the absence of colored pigment, are reminiscent of those of the famous axolotl *Ambystoma mexicanum*, a Mexican newt. The colonization of such environments does not appear to have been accidental and could be explained by their quality as climatic refuges during ice ages and as secure habitats, given the scarcity of predators (except bats, *Noctilio leporinus*).

Many of these species found in caves, karsts* and groundwater are still largely unknown. Periodically, new species are discovered and described, such as *Triplophysa* sp., a blind loach, in China in 2002.

Bibliography: *Anim.Behav.,* 2004, **68**: 291-295 & DOI:10.1016/j.anbehav.2003.11.009, 2005, **70**: 405409 & DOI:10.1016/j.anbehav.2004.11.007, 2013, **86**: 1077-1083 & DOI:10.1016/j.anbehav.2013.09.014, *Curr. Biol.,* 2013, **23**: 1874-1883 & DOI:10.1016/j.cub.2013.07.056, *J.Exp.Biol.,* 2014, **217**: 886-895 & DOI:10.1242/jeb.064599, 1955-1962 & DOI:10.1242/jeb.098384, *J.Fish Biol.,* 2005, **67**: 3-32 & DOI:10.1111/j.1095-8649.2005.00776.x1.1.16.3. Regressive evolution or proof of plasticity?

Biospeleologists have been interested in these cave forms, which are considered unique in comparison with those of the epigeal* conspecific populations from which they seem to derive, sometimes leading, due to a loss of pigmentation and the disappearance of the eyes, to the idea of the existence of a "regressive evolution" that is both anatomo-morpho-physiological and behavioral. However, the hypothesis of the accidental colonization of hypogeal* waters does not seem to be accredited and has given way, on the contrary, to the concept of a biological evolution based on a remarkable organic plasticity aimed at exploiting "underground niches" as "new" niches, which are both under-exploited by other species and lacking predators. These cave fish are said to be pioneers rather than refugees.

The evidence would be provided by comparative genetic examinations of the epi- and hypogeal* populations of the Mexican characin, *Astyanax fasciatus*, whose "divergence", said to have occurred between –525,000 and –700,000 years ago, predates the most recent glaciations (see *Amblyopsis spelæa*). These fish can serve as models for studying the plasticity of organisms, demonstrating that "phenotype = genotype + environment".

Bibliography: *J. Fish Biol.,* 2005, **67**: 3-32 & DOI:10.1111/d.1095-8649.2005.00776.x

1.1.16.3. *The advantages of an underground life*

Living in environments deprived of light and, as a result, of resources related to photosynthesis, seems, *a priori*, difficult, and hypogeal* populations appear to have to endure physiological handicaps and are therefore "to be pitied". Yet, these environments offer a number of eco-physiological advantages: an almost constant temperature and a scarcity of predators, which are usually of major concern to species in light environments. As for *nutrient** poverty, this is sometimes compensated for by a high food detection capacity. For example, all catfish have barbels, but those of hypogeal species such as the blind catfish, *Trogloglanis* *pattersoni*, present in Texas groundwater, are hyper-developed and very rich in chemosensory cells. Taking advantage of their “colonizing spirit”, these fish have had access to a vast and complex underground domain and a rich network of underground interconnections, most of which are still ignored.

These environments are known to be particularly soothing, to the point that their inhabitants are almost completely unaware of competition, combativeness and competition, sexual harassment and all other factors of agitation in enlightened environments.

Bibliography: *Behav*., 2008, **145**: 73-98, 931-947

1.1.16.4. *Opaque environments*

Weakly electric gymnotiform fish use the distortions of the electrical signals (electrical waves) produced by their electrical organ, EOD*, and reflected back to their electrical receptors, forming a 3D “electrical image” of moving or immobile bodies in their environment. Such electro-localization constitutes a “sixth sense” (Volume 1, section 3.1) that allows them to navigate in opaque tropical waters, as well as at night. Spawners among *Petromyzon marinus* sea lampreys do not use any visual signals to migrate to their continental spawning grounds at night, although they have, in addition to eyes, epiphyseal* (pineal gland*) and dermal photoreceptors in the tail that function as effective “radar” if they cannot navigate by sight.

1.1.17. *Living in the abyss*

1.1.17.1. *A difficult world*

Life in the depths of the oceans is particularly difficult because of the “extreme” conditions prevailing in this cold environment (0–4°C), which is deprived of light –in fact, there is weak light in the mesopelagic zone* between –150 m and –1,000 m and an almost totally aphotic environment* above –1,000 m (although bioluminescence is not insignificant) – characterized by very high pressures, a low *oxygen* concentration and often a high poverty of food resources, although the bodies of large pelagic fish and, in particular, those of marine mammals (whales, killer whales, dolphins) constitute significant nutrient inputs. The corpse of a whale is a blessing for an entire sector of the abyssal ecosystem.

The number of species that have managed to adapt to such an “extreme” environment is limited by this relative scarcity of food, to the point that it has long been accepted (Forbes 1844) that these deep waters were deprived of life and are azoic* from more than –550 meter deep. This is not the case, as demonstrated by the expedition of the Challenger (1876). Some groups of fish, generally endemic* ones, have successfully colonized these deep waters with varying degrees of success: hagfish (Volume 1, section 1.2.1.8) down to –2,750 meter deep, cartilaginous fish up to –3,000 m and chimeras (holocephalic) up to –8,300 m, with the depth record for *Abyssobrotula galatheae* (ophiidae) at –8,370 m. These species are considered “extremophilic”.

Anoxic attacks* have occurred on various occasions since the dawn of the fish (Devonian: –400 MA, sometimes referred to as the “fish age”) and current fauna result from the recolonization of surface species, which is believed to have occurred since the Cretaceous period (–94 MA). Specialized invasive families (ophidiids, liparids, ceratoids) are dominant at depths greater than –6,000 m.

Fish adapted to the ambient conditions of the deep waters mentioned above often, but not exclusively, have elongated morphologies and practice an “anguilliform” mode of locomotion, with the degree of elongation increasing with depth between –300 and –2,030 m in the northwest Atlantic. The *Coryphænoides rupestris* (macrouridae) grenadier dominates in these oceanic areas, with sharks and rays rare and flatfish completely absent. In depths greater than –1,000 m in the western Mediterranean, *Coryphænoides mediterraneus* grenadiers and other deep-sea species feed at daily rates that correspond to the temporary availability of pelagic prey* that migrate vertically, unlike their counterparts who, consuming permanent benthic* prey, do not show any feeding pattern. A certain lack of knowledge of these species comes from the fact that they are difficult to access and victims of the sudden decompressions suffered during their surface rise during deep fishing operations that cause the formation of gas bubbles in the blood, internal bleeding, exophthalmia* and gastric extroversion that are followed by death. The use of hyperbaric* chambers to bring back caught samples alive, effective in shallower fish (redfish, *Sebastes* sp., caught from –100 to –150 m), is rarely sufficient for more abyssal species.

Particular attention was paid to the visual devices used in bathypelagic* and bathybenthic* species (tubular or bidirectional eyes, large pupil, reflective mirrors). In deep water, where the absence of light is compensated for by the production of biological light (bioluminescence) (Volume 1, section 1.1.17.2), vision is provided by anatomical–physiological eye structures that are generally very complex and often associated with specialized bacteria.

While it was generally accepted that color vision did not exist in the dark depths of the abyss (“where all cats are gray”!) due to the single *opsin* in their retinal* sticks that is responsible monochrome vision, it has just been demonstrated that certain abyssal species such as the silver spinyfin, *Diretmus silvery*, are endowed with the ability to perceive certain colors, in this case certain shades of blue, thanks to the cones and rods of their retinas of 14 genes encoding several *rhodopsins* that are sensitive to several portions of the blue light spectrum. This fish can thereby capture residual sunlight and, above all, discern congeners, prey and predators, particularly those that produce blue bioluminescence.

Bibliography: *Biol.Rev.*2004, **79**: 671-712 & DOI:10.1017/S1464793103006420, *J.Fish Biol.*, 2007, **70**: 867-878 & DOI:10.1111.1095-8649.2007, 01347.x, 2013, **83**: 1528-1550 & DOI:10.1111/jfb.2013.83, 1576-1591 & DOI:10.1111/jfb.12266, *Proc.Roy.Soc.B*, 2014, **281**: 20133223 & DOI:10.1098/rspb.2013.3223, *Science*, 2019, **364**, 6440 : 588-592 & DOI:10.1126/science.aav4632

1.1.17.2. *One exception: hydrothermal springs*

A special and original case concerns the ichthyofauna (*Hydrolagus* sp., *Epigonus* sp., *Mora* sp., etc.) of the deep hydrothermal springs of the Atlantic Rift (–3,200 m) which are distinguished by their high chemosynthetic productivity, low O_2 concentration, high *hydrogen sulfide,* H_2S, content and high *metal* content, particularly *methyl mercury*, with high muscle and liver contamination (1.9 and 1.7 µg *Hg*/g respectively) due to bioconcentration* caused by their situation as “top predators” (biomagnification*). These hydrothermal springs with naturally hypertoxic waters are nevertheless considered “islands of productivity” on the ocean floor, compared to a particularly poor bathyal* environment. At least 40 species of bathyal fish* have been inventoried (bottom longlines) on this mid-Atlantic ridge at depths ranging from –900 to –1,760 m. They are all endemic* and feed, like the rabbit fish, *Hydrolagus pallidus*, on hydrothermal prey, with their richness in n-7 *fatty acids* confirming their chemosynthetic origin.

Bibliography: *Cybium,* 2004, **28**: 33-44, *Mar.Ecol.Prog.Ser.*, 2006, **320**: 253-258

1.1.17.3. *An abyss sometimes enlightened*

In the absence of sunlight, many organisms, including deep-sea fish, produce “biological light” (bioluminescence*) for predator camouflage (Volume 1, section 1.3.4), predator deterrence (Volume 1, section 1.3.3), prey capture and communication between sexes (Volume 1, section 3.1.2).

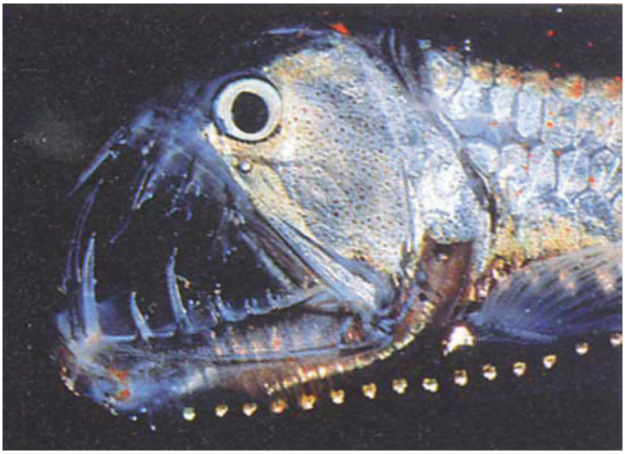

Figure 1.3. *Abyssal fish carrying ventral photophores*

1.1.17.4. *A hope of improving our knowledge*

Much remains to be learned about these deep faunas. Are our achievements less than those of the Moon, Mars or Venus? The technical improvements made to submarines and on-board vehicles hold great promise for progress in terms of improving our knowledge of the abyss and its occupants. For example, the snail fish, *Careproctus rhodomelas*, has recently been described from Pacific hydrothermal springs (Okinawa) that have been explored by a remotely operated vehicle (ROV). It lives at a depth of –1,530 m (3.8°C, 1.3 ml O_2/l) and lays a small number of large eggs (6 mm in diameter).

Bibliography: *J.Fish Biol*., 2010, **77**: 1709-1715 & DOI:10.1111/j.1095-8649.2010.02789.x

1.2. Food: the use of trophic habitats

The search for food and its consumption is, for fish as for all other animals, a major and essential activity. All of their senses are used for the precise detection of prey, and all of their energy is mobilized for its capture and ingestion in order to satisfy their appetite and meet their energy needs.

1.2.1. *Choose more or less energy-giving foods*

Fish adopt a variety of diets and consume prey that often has highly variable nutritional values. Some generalist species or euryphagous*, with a strong appetite, use all kinds of prey to satisfy it. As a result, the catfish, *Ameiurus melas*, native to North America, feeds indifferently on plant material, detritus and animal prey, living or dead – chironomids, worms, crustaceans, mollusks and fish, as well as their eggs and larva. Its sensory potential to use smell to discriminate between mixtures of amino acids* is considerable: it recognizes 10 of them from a mixture of 12, with the stimulating effect of *cysteine*. Its wide diet favors its potential for the colonization of European fresh waters (Volume 1, section 2.3.2). This voracious benthophagous* seriously damages native European species, even being capable of limiting the trophic activity of the *Esox lucius* pike with which it competes for food in fresh waters.

The European wels catfish, *Silurus glanis*, also consumes all kinds of prey: invertebrates in its early years, then crayfish, carps, water birds and even, exceptionally, pigeons (Volume 1, section 1.2.2.2.7.2).

The deep-sea shark, *Dalatias licha*, is a predator at the top of the food pyramid in the Mediterranean, with its diet made up of various animal prey: crustaceans, cephalopods, fish and even small sharks.

Other species are monophagous by adopting a specialized diet such as some large pelagic* planktonophagous that consume masses of food and do not make any selections, such as the megamouth shark, *Megachasma pelagos*, that travels the oceans in search of planktonic aggregations – hot spots – that it captures by swimming with its mouth wide open, by a process of suction, bucco-pharyngeal suction and branch filtration.

Dolly Varden trout, *Salvelinus malma*, residing in Alaskan coastal streams make extensive use of the nutritional resources of *Onchorhynchus nerka* sockeye salmon, which cover 80–90% of their diet, especially during their juvenile phase. They feed easily on salmon eggs because of the absence of a limit on their ability to open their mouths, but they also, following the death of spawners on the spawning grounds, feed on the flesh of their corpses and maggots – diptera larvae – which develop on their partially emerged carcasses. *Isotope* analysis* at $\delta^{15}N$ and $\delta^{13}C$ confirms the essential role played by these migratory salmon – 2–6 million adult individuals returning annually to Alaska rivers to breed and perish (Volume 1, section 2.2.1.1.1) – in feeding trout resident in freshwater streams. These salmon will ultimately also be preyed upon by bears and eagles.

An oophagous diet, such as that of the American sawfly, *Sciænops ocellatus*, is a source of essential *fatty acids* such as *arachidonic acid*, which promotes the growth and survival of embryos and larvae and increases their recruitment potential*. Their development is boosted by the maternal diet. Lake trout eggs, *Salvelinus namaycush*, attract various predators, such as the sculpin, *Cottus cognatus*, as a result of the production of olfactory signals emitted during spawning on Canadian spawning grounds.

Bibliography: *Biol.Lett*., 2013, **9** & DOI:10.1098/rspb.2013.0593, *Env.Biol.Fish,* 2014, **97**: 1323-1333 & DOI:10.1007/s10641-014-0221-3, *Eur.J.Physiol.,* 2010, **459**: 413-425 & DOI:10.1007/s00424-009-0720-9*, J.Fish Biol.,* 2008, **73**: 17-34 & DOI:10.1111/j.1095-8649.2008.01880.x, 96-114 & DOI:10.1111/j.1095-8649.2008.01908.x, 2011, **79**: 33-52 & DOI:10.1111/j.1095-2011.02976x, 2014, **84**: 1562-1573 & DOI:10.1111/jfb.12388, *Mar.Biol.*2014, **161**: 1697-1707 & DOI:101007/s00227-014-2454-2

1.2.1.1. *Eating behaviors that vary by species, sex, and physiological and ecological conditions*

Seahorses, camouflaged in the meadows of phanerogams – eelgrass, posidonia – where they hunt for animal prey made of small planktonic crustaceans (amphipods, mysides, decapod larvae), show differences in the composition of their diet, both between sympatric* Aegean Sea species such as *Hippocampus hippocampus*, *H.guttulatus*, between males and females, between incubating males – an incubation of eggs in a marsupial pouch – and non-pregnant males (Volume 2, section 2.12.7; Figure 2.9), but it is females that exhibit the greatest trophic activity and selectivity, in order to better court males, in view of the reversal of sexual selection behaviors in these syngnathids (Volume 2, section 1.4.1.1)?

Subjected to learning tests, guppy females, *Poecilia reticulata*, appear to have greater capacities for innovation in foraging than males, who make twice as many mistakes as their mates when subjected to prey finding tests, reflecting the behavioral flexibility of the “weaker sex” in capturing prey.

Brown trout varieties, *Salmo trutta*, are known in oligotrophic lakes in Great Britain and Ireland, characterized by their accelerated growth, early piscivorous feeding and remarkable longevity (23 years) compared to local insectivorous and invertivorous trout strains*. A piscivorous diet is a strategy that promotes hyper-growth and longevity.

Fish generally exhibit seasonal patterns of trophic activity and have a high capacity to withstand fairly long periods of fasting without severe sub-lethal effects, as in the European seabass, *Dicentrarchus labrax,* which can go without food for 45 days. An interruption in food activity can result from disturbances caused by ambient noise, with sticklebacks, *Gasterosteus aculeatus,* ceasing to feed – consumption of daphnia – when stress-generating boats pass by. Fall and especially winter thermal conditions lead to a cessation of feeding, as in Canadian brook salmon, *Salvelinus fontinalis*, with body temperatures near zero stopping all the secretion of digestive enzymes* and gastric emptying during a winter fast.

Food overactivity usually occurs after a period of famine responsible for growth depression. Growth retardation linked to an increase in temperatures concerns the marine pleuronectids in the high latitudes of the Pacific *Hippoglossus stenolepis*, which compensates for its energy losses by an increase in food activity. Such hyperphagia then allows so-called "compensatory" growth, as in carp, *Cyprinus carpio,* roach, *Rutilus rutilus*, stickleback, *Gasterosteus aculeatus*, and tilapia, *Oreochromis mossambicus*, in which digestive enzyme activities – *trypsin*, *chymotrypsin*, etc. – are stimulated. This reflects digestive plasticity and the economical use of scarce food.

The dietary success of most species is also based on the richness of their symbiotic* digestive microflora (bacterial microbiota), which varies from one population to another and from one individual to another, as in the stickleback, *Gasterosteus aculeatus*, and which plays an essential role in the digestion and assimilation of food. It is dependent on the major histocompatibility complex (MHC) (Volume 1, section 3.7.4.2.6), which controls the health status of each individual. The health of fish, like ours, would therefore depend on their gastric and intestinal bacterial flora.

Bibliography: *Anim.Behav.,* 2014, **89**: 191-198 & DOI:10.1016/j.anbehav.2013.12.029, *Behav.,* 2004, **141**: 1543-1553, *Biol.Lett.,* 2014, **10**: 20140206 & DOI:10.1098/rsbl.2014.0206, *Ecol.Freshwat.Fish,* 2018, **28** : 4-10 & Doi.org /10.1111/eff.12421, *Ecol.Lett.,* 2014, **17**: 979-987 & DOI:10.1111/ele.12301, *Funct.Ecol.,* 2014, **28** : 878-885 & DOI:10.1111/1365-2435.12230, *J.Exp.Biol.,* 2014, **217**: 859-865 & DOI:10.1242/jeb.097899, *J.Fish Biol.*, 2003, **62**: 195-205 & DOI:10.1046/j.0022-1112.2003.00019.x, 2005, **66**: 167-181 & DOI:10.1111/j.1095-8649.2004.00590.x, 2007, **71**, supplt B: 174-185 & DOI:10.1111/j.1095-8649.2007.01401.x, 2008, **72**: 1259-1267 & DOI:10.1111/j.1095-8649.2007.01789.x, **73**: 196-205 & DOI:10.1111/j.1095-8649.2008.01936x, 2014, **84**: 1099-1116 & DOI:10.1111/jfb.12351, 2014, **85**: 621-644 & DOI:10.1111/jfb.12447, *Mar.Ecol.Prog.Ser.,* 2005, **293**: 233-240, *Mol.Ecol.*, 2014, **23**: 1891-1898 & DOI:10.1111/mec.12699, 4831-4845 & DOI:10.1111/mec.12846, *Nature Comm.,* 2014, DOI:10.1038/ncomms5500, *Zool.Stud.*, 2008, **47**: 207-2141.2.1.2. Nycthemeral feeding rhythms

Research and feeding activities vary according to environmental parameters – temperature, light – and the availability of prey. Daily feeding rates are generally synchronized with the sunlight cycle and its seasonal variations. In the Mediterranean, however, fish at depths greater than –1,000 m, such as grenadiers, *Coryphaenoides mediterraneus*, which live in total darkness, exhibit rhythmic activity dependent on the availability of pelagic prey that migrate vertically, unlike species such as *Coryphaenoides guentheri*, which eat benthic prey* and have no rhythmic feeding activity. There are temporal encounters between predators and their prey.

Bibliography: *J. Fish Biol.*, 2014, **85**: 800-820 & DOI:10.1111/jfb.12459

1.2.1.2. *Relationship between predator and prey size*

The size of the prey ingested by carnivorous species depends mainly on the diameter of the mouth opening that enables ingestion. This is why the size of the prey generally increases with that of the predator, which consumes larger prey as it grows, with the larger prey having a higher energy value. However, there are exceptions, as opportunistic predators such as the yellowfin tuna, *Thunnus albacares*, continue to feed on small prey – sardines, sardinella, anchovies – during their day dives and in which there is a clear asymmetry between the size of the predators and their prey in Polynesia.

Bibliography: *Mar Ecol.Prog.Ser.,* 2006, **323**: 223-231

1.2.1.3. *Loyalty to a standard plan*

The guppy, *Poecilia reticulata*, shows a strong attachment to tradition in its feeding, with little monitoring of the effects of participation in a group that offers social learning alongside consumers of new prey. In a population of sticklebacks, *Gasterosteus aculeatus*, some individuals even refuse to eat a food that is new to them. These risk-averse consumers are food conservative.

Bibliography: *Anim.Behav.,* 2008, **75**:565-572 &
DOI:10.1016/j.anbehav.2007.06.014, 2014, **88**: 49-56

1.2.1.4. *Zoo-geographical differences*

The diet of sardines, *Sardina pilchardus*, seems, at first glance, to be very commonplace as it is plankton-like. However, the anatomical collection system constituted by the branchiospines* located on the gill arches, which act as a filter to planktonic particles, varies from one population to another depending on the size of the planktonic prey present in the ocean waters they frequent. As a result, populations on the Spanish coasts of the western Mediterranean collect prey (copepods, water fleas, decapod larvae) of larger size (750–4,000 µm*) than those on the Atlantic coasts of Spain (phytoplankton and 50–1,500 µm copepods) according to a perfectly calibrated planktonic filtration.

Bibliography: *J.Fish Biol.,* 2015, **86**: 1348-1362 & DOI:10.1111/jfb.2015.86.issue-4/issuetoc

1.2.1.5. *Food competition*

Strong competition for food often occurs in natural environments between individuals of the same population, to the benefit of the largest, strongest and most dominant. The smallest individuals of Arctic char, *Salvelinus alpinus*, victims of competition from the larger ones, are often forced to adopt unusual feeding patterns, such as feeding at night to reduce the aggressive interactions that are common during the day. Such competition is amplified when humans intervene by producing, in hatcheries, juveniles that are very well fed and whose growth rates are higher than those of their wild counterparts, as occurs in Japanese char, *Salvelinus leucomaenis*. Released into the wild, these individuals, whose sizes are 14% larger than their wild counterparts, have a competitive advantage over wild individuals, although they often exhibit less aggression. An increase in aggressiveness is then sought by planners who carry out breeding operations designed to release young who are both early and combative into the natural environment.

Aggressive behavior, which occurs in situations of competition between congeners for access to food, tends to decrease when the risk of predation increases, especially in the most vulnerable small groups, such as the convict cichlid, *Amatitlania nigrofasciata* ex *Archocentrus nigrofasciatus*. Predators pacify competitive relationships.

Bibliography: *J. Fish Biol*., 2008, **73**: 524-535 & DOI:10.1111/d.1095-8649.2008.01941.x

1.2.1.6. *Eating differently avoids competition*

Not eating like others avoids the problems of interspecies competition. Cichlids, *Perissodus straeleni*, from Lake Tanganyika are scale eaters who take samples using jaw devices – mouth openings oriented to the left or right – and specific dental specializations – in slides, curved, truncated, etc. – which allow the implementation of original processes for scratching and/or tearing off scales during bites directed against the sides of prey fish, some of which are accompanied by the predator's body rotation. A diversification of dental devices and scale removal procedures can be observed in the related species *P. microlepis*. The success of attacks, which are fast and follow ambushes, remains relatively low, at 20% of attempts, because the target species are constantly on guard. Such a diet, called "lepidophagous", is found in 39 genera of fish belonging to various families and is proof of a spectacular phylogenetic diversity. Various anatomo-morphological devices involving dentition and musculoskeletal movements of the jaws promote specific scaly rasping operations and mucus coating, as evidenced by scanning studies of the oral morphologies of a characin, *Roeboides affinis*, and a piranha, *Catoprion mento*, which reflect specific anatomical and behavioral features.

Bibliography: *J. Fish Biol.*, 2007, **70**: 1458-1469 & DOI:10.1111/d.1095-8649.2007.01423.x, 2013**, 83**: 1210-1220 & DOI:10.1111/jfb.12217, *Roy.Soc.Open Sci*, 2018, **5**, 1 & DOI:10.1098/rsos.171581

1.2.1.7. *Knowing how to be satisfied with little… and even the worst*

Not all fish are fortunate enough to have access to rich prey, and some are forced to be satisfied with lower quality food, which is sometimes available in random quantities. The roach, *Rutilus rutilus*, is known for its hardiness, because it is able to consume all kinds of prey, from algae to worms, mollusks, insects, in open water (plankton, pelagic prey*) or on the seabed (benthic prey*). Such flexibility allows it to live in rivers and lakes and to exploit all available resources, which favors its colonization of new environments such as Irish lakes. Similarly, the common rudd, *Scardinius erythrophthalmus*, is a euryphagous omnivore that exploits both filamentous algae and plants (renoncules, potamogetons) and animal prey (chironomes, mollusks) as well as various detritus of low energy value, which sometimes explains its low growth.

Other species target specific prey and have a specialized and sometimes even hyper-specialized diet. The Patagonian cod, *Patagonotothen ramsayi*, is unique because, at the end of summer and in autumn, it uses resources of low energy value whose water content is 95–98% of their mass and that are neglected by most other species: the so-called gelatinous plankton, composed of jellyfish and ctenophores which are very abundant at those times of the year. The stomach contents attest to this opportunistic feeding that occurs without significant competition from other fish species present in this sector. In the Irish Sea, jellyfish, *Aurelia aurita*, participate in the food chain of various fish species, in particular, herring, *Clupea harengus*, and whiting, *Merlangius merlangus*, as well as gray gunard, *Eutrigla gunardus*, capelin, *Trisopterus minutus*, dogfish, *Scyliorhinus canicula*, sole, *Solea solea*, and so on. Such food is poor but often abundant and easily accessible. The moonfish, *Mola mola*, is a large consumer of jellyfish, salps and siphonophores. An adult of 120 kg would consume 70 kg of these jellyfish daily. The increasing abundance of this geological plankton in the western Mediterranean and the eastern Atlantic, in relation to current global warming, is accompanied by an increase in moonfish populations, which in the Gulf of Lion are estimated at 475 individuals/km^2. Such a general phenomenon is recent, and English-language authors refer to it as *the rise of slime*.

And what about the scavengers and other garbage collectors, the Atlantic hagfish, *Myxine glutinosa*, who live at a depth of 1,100 m on muddy substrates and consume all kinds of dead prey – invertebrates, fish, cetaceans – deposited on the seabed, even if these bodies are in the process of decomposition. The round goby, *Neogobius melanostomus*, invasive in many regions (Volume 1, section 2.3.3), generally consumes soft and easily accessible tissues: successively. the eyes, viscera and muscles of dead fish.

Individuals of the black triggerfish, *Melichthys niger*, exploit the feces and vomit of marine mammals such as dolphins, *Stenella* sp., whose movements on the reefs of the Brazilian coast they closely follow, watching for the slightest sign of defecation by their fellow travelers, although fecal particles may also be accompanied by intestinal parasites. They should not be considered species that are content with little because their food is richer, more valuable and much more respectable than some think. It is important to avoid any anthropomorphic judgment because, for those concerned, it is a real feast.

Bibliography: *Banyuls Obs Sea Service*, mai 2018, 4, *Curr.Biol.*2017, **27**: R1263-R1264 & DOI:10.1016/j.cub.2017.09.027, *J.Fish Biol.*, 2009, **75**: 1230-1243 & DOI:10.1111/j.1095-8649.2009.02359.x, 2014, **84**: 1099-1116, 2015, **87**: 194-199 & DOI:10.1111/jfb.12708, *Roy.Soc.Open Sea*, 2017, **4**, 11 & DOI:10.1098/rsos.171421, *Scientia Mar.,* 2007, **71**: 505-511

1.2.1.8. *The quantity is more important than the quality*

Sometimes, it is necessary to eat a lot, all day long, to satisfy hunger and accumulate a minimum amount of energy from poor food. In the Great Barrier Reef, the exploitation of natural resources involves a series of diets, from the richest – carnivorous predators, consumers of animal plankton – to herbivores – surgeons, parrot fish – to detritivores*, consumers of energy-poor elements – detritus material, plant detritus in the process of bacterial decomposition – and sedimentary – bacterial microfilm – all poor in *fatty acids*. The latter, such as surgeon fish, *Ctenochætus striatus*, and parrotfish, *Chlorurus* sp., *Scarus* sp., begin to feed at dawn, with their digestive tracts, empty at that time, showing a rapid turnover of digestive content with low energy value during the night. In such detritivores, the quantitative is more important than the qualitative.

1.2.2. *Adopt original hunting methods*

1.2.2.1. *Experiencing through social learning and/or copying others*

Every individual, during youth, has innate genetic abilities, transmitted by their parents and which often prove insufficient to enable them to capture prey. Indeed, they are initially naive and must acquire experience, either individually as a result of trial and error or collectively with older and experienced colleagues who must be observed so that their know-how can be absorbed and copied. Regardless of the innate patterns of food consumption, the search for and ingestion of prey also depend on education from congeners who act as “leaders” in groups (Volume 1, section 3.3) and the “followers” who accompany them, such as the Arctic char, *Salvelinus alpinus*, when, where and what to eat in Swedish waters: forms of copying. Fish, who generally have a keen sense of observation, with vision being one of their most commonly used sensory functions, become capable, through careful observation of their congeners, of acquiring useful information about their food and the capture of their prey, as part of a social transmission of signals that have some economic value – saving time and energy – in order to benefit from it. This is the value of having good teachers.

Young minnows, *Phoxinus phoxinus*, use social information by swimming in schools (Volume 1, section 3.3.4) with older congeners to improve their foraging while remaining less exposed to risks of predation. The more others they work with, the faster they make progress. Similarly, common carp, *Cyprinus carpio*, benefit from learning to search for their food when associating with congeners acting as teachers. Their food intake performance is optimal when combined, in mixed schools, with tilapia, *Oreochromis niloticus*. These cyprinids, who are slow learners, then benefit from the know-how of faster learners. On the other hand, a certain inhibition of the performance of the latter is linked to the presence of less intelligent carp: two species with different cognitive abilities.

Learning can be experimentally demonstrated by offering young brook salmon, *Salvelinus fontinalis*, a new prey they do not know, such as worms quite different from the dry pellets* that form their usual food. These young individuals learn quickly (<1 day) to consume the new prey when they have been spectators of the food intake by means of adults acting as demonstrators, whereas it takes them 7 days to acquire the same approach alone. Such social learning, through copying, is beneficial because it reduces the energy cost of finding food. Gathering information from others is preferable to a long and difficult individual search.

Bibliography: *Behav*., 2007, **144**: 611-630, *Env.Biol.Fish,* 2014, **97**: 523-528 & DOI:10.1007/s10641-013-0171-1, *Fish Fish*., 2003, **4**: 203-215, *J.Fish Biol*., 2007, **71**: 1023-1034 & DOI:10.1111/j.1095-8649.2007.01568.x, 2014, **84**: 133-144 & DOI:10.1111/jfb.12259

1.2.2.2. *Accurate detection of the location of prey buried in the sediment*

Some elasmobranch predators such as the dogfish, *Scyliorhinus canicula*, are able to locate prey – crustaceans, worms, etc. – with great precision, even when they are not directly visible or directly accessible, thanks to the weak bio-electric fields (15 μA*) they produce and which are detected by an electroreception process. The effectiveness of catching organisms buried in surface sediment (0–50 mm) depends on the depth and nature of the substrate (sand, pebbles, rock) whose physical properties can create distortions in the electric field. A sandy sediment of low resistivity –

<200 Ωm* – is favorable to the optimal feeding activity of these benthic invertebrate predators*. It is a “bio-electric” hunt.

Bibliography: *Anim.Cogn.,* 2014, **17**: 55-65, *J.Fish Biol.*, 2008, **72**: 1450-1462 & DOI:10.1111/j.1095-8649.2008.01807.x

1.2.2.3. *Discrete prey capture strategies, very precise in time and space*

The capture of flighty prey is generally crucial for the survival of predators who are condemned to feed relentlessly and avoid a fasting situation that is particularly critical in their early years, when they do not yet have sufficient energy reserves. Their success depends on both predator performance and the capabilities of prey to escape. All species that feed on live and mobile prey, known as vagiles*, require, in order to obtain a successful capture, the ability to precisely detect these prey by integrating their direction and their swimming and escape speeds. Properly targeting the point of attack allows for a successful interception. With the black bass, *Micropterus salmoides*, a video image visualization study showed that the chances of catching large prey, which have a high escape capacity, are linked, on the one hand, to the position of the predator in relation to the prey and, on the other hand, to the timing of its attack, according to a perfect coordination of its swimming movements – propulsion speed – when approaching the prey and, in particular, the suction force it can deploy when located in its immediate vicinity. This depends on the volume of the water ingested, which is related to the protrusion* of its jaws, the size of its mouth opening in a terminal cephalic position and the hydrodynamic–hydraulic pressure gradient of its mouth cavity. Attacking prey at a high speed, even if it is still at a fairly long distance, in order to give it very little time to escape, is a complex and often, but not always, successful strategy. The precise timing of well-coordinated attack movements conditions the supply of this centrarchid.

Many small fish on coral reefs, such as the damselfish, *Chromis viridis*, regularly feed on benthic prey* – copepods, isopods – living among corals and algae. Capturing these highly mobile prey that are able to quickly escape their approach requires a stealthy movement strategy designed to avoid mistrust on the part of the targeted prey and to allow instant capture that leaves them no chance of escape. This type of “hidden” hunt is practiced by means of powerful oral suction. Such rapid aspiration of a volume of water, including prey, requires a certain proximity – a few centimeters – between the prey and the predator to be successful. How can a fish that approaches its prey not denounce itself by its swimming movement generating a hydraulic displacement wave in the form of a wave that precedes the fish? How does it avoid being immediately detected by the prey that is always on the alert? The damselfish manages to reduce this “bow wave” so as not to alert its prey or encourage mistrust by reducing the liquid flow by opening its mouth, as shown by a

3D kinematics visualization: prey that does not have time to see the danger coming. A perfectly stealthy hydro-dynamism is achieved by these smart fish.

The stickleback, *Gasterosteus aculeatus*, also exhibits stealthy feeding behavior in small crustaceans – copepods, isopods, amphipods – through buccal suction and suction associated with protrusion* from its mouth, following skeletal-muscular jaw movements that cause a lowering of the buccal floor and an increase in the volume of the buccal cavity, movements that are responsible for an increased incoming hydraulic flow. This behavior is sexualized. It differs between females, which are capable of greater protrusion and oral depression, and males, which allows them to capture fleeing prey from a greater distance. Males therefore suck their prey closer together than females, but the protrusion of their mouth is 11 ms* faster than theirs. Less able to feed on nectonic prey* by suction than females, they feed on less vagile benthic prey and have stronger jaws that are especially adapted to biting, which also allows them to harvest and transport the plant material with which they build their nests (Volume 2, section 2.5; Figure 2.3). These males have "exchanged" hunters' jaws for those of builders. Such discreet hunting is particularly effective.

Bibliography: *J.Exp.Biol.*, 2013, **216**: 835-840 & DOI:10.1242/jeb.085258, DOI:10.242/jeb.074948, 2014, **217**: 1423 & DOI:10.1242/jeb.094813, *J.Roy.Soc.Interface*, 2014, **11** & DOI:101098/rsif.2014.0223

1.2.2.4. *Particularly clever egg eaters*

The male of the endemic *Telmatherina saranisorum* from an Indonesian lake in Sulawesi swims in a spectacular circuit – in large circles – in front of the females he encourages to lay eggs. Not interested in mating and only concerned with feeding, he consumes the eggs fresh as soon as they are deposited. A simulated courtier behavior is intended to deceive females. One of the neighboring species, *T. antoniae*, simply follows a couple ready to spawn and then cannibalizes their freshly laid eggs: oophagous specialists*.

Bibliography: *J. Fish Biol.*, 2008, **73**: 728-731 & DOI:10.1111/d.1095-8649.2008.01949.x

1.2.2.5. *A convergence of food motivations*

An aggregation of prey generally leads to the formation of an aggregation of predators. For example, there is a co-migration of Atlantic capelin, *Mallotus villosus*, which seasonally move in schools along the Norwegian coast to feed and then constitute rich spawning aggregations in spring (Volume 2, section 1.1.6), benefiting their natural predators, gadids such as cod, *Gadus morhua*, and haddock, *Melanogrammus aeglefinus*, as reflected in their stomach contents. These predators therefore follow the migratory movements of capelin each year, whose stocks they greatly exploit, although a minority of spawners manage to survive and return to reproduce in these same areas the following year, thereby demonstrating a strong capacity for resilience.

Fish aggregations can therefore result from such a convergence of interest in the same site. Attractiveness towards prey justifies a concentration of predators on these "hot spots". In Belize, for example, the seasonal concentrations of *Lutjanus cyanopterus* and *L. jocu* snappers on their breeding grounds explain the large numbers of whale sharks, *Rhincodon typus*, which consume large quantities of freshly laid eggs, a food of high energy value. Summer concentrations of whale sharks in the Caribbean are located on advantageous upwelling sites* rich in *nitrogenous nutrients* and therefore in phytoplankton – *chlorophyll a* – and zooplankton – copepods and especially fish eggs. Areas of high productivity are greatly appreciated by plankton eaters.

Bibliography: *Mar.Ecol.Prog.Ser.*, 2001, **215**: 275-282.

1.2.2.6. *Particularly gifted larvae at an early age: their survival depends on it*

Stealth hunting strategies do not only involve experienced adults who have experienced learning phases characterized by trial and error. Fish larvae, which generally have reduced mobility due to their very small size and poor swimming performance, face feeding difficulties in the first few days after hatching. Subjected to energy imperatives because they generally have only low energy reserves, having exhausted more or less completely their yolks, they must not miss their targets, such as protozoa – paramecia and other ciliates – otherwise they risk quickly starving to death. They should be able to position themselves promptly at a suitable distance from the mobile prey in order to capture it successfully by oral suction movement. The visual identification of the movements of target prey in a catch area has been studied in the laboratory in the larvae of the zebrafish, *Danio rerio*, which, as early as 4–5 days after hatching, are able to hunt mobile prey that they detect visually. The neural circuits of the optical roof – *tectum opticum** – involved in visual detection and prey capture are quite well known (Volume 2, section 5.3.1; Figure 4.3). Brain activity at this optic roof can be monitored by visualizing neural activity. An evolutionary neural organization is located at the 5th–6th day after hatching, which conditions the success of ciliate capture. The emergence of spontaneous neural activity in this part of the brain connected to the retinal axons is essential. It is closely synchronized with the beginning of hunting behavior, in relation to light conditions, with darkness causing a lack of catches.

However, if such mechanisms allow daytime feeding, catches are also made at night, which implies a non-visual sensitivity based on a "somato-sensitivity" linked to direct physical contact between prey and predator or indirect contact resulting from a hydraulic wave created by the movement of the prey. In the case of larvae of the American striped bass, *Morone saxatilis*, it is the neuromasts* of the lateral line that allow a non-visual capture of *Artemia salina* prey, as shown by a deadly juvenile induced by the experimental destruction, by *neomycin*, of the hair cells of their neuromasts*. Larvae can successfully feed both at night and during the day continuously in order to survive and grow rapidly. This vital episode is extremely delicate: knowing how to hunt from birth or die. The survival of the most suitable begins early in fish.

The visual acuity of young zooplankton-consuming fish is based on the possession of UV cones in their retinas, whose sensitivity increases the contrast of prey and facilitates visual identification. During development and with a change in diet towards larger nectobenthic* prey, UV cones are replaced by blue-sensitive cones, which can be experimentally achieved in brown trout, *Salmo trutta*, larvae treated with a *thyroid hormone* and whose catch performance of *Daphnia magna* daphnia is then reduced. High sensitivity to UV rays is necessary for juvenile feeding. Their diet is dependent on retinal *opsins**. Oral expansion or protrusion* allows the development of suction forces that determine the larvae' feeding success, following a computerized model established in the larvae of the sea bream, *Sparus aurata*: oral hydrodynamics that is effective from birth.

Bibliography: *Curr.Biol.*, 2015, **25**: R273-R275 & DOI.org/10.1016/j.cub.2015.02.005, 2016, **26**: R377-R385 & DOI: 10.1016/j.cub.2016.03.054, 2017, **27**: 2407-2419 & DOI:10.1016/j.cub.2017.06.056, *J.Exp.Biol.*, 2013, **216**: 3071-3083 & DOI:10.1242/jeb.087742, 3522-3530 & DOI:10.1242/jeb.087395, 2014, **217**: 3748-3757 & DOI:10.1242/jeb.104331, *J.Proc.Roy.Soc.B,* 2012, **280** & DOI:10.1098/rspb.2012.2490

1.2.2.7. *Various clever and effective strategies for fish-eating predators*

Carnivorous species display the most imagination in the implementation of schemes designed, individually or collectively, to obtain maximum efficiency in catching their prey, whether insects, fish, birds or mammals. Each predator species has a specific plan of attack on its prey, the effectiveness of which is increased with experience acquired individually and/or collectively. Some of them show a particular ability to organize hunts, individual or collective, and show an astonishing agility and dexterity.

1.2.2.7.1. The swallow hunt is open

Fish, on the one hand, and birds and mammals, on the other, which live in two very different environments, are usually unlikely to meet. However, some fish, carnivorous predators, do not deprive themselves of catching relatively accessible prey such as water birds – ducks, water hens, grebes – that swim on the surface of the water or dive into the liquid element, as evidenced by the accounts of their capture by pike, pike perch, catfish and piranhas; but catching birds in flight, especially if they are known to possess a fast flight, is an extraordinary performance and hunting achievement.

For example, in a lake in South Africa, the tigerfish, *Hydrocynus vittatus*, a carnivore with strong sharp canines (32 teeth) that earned it the name tigerfish, practices such a sport hunt in the summer, in the middle of the morning. During the 15 days of scientific observation, 300 swallows, *Hirundo rustica*, were seen and filmed as they were caught by tigerfish that jump out of the water to catch birds flying near the surface. Such hunting consists of either vertical jumps out of the water (up to 1 meter high) or a chase below the surface of the water. This hunt is particularly difficult to conduct and is not always successful, as they are estimated to constitute about 25% of attempts and much more (4 out of 7) in the case of a chase. In addition to the speed of the bird's flight, even if it is reduced when it flies near the surface of the water for food or drinking, the fish must integrate the existence of optical distortions associated with the refraction of light at the water–air interface.

It is likely that such a diet is not accidental and is an adaptive strategy when these aerial prey are abundant while underwater lake prey are rarer. However, it is not without danger for tigerfish because predatory birds, such as vociferous *Haliæetus* eagles, can take advantage of the circumstances and seize them: they are ballistic experts.

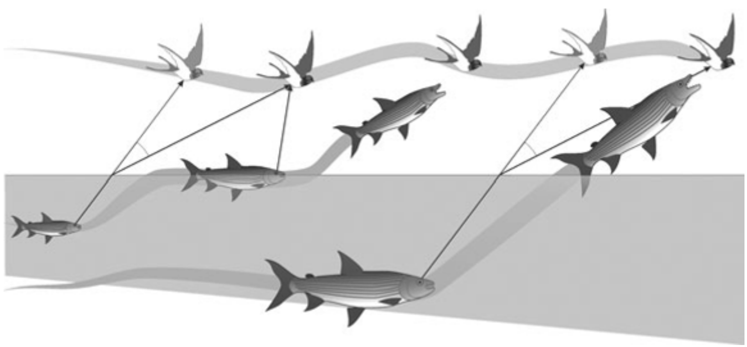

Figure 1.4. *Diagram of the flight paths of swallows and tigerfish,* Hydrocynus vittatus*, that pursue them and attempt to catch them in a lake in South Africa (source: O'Brien* et al. *2014, J.F.B, 84: 263)*

Bibliography: *J. Fish Biol.*, 2014, **84**: 263-266 & DOI:10.1111/jfb.12278

1.2.2.7.2. A new unconventional hunting strategy

Some examples of the predation of birds by fish are known and do not seem exceptional. However, a highly unusual case has recently been reported, which demonstrates an ability for some fish to modify their usual feeding behavior to adapt to hunting conditions that are totally different from those they usually practice in their natural ecosystem: they demonstrate an innovative spirit.

For example, the wels catfish, *Silurus glanis*, which are large fish-eating predators, are constantly expanding and colonizing rivers in Western Europe from their original ecosystems: the Danube waters (Volume 1, section 2.3.3). They are classically known to occupy deep and dark biotopes in the Rhône, Saône, Seille and other rivers, with their usual prey being freshwater fish that they often catch at dusk and at night as their vision is not their most developed sensory system, but they are able through their long barbels, of the acoustic vibrations emitted by their preys. Daytime activity has rarely been observed, limited to short winter and spring episodes.

That some large catfish (1–2 m in length) have specialized in catching *Columbia livia* pigeons by day and in full sunlight, on the banks of the Tarn river in the town of Albi, and that their hunting strategy leads them to have to leave the water, on islets of gravel, to complete their task, is therefore quite surprising and new.

Studies conducted during the summer season, from late June to mid-October, have shown a remarkable adaptation to hunting pigeons that drink and wash on the gravel banks of the river's banks or on small islands. Some individuals have developed a strategy of taking a stealth approach to pigeons, such as crocodiles that hunt antelope. The attacks only concern moving birds, and the predator must make a capture jump out of the water to capture its prey. Of the 54 pigeon attacks observed and filmed, 28%, or 15, were successful, performed by the same larger individuals who are supposed to have enough energy to propel themselves on land, at the risk of crashing, and immediately afterwards regain their liquid element, the duration of the attack not exceeding 4 sec. Pigeons then form the basis of their diet for these fish, as evidenced by the measurements of *carbon isotopes** $\delta^{13}C$ *and nitrogen* $\delta^{15}N$ of their flesh, which proves that the pigeon has become an important prey and a trophic specialty of some of these wels catfish, the others being content to consume carp, roaches, breams and crayfish. These invasive wels catfish have been implanted in this river since 1983, but no such behavior has ever been observed. This is a remarkable adaptation to a new environment aimed at optimizing their food by exploiting a previously neglected resource. It is therefore an ecological opportunity and a recent hunt practiced by particularly inventive wels catfish.

Figure 1.5. *Strategy for approaching the* Silurus glanis *on a river beach of the Tarn, in Albi, where a group of pigeons wash and where one of them is caught by a Wels catfish jumping out of the water (source: Cucheronnet* et al. *2012, PlOs One, 7, 12, Figure 1)*

A dusky grouper, *Epinephelus marginatus*, was filmed in Port-Cros, consuming a cormorant, an opportunity to be taken when it arises.

Figure 1.6. *Mediterranean dusky grouper,* Epinephelus marginatus*, having seized a cormorant during its diving (source: Jomard, J.)*

In the Seychelles, seabirds, the *Oceanites* sp., are hunted and captured, both when they are landed on the surface and when they fly near it, by large-headed jacks, *Caranx ignobilis*.

These carnivorous predators, whose diet is traditionally based on crustaceans, cephalopods and fish (sardines, wrasse, parrot fish, etc.), therefore broaden their trophic spectrum, hunting alone or in organized groups, thus demonstrating an original ornithophagy. The capture of small mammals is occasionally observed among opportunistic predators. These are generally large fish with large mouth openings. For example, in Alaska, rainbow trout, *Onchorhynchus mykiss*, and Arctic char, *Salvelinus namaycush*, under 30 cm in size consume shrews, *Sorex* sp., that are periodic prey. One original case, which had never been seen, concerns the catfish, *Neoarius graeffei*, which, in a desert in Western Australia, catches small terrestrial rodents, *Notomys alexis*, with these prey constituting up to 94% of its stomach content and representing a considerable energy supply in these low-food environments. They know how to adapt to available food, even unconventional food.

No convincing link can be established between the immediate and punctual behaviors of fish using unique cognitive abilities and the implementation of permanent adaptations. Unless some future catfish (in a few million years!) can be imagined to adopt a pigeon-eating diet (by refining their ability to jump out of the water? and why not by learning to fly to better pursue birds?), such a futuristic scenario must take into account the fact that pigeons could also, for their part, develop parallel anti-predatory behaviors, in accordance with an endless race between the evolution of predators and that of prey that simultaneously and in parallel develop adaptations to changes in food availability.

Bibliography: *Ecol.Freswat.Fish,* 2013, **23**: 622-630 & DOI:10.1111/eff.12117, *PLOS ONE,* 2012, **7***,* 12: e50840, *J.Arid Env*., 2016, **135**: 9-11 & DOI.org/10.1016/j.jaridenv.2016.08.005, *J.Fish Biol.,* 2007, **71**: 101-114 & DOI:10.1111/j.1065-8649.2007.01471.x

1.2.2.7.3. An ace from ballistics

The Thai archerfish, *Toxotes chatareus*, feeds on aerial insects placed on the foliage of plants along the banks of rivers. It does not wait for them to fall into the water by chance, but seeks to destabilize its potential prey through a jet of water from its mouth to cause its prey to fall into the aquatic environment. The direction of the jet and its propulsion force as a function of the prey's height are calculated with great precision, by taking into account the classical optical deformation of the images at the water–air interface.

Such a tactic is particularly complex and involves learning and training using various visual stimuli that have been tested in the laboratory. These tests reveal the remarkable ability of this fish to discriminate between a wide variety of shapes and to make good choices about the angle of fire most likely to be effective. In the laboratory, it even manages to innovate by targeting types of prey that are new to it, while it loses interest in unpleasant or toxic prey. The accurate identification and calculation of the water jet to be projected onto the desired target is usually accompanied by a jump out of the water, which reduces the distance from the prey and increases the power of the jet to destabilize the target insect. In addition to the mental devices (Volume 2, section 2.3.15) developed, there is then a physical performance, that of a powerful jump resulting from a characteristic body curvature – the *C-start* – and a tailbeat allowing to lean on the water, with force and elasticity, during the take-off phase. The power of this upward movement, complemented by a fast swimming speed to be at the precise point of fall of the targeted insect, is controlled by a musculature developed innervated by brain motor neurons, some of which are identified – Mauthner cells – and which control the body's curves to the left and to the right. The ambient temperature plays a significant role in the performance of the jump. In generally warm mangrove waters (26°C), a decrease of 1°C results in a 4 ms take-off delay, which can cause the prey's capture to fail. Fish can certainly implement a mechanism to compensate for the effect of thermal changes, allowing them to continue to feed during sudden temperature changes. Such hunting is extremely accurate and efficient.

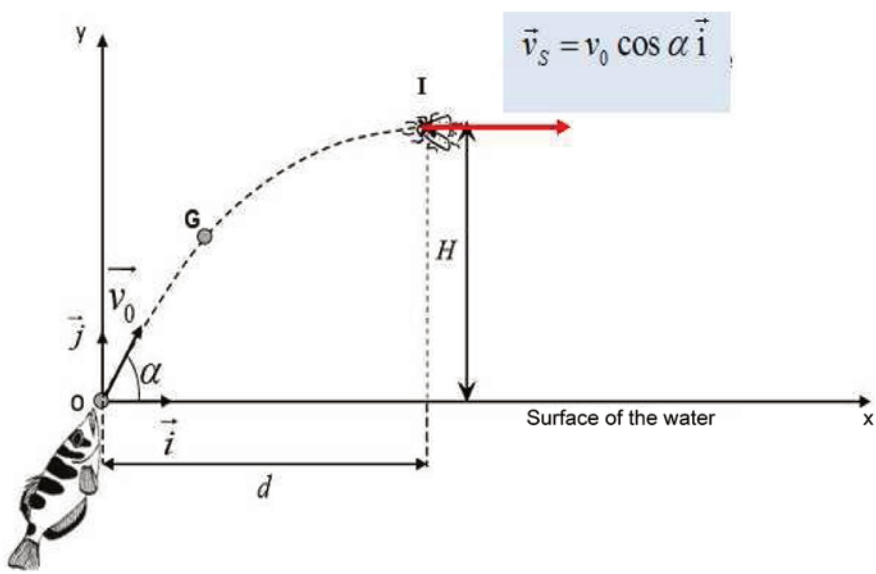

Figure 1.7. *Trajectory of the water jet propelled by the archerfish,* Toxotes *sp., towards an insect placed on the river foliage (source: "Les prouesses du poisson archer", Bachelor of Science of South Africa 2012 and Insects Magazine No. 130, Sept. 2003, p. 23)*

The psychomotor mechanisms used to dislodge the prey and calculate, with very high precision, the precise take-off point and the speed of the *C-start* have never ceased to amaze researchers. This is a remarkable adaptive maneuver, in which the fish turns to its right and then accurately evaluates both the precise point of fall and, taking into account the height and rate of the fall of its victim, the time required to be present at the exact moment of its landing impact on the water surface in order to recover before it is caught by a rival. In Thai mangroves, surface prey hunters such as the beloniforme Buffon's river garfish *Zenarchopterus buffonis*, who have the ability to detect the slightest local hydraulic movement by their mechanoreceptor sensory cells, the neuromasts* on the lateral surface of the lateral line, rush onto the prey when it hits the water. As these competitors are numerous, the archerfish is not always rewarded for its skill. It relies on its visual acuity and swimming acceleration potential – the average capture time is 2.7 sec – to avoid being overtaken, at least during the day, as it is forced to stop hunting at night when heterospecific competitors are present and become too efficient. It is not enough to be a skilled archer.

The banded archerfish, *Toxotes jaculatrix*, is sensitive to its social environment, with any presence of a congener delaying its decision to shoot. It fears any foreign presence and remains efficient only in the absence of any "audience" because it is advisable not to be disturbed.

The capture maneuver of the archerfish was filmed in the laboratory during tests with dead flies during the 40 ms of the hunter's takeoff, which allows the hunter to make a detailed analysis of their decision-making, which is considered extraordinary by those carrying out the experiment. It should also be noted that the visual identification of the target of a stationary insect on a foliage is particularly difficult in a rich, complex and structured environment such as that of mangroves in the tropical forest. Detecting the image of a static prey – insects, spiders, small lizards – in such a rich landscape that distracts the eye and targeting the spray with such precision and vigor that it overcomes the adhesion forces it exerts on the foliage overhanging the water seem to constitute a tour de force. The memory of the places in its hunting territory cannot be retained, given the instability of water levels linked to tidal movements in the mangrove swamp. This is therefore an exceptional performance. The optical mechanisms that allow archerfish to scan an image within the multicolored visual scene of their static environment would not be unlike those known to humans. Common serial vision tests, carried out in the laboratory in both countries, show such similarities that they lead us to believe that the mental mechanisms – the algorithms – are the same and apparently quite common. Yet, humans have a cerebral cortex that is missing in fish with small brains (Volume 2, section 5.3.1; Figure 4.2). Are such extra-cortical mechanisms possible in a fish that would then be somewhat "para-human"?

Bibliography: *Curr.Sci.*, 2015, **14**: R595-R597 & DOI:10.1016/j.cub.2015.06.005, *J.Exp.Biol.*, 2013, **216**: 1265-1274 & DOI:10.1016/j.anbehav.2013.09.031, 3096-3103 & DOI:10.1042/jeb.087734, 3450-3450 & DOI:10.1242/jeb.088856, 2014, **217**: 2816 & DOI:10.1242/jeb.111534, 2866-2875 & DOI:10.1242/jeb.105510

1.2.2.7.4. The seal hunt

Large carnivorous predators, whose appetite seems insatiable, develop subtle hunting tactics to ensure the best catch performance in view of the defensive behavior of their traditional prey. Such a prey–predator relationship has been analyzed in South Africa in relation to the white shark, *Carcharodon carcharias*, and the colonial seals, *Arctocephalus* sp., living in colonies on the coasts of the Cape Town region. Shark attacks, which are their almost exclusive predators, preferentially target young seals that can be caught near the shore. Sharks patrol along these shores and take advantage of the carelessness and naivety of these young seals occupied by their activity in shallow waters. Monitoring the respective behavior of predators and prey, each marked by acoustic transmitters, made it possible to specify the modalities of the attack, which depend mainly on lighting, with the light conditions of dawn and dusk being the most favorable, both for the relative concealment of sharks swimming in shallow ambush and for the visual identification of seals whose surface image is contrasted on the clear sky background. A comparable contrast explains the attack of windsurfers and their surfers. In this prey–predator model, the smartest is always the winner: the shark! However, many seals manage, with age, to avoid always being the losers.

The trophic ecology of two sympatric species, the tiger shark, *Galeocerdo cuvier*, and the bulldog shark, *Carcharhinus leucas*, in Reunion Island, has been clarified by analyzing the stomach contents and *isotopes* $\delta^{13}C$ and $\delta^{15}N$ of their prey, with their piscivorous and teutophagous character* being more marked than previously indicated in other places. They would only be interested in humans very accidentally.

Bibliography: *Anim.Behav.,* 2008, **76**: 1901-1917 & DOI:10.1016/j.anbehav.2008.06.025, *Canad.J.Fish.Aquat.Sc*i., 2014, **74** : 216-227 & DOI.org/10.1139/cifas-2016-0105, *Env.Biol.Fishes*, 2015, **98**: 805-812 & DOI:10.1017/s10641-016-0515-8, *J.Fish Biol.*, 2017, **91**: 460-472 & DOI:10.1111/jfb.13351, *Roy.Soc.Open Sea*, 2017, **4**, 9 & DOI:10.1096 /rsos.170674

1.2.2.7.5. Stunned prey

The electric eel or gymnote, *Electrophorus electricus*, an electric fish that has nothing to do with eels of the *Anguilla* genus, is an aquatic monster 2–3 meters long and weighing 20–25 kg. It has a remarkable weapon for capturing its prey: its electrical organ. Indeed, part of its caudal musculature has seen its muscle cells specialize in electrocytes which, combined in series according to the principle of electric batteries, are capable of producing sudden and powerful discharges, of up to 600 V, which cause the instant paralysis of its prey. These are usually fish, sometimes even large ones, but the victims can also be cattle and humans. Even a horse cannot resist it.

Before carrying out a deadly attack on its prey by a high-voltage discharge, the predator carries out an initial detection by a series of small, double or triple electrical discharges, whose signals are reflected on its own electrical receivers, in order to confirm the presence of a living prey in the dark, muddy swampy waters of the Amazon and Orinoco basins. After that, the electric eel strikes its prey, like a teaser, with a violent discharge that causes the instant paralysis of its motor muscles and immobilizes it completely. It has been shown that the eel modifies its body conformation by moving its head and tail closer together in order to increase the power of its electrical discharge according to the size of the target prey. It is also important to avoid producing electrical discharges on environmental objects. Only the prey are destined to undergo incapacitating lightning according to a well-targeted tetanization. Such a fish, a real living teaser, is called “a trembler” by the indigenous people of the region.

This ability to convert food energy into several hundred volts of electrical energy using the electrocytes of the electrical organ is original. It involves neuromuscular specialization that can serve as a useful neuro-chemical model for understanding the specialized cellular mechanisms common to all vertebrates and that are therefore of general application. Such data are valuable in physiology.

Bibliography: *J.Exp.Biol.*, 2015, **218**: 650 & DOI:10.1242/jeb.112078, *J.Fish Biol.*, 2008, **72**: 331-354 & DOI:10.1111/j.1095-8649.2007.01631.x

1.2.2.7.6. The effectiveness of a collective hunt

The effectiveness of a collective hunt is demonstrated in lionfish, scorpionfish or flying scorpionfish, *Dendrochirus zebra*, from the Indo-Pacific. A beat of its fins is used to signal to its congeners the presence of prey that together they can push into the corners of the reef using their long pectoral fins and dorsal fin with venomous spines. Such collaboration between these scorpaenidae maximizes the effectiveness of these predators, but this cooperation is limited to the hunting strategy, with the prey not shared as it is immediately swallowed by the first one who succeeds and with the hunter behaving, 8 times out of 10, upon its first arrival. The effectiveness of these common hunts is such that, in the Caribbean, where several lionfish species have become invasive (Volume 1, section 2.3.8), the stability of prey species stands is now compromised on coral reefs. An attempt to teach sharks to feed on these fish, which usually have no natural predators, has been undertaken in Honduras. Sharks dragged into ponds are released on sites where these potential prey thrive, with the hope that they will feed on them.

Bibliography: *Biol.Lett*., 2014, **10**: 20140281 & DOI:10.1098/rsbl.2014.0281

1.2.2.7.7. Cooperation between different species

Collaborations between species that join forces for the same offensive purpose are sometimes surprising, a cooperation that was thought to be reserved (sometimes!) for great apes and humans. A remarkable example of cooperation during an interspecies hunt has been observed in the Red Sea between the grouper, *Plectropomus pessuliferus*, and the giant moray eel, *Gymnothorax javanicus*. The grouper calls upon its partner when the situation requires it owing to the difficulty of reaching a reef fish sheltering in an inaccessible cavity or a crevasse. He initiates the hunt by standing in front of his partner and shaking his head 3–6 times a second, which is a motivational signal that acts as a stimulus to trigger the positive response of the moray eel that then leaves its hole. He works with a partner whose skills he knows in this task, following previous successful experiences. Their collaboration results in a great success in catching prey; the grouper seems to benefit only from this hunting method insofar as it monopolizes the prey by swallowing it directly, without the slightest sharing for its teammate and without the risk of seeing any competition taking place with aggressiveness between them. The grouper is not a sharer!

Another form of association has been described and filmed on the Brazilian coast where the dusky grouper, *Epinephelus marginatus*, follows the snakefish, ophichthidae *Myrichthys ocellatus*, and, acting as an opportunistic thief, quickly swallows the cryptic prey* that the latter skims into rocky crevices. It would therefore be more of an individual hunt taking place simultaneously, as one individual can take advantage of the presence of the other to maximize his chances of capturing prey. Another original case, described only once in the Azores, concerns a temporary association (6 minutes) of hunting between a young 15-centimeter dusky grouper and a 30-centimeter *Octopus vulgaris*, with the usual relationships between these two species usually being predation, at least when the force ratio is reversed.

Bibliography: *Curr.Biol.,* 2014, **24**: R791-R793 & DOI:10.1016/jcub.2014.07.033, *Cybium*, 2006, **30**: 82-84, 2008, **32**: 187-188, *PLoS Biol*., 2006, **4**: e431 & DOI:10.137/journal.php.0040431, *Sci.Avenir,* 2007, 720: 27

1.2.2.7.8. Other opportunistic species strategies

An original hunting tactic concerns the sail swordfish, *Istiophorus albicans*, large tropical pelagic swimmers, who target schools of sardines, sardinella and other small pelagic fish in the open ocean. Equipped with a long, tapered, pointed, slightly conical and rigid rostrum extending their skull, this sword or halberd not only plays a locomotive role by reducing hydrodynamic drag, which allows them to reach a high swimming speed (15–20 m/sec) but also functions, during attacks, as a weapon designed to kill as many small fish as possible. After initially regrouping and concentrating them into a ball, each individual hurls himself and penetrates his rostrum into this concentration of prey gathered into a ball, then hits them violently with powerful and rapid lateral sword movements – accelerations are among the fastest known in aquatic organisms – thanks to the flexibility of his vertebral spine, with the intention of knocking out and cutting to pieces as many victims as possible who will then be consumed. Monitoring of catches of *Sardinella aurita* sardinella by groups of sailfish, *Istiophorus platypterus*, in the Gulf of Mexico showed the existence of a lateralization (Volume 2, section 4.3.7) marked by attacks at the individual level, as evidenced by lateral wear: left or right abrasion of the microteeth bordering the rostrum. The most lateralized individuals, who have a clear preference on the left or right side of the sword's movements, have the greatest capture success, with specialists more efficient than ambidextrous ones. While the lateralized attack mode of an isolated individual is highly predictable for a prey knowing that an attack can last 1 hour or more, attacks on sardinella shoals by groups of variously lateralized hunters, as they most often occur, reduce this predictability and become highly beneficial to a given hunter group. Such a group hunt, with unpredictable attacks, is particularly effective.

1.2.3. *Use of cannibalism*

1.2.3.1. *Behaving like savages?*

The best, most nutritious and easily accessible prey is often its own congeners, especially if they are defenseless as they are early, in the egg, larvae and juvenile stages. Consuming congeners as live prey is a common behavior in fish and involves about 17 families of teleosts. Far from appearing to be a behavioral anomaly and reprehensible, cannibalism is now considered completely normal and is even considered to be a fairly normal survival strategy, playing a regulatory role in the dynamics of natural populations, leading to the trivialization of this crime linked to the convenient avoiding of overpopulation.

Trout, like other salmonids, have a clear tendency to practice cannibalism. Thus, in a Slovenian river where they have both been introduced, the brown trout, *Salmo trutta*, and the rainbow trout, *O.mykiss*, the consumption of their congeners contributes 27.9% and 7.7% respectively of their respective energy intake measured by the isotopic values* of *carbon* $^{13}\delta C$ and *nitrogen* $^{15}\delta N$. Such cannibalism begins at 16.6 cm (age 3+) and 24.7 cm (age 2+) respectively. The consequences on the dynamics of natural populations must be taken into account in the fisheries management of watercourses. The trophic benefits of cannibalism are spectacular in the 6-spine stickleback, *Pungitius pungitius*, in Finnish waters: adults who eat eggs and juveniles of their species reach large sizes (100 mm), with such a size being exceptional.

Bibliography: *Ecol.Freshwat.Fish,* 2017, **26**: 686-694 & DOI:10.1111/eff.12316, *Fish Biol*., 2017, **91**: 1737-1744 & DOI:10.1111/jfb.13477

1.2.3.2. *Avoid starving to death*

It is not uncommon for hungry fish to use this means of survival in times of famine, especially if they are brood stock who are under an obligation to perform their reproductive duties. As a result, a few days before laying and while benthic prey* is rare, adults of the Adriatic dwarf goby, *Knipowitschia panizzae*, engage in active cannibalism towards the eggs and juveniles of their congeners. This fish is not usually piscivorous, but find their hunger justifying the means.

It is common for herring, *Clupea harengus,* to cannibalize some of the benthic spawn* they lay in their spawning grounds in southern Norway, with cod and other clupeids also preying on eggs; the stomachs of these egg-mass feeders sometimes contain more than 20 eggs, with the record in a herring stomach being 4,320 eggs. The seabed, made of stones and gravel, is sometimes covered with eggs to a thickness of 5 cm so that this removal is not considered too damaging to the stock, as spent spawners quickly leave the spawning grounds after accumulating genetic energy reserves useful for the winter.

Such cannibalism is highly dependent on environmental conditions related to congeneric density and the availability of other prey, but it is also genetically based, with some individuals having a clear propensity to be more cannibalistic than their neighbors, such as Arctic char, *Salvelinus alpinus*, among whom individuals raised in hatcheries, and who have therefore never consumed live prey, become cannibals as soon as they are released into Norwegian lakes, with such innate dispositions particularly common among large individuals.

The temptation is great for the grunions, *Leuresthes tenuis*; when they are in large numbers mixed with their eggs in the wet sand of Californian beaches (Volume 2, section 3.8.2; Figure 3.4), and even before leaving them definitively at the next ebb tide, they may consume some of them, with their consumption and digestion resulting in a supply of *proteins* and *lipids* that can prove very useful for their journey back to the open sea owing to the large amount of energy needed to get back out to sea.

Bibliography: *Ethol.Ecol.Evol.,* 2001, **13**: 385-391 & DOI:10.1080/ 089227014.2001.9522769, *J.Fish Biol*, 2002, **61**: 1050-1052 & DOI:10.1006/jfbi.2002.2055, 2005, **66**: 957-965 & DOI:10.1111/j.1095-8649.2005.00646.x

1.2.3.3. *A necessary energy investment to ensure the future*

The males of the stickleback, *Gasterosteus aculeatus*, who act as guardians of the nests they have built, devote themselves fully to cleaning and ventilating the eggs (Volume 2, section 2.5; Figure 2.3), to the extent that they do not have the time to search for their own food. As a result, in order to compensate for their energy losses, they tend to consume some of the eggs entrusted to them. Such filial cannibalism allows them to preserve their physical condition so as to successfully continue their guard duty. This sampling, which generally only affects a small fraction of the eggs deposited in nests, has only a slight impact on the final reproductive success of these males, who must remain in good shape, both in the short-term to successfully raise the young under their care and with a view to future mating. Such an energy boost allows them to succeed in fertilization, which is a sustainable energy investment.

Juveniles of the round goby, *Neogobius melanostomus*, use olfactory signals to identify eggs of their own species, which they prefer to eat given the choice of other eggs, such as those of the rainbow trout, *O. mykiss*, that are offered to them in the laboratory. This preference, experimentally demonstrated by tests using waters in which eggs of different species have been bathed, may prove harmful to it, as odor traps can be used by humans to try to eradicate this harmful species from North America (Volume 1, section 2.3.3).

In Finnish waters, the male sand goby, *Pomatoschistus minutus*, which breeds successively with two females, prefers to eat the large eggs spawned by the latter in order to save time in its breeding cycle, with the large eggs having a slower development and being nutritionally richer; this makes it disadvantageous to lengthen parental care, even by 1–2 days, as it delays its subsequent mating by the same amount. This male therefore seeks to optimize his breeding calendar.

Fish that practice parental care (Volume 2, section 2.12.13), such as the cichlid, *Neolamprologus caudopunctatus*, from Lake Tanganyika, use filial cannibalism. Females, who, unlike males, are usually respectful of their own eggs, would use this process to recover energy and ensure the quality of care they then provide to those of their offspring who have been spared. It is rare for females to deviate from their "conservative" traditions.

Bibliography: *Biol.Lett,* 2008, **4**: 160-162 & DOI:10.1098/rsbl.2007.0589, *Biol.Rev.*, 2002, **77**: 261-277 & DOI:10.1017/S1464793101005905, *J.Fish Biol.,* 2011, **78**: 1944-1953 & DOI:10.1111/j.1095-8649.2011.02964.x, *Naturwissench*., 2009, **96**: 399-403 & DOI:10.1007/s00114-008-0485-6

1.2.3.4. *Murderous males and hardworking females*

Cannibalism is common among salmonids such as the brown trout, *Salmo trutta*, during its fall spawning season. On spawning grounds, freshly laid eggs are vulnerable for the first 2 minutes after spawning, while the female, using her tail, covers them with fine sediment – gravel – for burial (Volume 2, section 2.1.3; Figure 2.1). It is during this burial that most rapines occur. The speed of recovery is therefore crucial for the survival of eggs. As seen in video images, these acts of cannibalism occur in 25% of egg-laying activities and are carried out by peripheral males who do not participate in fertilization, as well as sometimes by the males who fertilized the eggs in question, which has a negative impact on the couple's offspring. Females do not engage in such criminal acts at any time, as they are too busy multiplying the number of eggs laid and working on their burial. On the Norwegian coast, juvenile Atlantic salmon, *Salmo salar*, eat the freshly laid eggs of their congeners. They are an important part of their diet and a rich source of marine nutrients. This energy supply has a positive influence on their winter survival.

Bibliography: *Ecol.Freshwat. Fish*, 2011, **20**: 580-587 & DOI:10.1111/j.1600-0633.2011.00507.x, *Env.Biol.Fishes*, 2015, **98**: 2305-2313 & DOI:10.1017/s10641-015-0436-y, *Naturwissenschaft*., 2010, **97**: 435-439 & DOI:10.1007/s00114-0656-0

1.2.3.5. *Preparing for the future by sacrificing the present*

Filial cannibalism can be considered somewhat paradoxical insofar as parents are intended to give life to their descendants, not to destroy them. This behavior is generally considered a way for a spawner to survive and increase his subsequent reproductive potential from the energy accumulated through the consumption of his own eggs, especially when food resources are scarce or there is little time to search for food. Yet, with the toadfish, *Porichthys notatus*, from the Pacific coast, this cannibalism occurs even if trophic conditions are favorable and even though these males are not suffering any deterioration in the condition of their body. On the other hand, the situation is all the more intense when intrasexual competition is strong because of the competition between males for access to females and possession of nests.

Male pipefish, such as *Syngnathus abaster* from the Portuguese coast, invest a lot of energy in breeding their embryos in their marsupium* (Volume 2, section 2.12.7). However, these males, both during the development period of the juveniles inside their incubator pouches and later after this pregnancy – postpartum* males – do not engage in any cannibalism that might appear natural and excusable. A reduction in their appetite and a limitation of their trophic needs allow these males to avoid cannibalism and thereby safeguard their offspring. In contrast, females and non-reproducing males of this species cannibalize the newborns of their congeners.

Male *Syngnathus typhle* in the Venice lagoon behave like cannibals among the juveniles of their species.

It should be noted that in addition to active cannibalism, there is, among pipefish, passive oophagy through the natural lysis, in their incubator pouch, of certain eggs and absorption of *nutrients** from them for the benefit of other embryos, as well as for pregnant fathers (Volume 2, section 2.12.7). The filial cannibalism of the male pipefish, *Syngnathus schlegeli*, is confirmed by the marking by *isotopes* $\delta^{15}N$ of the eggs absorbed by the epithelium of his incubator pouch and whose nutrients are found in his liver, which is irrefutable proof of the personal benefit he derives from the activity.

Bibliography: *Behav.*, 2016, DOI:10.1163/1568539X-00003328, *J.appl.Ichthyol.*, 2009, **25**: 479-480 & DOI:10.1111/j.1439-0426.2009.01267.x

1.2.3.6. *A means of strengthening the social status of dominant males*

The practice of infanticide by cannibalizing spawn, as observed among the dominant males of the cichlid lamprologus, *Neolamprologus pulcher*, can also be interpreted as a means of establishing social status by destroying the offspring of rivals and ensuring that a new generation carries their own genes, in line with the behavior of lions and other beasts. The female has no alternative but to use her reproductive potential to try to compensate for the damage and ensure the prosperity of the social group without delay.

Bibliography: *Roy.Soc.Open Sci.*, 2017, **4**, 3 & DOI:10.1098/rsos.160891

1.2.3.7. *Cuckolded and vengeful males*

Stickleback, *Gasterosteus aculeatus*, males are able to use olfactory information to identify foreign eggs resulting from fertilization flights by *sneakers** (Volume 2, section 1.2.1.1) and which are mixed with eggs that they have fathered. They eliminate them by cannibalizing them. On the other hand, they ensure the protection of their own people.

Among the *Telmatherina sarasinorum* endemic to an Indonesian lake of Celebes, males are numerous and highly promiscuous. They have two alternative reproductive tactics at their disposal: courting females and forming couples with them or impregnating them by surprise, in accordance with the terms of sneaking* (Volume 2, section 1.2.1.1). The higher the number of sneakers*, the more dominant males who court females practice filial cannibalism: cannibalism is multiplied by 3 in the presence of 1 sneaker* and by 6 in the presence of 2 or more sneakers*. It is estimated that 13% of eggs are cannibalized in the absence of sneakers* and 62% in the presence of 1 or 2 sneakers*. The presence of these small sneakers* leaves the dominant males with little hope of exclusive personal paternity, with the strong sperm competition of up to 400 males per 1 m^2, leaving them with little chance of escaping the ambient cuckoldry (Volume 2, section 1.2.7.3). Such oophagia is almost widespread, showing that it is viewed as better to have no offspring than to produce bastards.

Bibliography: *Env.Biol.Fish*, 2006, **75**: 471-482 & DOI:10.1007/s.10641-006-0037-x, *J.Fish Biol.*, 2007, **70**: 1295-1301 & DOI:10.1111/j.1095-8649.2007.01.390.x, *Naturwissenschaft.,* 2009, **96**: 399-403 & DOI:10.1007/s00114-008-0485-6, *The Amer.Natur.*, 2007, **169**: 258-263

1.2.3.8. *Counter-strategies developed by females*

Females, who almost never cannibalize egg-laying, either their own or that of their congeners owing to their respect for the value of eggs, are wary of males who are too cannibalistic. They observe the parental behavior of nesting males and avoid mating with those they have seen engage in cannibalism. Female blenny, *Rhabdoblennius ellipes*, on the Japanese coast therefore prefer to mate with males with fresh eggs in their nest, with young eggs, with those 0–2 days post spawning more attractive than eggs 3–5 days old, because they indicate a lack of cannibalistic behavior on the part of their guardian. In addition, their spawn, added to previous spawn, may benefit from the dilution of predation risks.

Bibliography: *Ethol.,* 2011, **117**: 227-236 & DOI:10.1111/d.1439-0310.2010.01868.x

1.2.3.9. *Early cannibals and ecological birth control*

Cannibalistic habits can occur particularly early as they sometimes appear even at the embryonic stage. With the viviparous salmon shark, *Lamna ditropis*, from Alaska, in the absence of maternal nutrient intakes through a placenta, the most developed embryos feed on the flesh of their brothers and sisters present, like them, in their mother's genital tract. They have fang-like teeth that allow them to cut the shells of neighboring eggs and then eat them so that only four or five newborns are delivered by each female, with all others having been cannibalized without her knowledge. Similarly, with the feeder shark, *Negaprion ferrugineus*, embryos move in their mother's genital tract (uterus) to capture the eggs and embryos they consume. The concept of the "sedentary embryo" has survived.

Cannibalism is a perfect part of a natural resource management policy. An original larval cannibalism occurs with the African catfish, *Clarias gariepinus*; the larvae with sharp teeth are aggressive towards other larvae and inflict skin injuries on them, the released pheromones* increasing the aggressiveness of these larvae which is at its peak in a light environment, with the chance of larval survival greater in the dark.

An even more unique behavior is that of the female catfish, *Bagrus meridionalis*, who voluntarily spawns oocytes in her nest to feed larvae from her previous reproductive activities!

Bibliography: *Ethol.,* 2018, **75**: 122-126 & DOI.org./10.1111/eth.12828, *Zool.Sci.,* 2013, **30**: 421-424

Finally, all the apparently negative activity of the desertion of offspring, infanticide and filial cannibalism cannot merely be considered the simple survival actions of tired and hungry fathers. The destruction of progeny allows males to form new couples with new partners and produce new generations that are more promising than the old ones. Is it not the case that lions and other felines practice this systematically?

1.2.4. *Practice grazing*

There are generally few herbivorous or phytophagous species in the marine environment, but their populations, sometimes abundant, are capable of intensely grazing seaweed and/or phanerogamous underwater meadows when many individuals form dense schools. They occur more frequently in fresh waters and their feeding behavior seems uninteresting at first sight. Is grazing common behavior? We will see that this is not the case.

1.2.4.1. *Grazing on freshwater plants or seaweed and marine phanerogams*

Grazing aquatic plants such as water hyacinths, as practiced by Chinese carp, *Ctenopharyngodon idella*, involves making a taste-based choice using the sensory cells belonging to taste buds and cutting abilities following moving the jaws in a rotary motion and then grinding with pharyngeal teeth, in order to effectively chew the cellulosic cell walls of plants prior to digestion using quantitatively abundant specialized *enzymes** – *α-amylase*, *α-glucosidase*. A pharyngeal musculoskeletal chewing system allows the mechanical treatment of the ingested material. Such adapted digestive systems leave no room for any original behavior.

Similarly, the various species of mbuna cichlids that coexist in Lake Tanganyika use the plant resources that cover the rocky beds, displaying specific preferences related to the position of the microhabitats distributed between the top, sides or base of boulders covered with various algal species. The diversity of feeding behaviors may, in turn, explain the diversity of herbivorous ichthyic populations in the African Great Lakes. On the Atlantic coast of Portugal, salema, *Sarpa salpa*, graze the coastal meadows of cymodoceae and eelgrass, preferring *Zostera noltii* and, to a lesser extent, *Cymodocea nodosa*, followed by *Z. marina*, whose *carbon* and *nitrogen, C/N*, levels are significantly different. Projects to restore coastal meadows must therefore take into account such food preferences.

In the meadows along the Australian coast, the herbivorous kyphosid, *Girella elevata* and *Kyphosus sydneyanus*, consume green algae, *Ulva australis* and *U. compressa*, which form a vegetative cover on intertidal rocks*. Their abundance is correlated with that of sea lettuces, which multiply by 5 between February–March and October–November. These algae are tastefully attractive. These fish behave omnivorously at fairly low temperatures of 12°C and become almost exclusively herbivores at hot temperatures of 22–27°C, with the nutritional value of the ingested plant material increasing in relation to the activity of their digestive *enzymes**: *proteases*, *carbohydrase*, *α-amylase*, *α-glucidase* which are heat sensitive, as has been shown among parrot fish, *Sparisoma cretense*, in southern Greece which are the beneficiaries of global warming and are promised a bright future.

Some Red Sea herbivores, such as the siganidae, *Siganus luridus* and *S. rivulatus*, which entered the Mediterranean after the opening of the Suez Canal (on the Syrian coast in 1931), became invasive (Volume 1, section 2.3.7) and spread their populations to the Adriatic, Sicily, Tunisia, Algeria and France taking advantage of global warming. These Lessepsian migrants* are in serious competition with the native species, salema, *Sarpa salpa*. These siganidae, particularly abundant in the Levant and around the Greek islands, consume algae abundantly by creating bare benthic* spaces.

Australian monacanthids of the *Meuschenia* genus choose older *Posidonia australis* leaves because young leaves are rich in *phenolic compounds* that act as chemical "repellents". Their preferences are for leaves covered with epiphytes* and an epifauna* – epibionts* – of high nutritional value that is much higher than that of plant components, making them "false herbivores". Surgeon fish, *Ctenochætus striatus*, graze heavily on the coral substrate, collecting the microalgal film and participating in its bio-erosion. This fish has complex oral structures consisting of rigid parts for surface rasping and palatal soft parts that function as a brush and shovel to collect particulate material from coral algal surfaces. Such adaptations to a herbivore-derived diet are particularly effective.

Bibliography: *Can.J.Fish Aquat.Sci*., 2007, **64**: 867-673 & DOI:10.1139/F07-063, *J.Exp.Biol*., 2014, **217**: 1925-1932 & DOI:10.1242/jeb.096248, 3057-3072 & DOI:10.1242/jeb.106575, *J.Fish Biol*., 2006, **69**: 130-140 & DOI:10.1111/j.1095-8649.2006.01082.x, 2007, **71**: 272-278 & DOI:10.1111/j.1095-8649.2007.01472.x, 2014, **84**: 1474-1489 & DOI:10.1111/jfb.12371, 2015, **86**: 375-384 & DOI:10.1111/jfb.2015.86.issue-1/issuetoc, *Mar.Ecol*.2014, **35**: 96-105 & DOI:10.1111/maec.12059*, Mar.Ecol.Prog.Ser.,* 2016, **553**: 81-92 & DOI:103354/meps11790*, Roy.Soc.Open Sci,* 2018, **5**, 1 & DOI:10.1098/rsos.171111

1.2.4.2. *Grazing microscopic epilithic algae**

On the shores of Lake Tanganyika, on hard bottoms of rocks, stones, pebbles and sandy sediments, various species (about 15) of cichlids adopt a diet of microscopic algae as the coating on these surfaces. With a wide variety of specialized structures (comb teeth, rakes, jaws, intestines of different lengths, digestive *enzymes*), these species constitute a variety of "ecomorphs" that depend on the type of substrate and depth and share algal resources. Defined as "grazers-browsers" such as *Pelmatochromis fasciolus* and *Telmatochromis temporalis* which harvest unicellular and filamentous algae, scrapers, such as *Eretmodus cyanostictus*, which grates epiliths*, and scoopers, which absorb and sort sedimentary and algal particles such as *Xenotilapia papilio*, all exploit these diversified resources according to their food preferences and their specialized gathering capabilities. Highly specialized morphoanatomical and physiological feeding adaptations allow them to exploit the full range of algal and plant resources.

Bibliography: *Roy.Soc.Open Sci,* 2016, **3**, 11 & DOI:10.1098/rsos.160229

1.2.4.3. *Grazing corals*

Of the 6,000 species of reef fish, only 123 species feed on corals, the latter being protected by their mucus and by the stinging nematocytes* of the tentacles of their polyps. Some corallivorous species such as the southern tubelip, *Labropsis australis*, have structures adapted to using suction to harvest the organic surface – the polyps – covering the mineral skeleton. Their lips are covered with a lamellar epithelium that secretes, by goblet cells, an abundant mucus made of *polysaccharides*. This mucus facilitates sucking and, above all, protects against damage caused by the multitude of nematocytes*, which is reminiscent of the mucosal protection of clownfish of the genus *Amphiprion* within the corolla of stinging tentacles of host anemones (Volume 1, section 3.4.1; Figure 3.3). However, this tubelip shows a preference for damaged corals richer in mucus than healthy corals.

Another form of grazing of mineralized corals concerns parrot fish (scarid fish of the *Scarus* genus) which feed on the organic part (the polyps) and reject, in their feces, the mineral part made of limestone *carbonate*, $CaCO_3$, which is at the origin of coral sand constituting the paradise beaches of tropical islands. The diet of these parrots is also herbivorous. Their consumption of macroalgae that grow on corals, especially those degraded by cyclones and that die – through bleaching – as a result of water acidification and global warming, a decline that has been observed for several decades in the Caribbean, the Great Barrier Reef, Polynesia, plays an important role in preserving natural coral reef habitats. An assessment of the intensity of grazing by parrot fish, *Scarus*, on Caribbean corals is necessary to establish plans for the protection of reef areas, taking into account the spatial competition between macroalgae and corals, as coral recruitment* by *Porite* larvae, one of the main coral species, may be made difficult as a result of excessive algal cover and lack of accessible mineral support. These grazers work to maintain coral health.

The intensity of grazing on algal species, particularly filamentous and encrusting calcareous algae, by parrot fish in Kenya determines the development of algal reef successions that modulate competitive interactions – space, nutrients, light – between macroalgae and corals. The feeding methods by scraping, grazing and crushing the various parrot species, especially those of large size which select algal species according to their palatability* within a vast home range* of 75–300 m^2, determine the development of reef covers, both algal – *Padina*, *Hypnea*, *Sargassum*, *Turbinaria* – and coral. As a result, herbivorous and corallivorous parrot fish shape the reef landscape in accordance with their respective consumption of algae and corals.

Algal consumption by parrot fish conditions the coral cover of Australian and Caribbean reefs. The population of coral reefs depends directly on the selective appetite of these fish. While corals have been declining for more than 35 years in the Caribbean and algal cover is steadily increasing, it has been shown in the Florida Keys that this is conditioned by the consumption of parrot fish according to their food preferences which vary during their development (juveniles, intermediates, adults).

Faunal fish invasions (Volume 1, section 2.3) can have opposite and opposing effects on marine ecosystems in the Eastern Mediterranean and the Caribbean. Mediterranean marine plant ecosystems are overexploited and in clear decline due to the Lessepsian* invasion of the eastern basin by herbivorous species of siganidae or rabbitfish originating from the Red Sea, *Siganus luridus* and *S. rivulatus*. In the Caribbean, on the other hand, the invasion of lionfish *Pterois volitans* and *P. miles*, which have decimated populations of small herbivorous fish, favor excessive algal development that negatively covers coral surfaces. Should we imagine an experimental immigration of rabbit fish? On other Caribbean reefs, the presence of these invasive lionfish results in a 50% reduction in the feeding activities of herbivorous species. A change in the grazing dynamics of microalgae has important consequences for benthic reef ecology.

Herbivore densities are higher on coral reefs in the Red Sea affected by coral bleaching than on those that have remained healthy and free of algal cover following coral death. These fish then benefit from anthropogenic disturbances. On the other hand, the populations of the wrasses of the *Symphodus* genus are victims of alterations in the canopy* of *Cystoseira* algae in the Mediterranean sublittoral zone. A transformation of coastal habitats and a decline in three-dimensional structures favorable to the protection of juveniles are responsible for a dramatic decrease in the recruitment* of these labridae. In addition, the depletion of this algae, which is widely used by nesting males, can seriously affect the reproductive success of these fish.

Bibliography: *Curr.Biol.*, 2017, **27**: R13-R14 & R399-R407, *Env.Biol.Fish*, 2013, **96** : 1065-1072 & DOI:10.1007/s10641-012-0103-5, 2016, **99**: 499-508 & DOI:10.1007/s10641-016-0486-9, *J.Exp.Mar.Biol Ecol.*, 2013, **442**: 70-79, *Mar.Biol.,* 2004, **145**: 445-454 & DOI:10.1007/s00227-004-1341-7, *Mar.Ecol.Prog.Ser.,* 2014, **504**: 110-132 & DOI:10.3354/meps.10744, **506**: 115-127 & DOI:10.3354/meps10764, 2015, **520**: 1-20, 2018, **597** : 207-220 & DOI.org/10.3354/meps12600, **603** : 175-187 & DOI.org/10.3354/meps12718

1.2.4.4. *Cultivating gardens and defending algae*

In tropical waters, parrotfish, *Sparisoma aurofrenatum*, consume various species of algae on coral reefs in the Caribbean, whose diversity sometimes increases with their number. These fish aggressively defend the algae gardens located in their territories in which they form social groups. They seem to have a certain sense of the value of algae that justifies their protection against intruders. Similarly, on Caribbean reefs, damselfish, *Stegastes planifrons*, create algae gardens and maintain them through selective grazing, especially in areas where dead corals cover. They defend these territories against the intrusion of rivals they suspect of being angry with their food resources. Their populations are tending to expand in line with current advances in coral bleaching, but are limited by the algal consumption pressure that controls their number. They behave like farmers and carry out original farming behavior.

In the Philippines, the jewel damselfish, *Plectroglyphidodon lacrymatus*, maintains its algal gardens on the reefs. Their size depends on their location in relation to their surroundings: the presence of conspecifics or heterospecifics (*Pomacentrus chrysurus*) with whom they have a conflicting relationship. Attacks between congeners are the most frequent (84% against 31%); the energy cost of defending a territory (1.2 m^2 in its absence) is responsible for a reduction of its surface area of approximately 50%. Conflicting relationships between neighboring farmers can be expensive.

Bibliography: *J.Fish Biol.,* 2018, **93** : 1197-1206 & DOI:10.1111/jfb,13841, *Mar.Ecol.Prog.Ser.*, 2014, **506**: 115-127 & DOI:10.3354/meps10764, **511**: 193-207 & DOI:10.3354/meps10921, 015, **528**: 289-296, & DOI:10.3354 meps11243

1.2.4.5. *Mechanisms for defending contaminated plants and grazers*

After being exploited by the herbivorous invertebrates, mollusks (chitons, gastropods) and echinoderms (sea urchins), aquatic algae and phanerogams are also exploited by vertebrates: turtles, dugongs and fish. Surgeon fish, *Acanthurus* sp., *Ctenochætus* sp., parrot fish, *Scarus* sp., *Sparisoma* sp., and rabbit fish or siganidae, *Siganus* sp., in the warm waters of subtropical and tropical regions, play an important role in the exploitation of algae. It should be noted that the Indopacific regions are particularly rich in herbivorous species, unlike the Atlantic fauna which, for paleontological and phylogenetic reasons, are rather poor.

The defense mechanisms of these plants against this predation have been mechanical, using calcification, and chemical, through the secretion of toxic substances such as *terpenoids – caulerpine, caulerpenine, caulerpicine* – and *tannins*. The marine herbivorous fish mentioned above have developed appropriate mechanisms for grazing calcified elements and neutralizing toxins, allowing them to take the best advantage, for their food, protection and reproduction, of this underwater kingdom which, given global warming, in particular, the tropicalization of the Mediterranean, promises to extend beyond the tropical and subtropical regions alone.

Some marine algae are invasive* in the Mediterranean, such as *Caulerpa taxifolia*, which contains a toxic compound: *caulerpine*. It is grazed by the white seabream, *Diplodus sargus*, which induces disturbances in its metabolism of *polyunsaturated fatty acids, PUFA*, which can cause health problems in human consumers of this fish due to a deficiency in essential *fatty acids* of the *ω6* series.

Bibliography: *Curr.Biol*., 2017, **27**: R484-R489, *Mar.Biol*., 2014, **161**:1275-1283 & DOI:10.1007/s00227-014-2417-7, *Proc.Roy.Soc.B, 2,*019, **286** : 20182672 & DOI.org./10.1098/rspb.2018.2672 2

1.2.4.6. *Vegetarian sharks(!)*

A unique diet is that of the hammerhead shark, *Sphyrna tiburo*, from the American coast which, in addition to fish, cephalopods and crustaceans, consumes turtle grass leaves, *Thalassoma testudinum*, a phanerogam. Previous observations indicated the presence of this plant material in their stomachs, suggesting accidental ingestion through the capture of crabs or octopus in seagrass beds. Recent studies show that this is not the case and that, in California, hammerhead sharks regularly ingest a significant quantity of plants that can constitute, in mass, 62% of their digestive content and represent up to 90% of their food targets, with cephalopods constituting the remaining 10%. Better, *isotope* markings $\delta^{13}C$ have revealed the existence of digestive *enzymes* (a *β-glucosidase* synthesized by the micro-organisms of its intestinal flora) capable of digesting this plant material, which shows that these dangerous carnivores with the fateful reputation of killers can also, at times, behave like peaceful grazers with omnivorous regimes. The “teeth of the sea” are no longer what we thought they were; could it be that they even count vegans* among their number?

Bibliography: *Proc.Roy.Soc,B,* 2018, **285**: 1886 & DOI:10.1098/rspb.2018.1583, *Soc. for Integrative & comparative Biology*, 2018 annual meeting. 109-1. S*amanthacleigh.weebly.com*

1.2.4.7. *Herbivorous plant propagation agents*

Aplodactylidae, *Aplodactylus trabeculata*, is a herbivore that consumes kelp*, *Lessonia trabeculata*, on the Chilean coast and whose spores (sporophytes) are not digested. Released viable into the feces, they ensure a dispersion of this laminaria algae in various marine habitats. It therefore acts as a facilitator of algal expansion.

Similarly, in Hawaii, the bluespine unicornfish, *Naso unicornis* is a herbivore that consumes the rhodophyte red algae, *Gracilaria salicornaria.* It releases viable algae fragments into its feces that, a few weeks later, form new algae using a natural propagation process.

Bibliography: *J.Exp.Mar.Biol.Ecol.,* 2018, **500** : 112-119 & DOI.org/10.1016/j.jembe.2017.12.007, *Mar.Biol.*, 2017, **164** : 25 & DOI:10.10007/s00227- 016-3049-x

The capture of live, mobile animal prey justifies much more elaborate behavior than simple plant grazing, and some hunting methods, both individual and collective, call for real and often very intelligent strategies, some of which will be presented here.

1.3. Individual and collective protective habitats

Fish, like all living beings, are confronted with a number of dangers arising from factors in their environment against which they must protect themselves, both through appropriate behavior and the implementation of physiological resistance mechanisms. They are also threatened by congeners and, especially, by predators who are only too willing to threaten their lives and against whom they must develop strategies of concealment, as well as flight to safe shelters. Such defensive and protective measures using both active (escape movements) and passive (mimicry) mechanisms concern adult individuals, as well as their offspring, eggs and larvae which are particularly vulnerable.

1.3.1. *Protecting oneself from environmental factors*

Protective physiological mechanisms will not be addressed here, where only protective behaviors against environmental aggressions related to ambient hydrodynamics, ultraviolet radiation and difficult or extreme habitats will be discussed.

Most of these defensive behaviors are based on an ability to escape from "environmental danger" and take refuge in sites where there is little or no threat. As a result, in the face of acoustic stress – noise pollution caused by anthropogenic noise from boat engines, seismic explosions, etc. – the basic reaction of all species is to leave the area and move away, in distance and depth, to enjoy a calmer environment.

1.3.1.1. *The value of having hydraulic shelters*

Fish living in rivers are often confronted, in this hydrologically heterogeneous environment, with differences in current speed and hydrodynamic turbulence that lead them to select areas and microhabitats that balance costs (swimming energy expenditure) and benefits (food opportunities). In addition to searching for the best trajectories, they adapt their swimming speed to the speed of the current by seeking to use hydraulic shelters they encounter to allow them to rest and save their energy. Consequently, ports, hitherto considered to be traps, are now being rehabilitated because their slow-flowing waters often serve as a haven of peace, at least for larvae and postlarvae looking for a favorable site to settle in when they are recruited*.

With the guppy, *Poecilia reticulata*, the tallest individuals, unlike the smallest, swim further away from their habitat and venture further between structures – boulders, wood debris, piers – that form obstacles to longitudinal water flow and create turbulence. They prefer areas of fast current, but low turbulence. Their strategy consists of maintaining the same position through an active yet stationary swimming to avoid being dragged downstream by the water flow. This practice is called "sit-and-wait". Males, regardless of their size, prefer slow currents because of the risk of entrainment caused by their long fins, a secondary sexual characteristic highly appreciated by females (Volume 2, section 1.1.2.6.6) but which constitutes, in this case, a motor disability. Females have better running and turbulent water movement skills than their partners, although they are often also disadvantaged by their pregnancy – a large abdomen, swollen by the development of their ovaries.

In Canadian rivers, char, *Salvelinus confluentus*, populations are all the more abundant because the bed is made up of blocks and cluttered with tree trunks and branches that provide hydraulic shelters. Intensive logging, which limits the number of submerged trees and branches, is responsible for the decline of up to 43% of their populations. Stream restoration operations, through a repository of wooden structures, are being carried out in U.S. streams for the purpose of improving salmonid habitats. Female rainbow trout, *O. mykiss*, migrate to upstream spawning grounds – anadromous* – and choose coarse substrate sites that can provide shelter for their offspring (Volume 2, section 2.1.3).

It is generally accepted that the anthropogenic effects of simplifying freshwater habitats during stream bank and bed operations to reduce flood risks result in a decrease in the density of salmonid populations. For this reason, it has been recommended that physical structures such as boulders, tree trunks and branches be added to American rivers, which generally results in an increase in trout and salmon density. This kind of physical habitat restoration programs that add large woody elements appears to have positive effects in salmonid streams in the northwestern United States. They are more controversial in other regions.

Such changes in natural habitats lead to behavioral differences, with fish being more active and aggressive (foraging and access to food, breeding opportunities, anti-predator defense, etc.) in so-called “open” habitats and being more faithful to their place of residence in more complex and structured habitats. Differences in visual distance (35 cm vs. 100 cm) may partly explain such differential behaviors.

Given the plasticity of the behaviors, it seemed predictable that the degree of habitat heterogeneity could be predictive of fish personality traits (Volume 2, section 3.7). A comparative study of the behavior of juvenile Atlantic salmon, *Salmo salar*, in a Canadian stream with both habitat types showed that this is not the case and that the physical structure of the habitats does not favor any particular personality type (brave or fearful, enterprising and exploratory or faithful to its microhabitat, etc.).

Bibliography: *Anim.Behav*., 2018, **135**: 139-146 & DOI.10.1016/j.anbehav.2017.11.006, *Can.J.Fish.Aquat.Sci*, 2015, **72**: 466-478 & DOI:10.1139/cjfas-2014-0344

Fish generally do a better job than just resisting hydraulic driving forces by seeking shelter. They use their swimming abilities and often make use of currents to take advantage of hydrodynamic forces to improve their individual or collective swimming performance during migrations (Volume 1, section 2.2.3).

1.3.1.2. *Adaptation to extreme habitats*

Various environments are particularly inhospitable to fish, such as caves, groundwater, temporary water points and abysses.

However, some species have managed to survive and exploit their resources. For example, some mollies, *Pœcilia mexicana*, colonize Mexican caves rich in sources that produce *hydrogen sulfide* H_2S, a toxic gas. These populations have developed detoxification mechanisms and the ability to consume bacterial prey, which requires remarkable digestive adaptations.

Marine species living in deep hydrothermal springs (Volume 1, section 1.1.17.2) are also perfectly adapted to these environments, which are very hot and also rich in toxic gases.

Resisting extreme conditions such as those resulting from the drying out of water points during the dry season is also a particularly remarkable feat achieved by some fish such as the West African lungfish, *Protopterus annectens*, which digs a burrow to take refuge during the dry season, wrapped in a cocoon of hard mucus. The topminnow, *Austrofundulus myerci*, like many other cyprinodonts, ensures the sustainability of the species by burying its eggs in the wet sediment before the pond dries up and dies. Eggs will hatch when the rains return and neonates will reproduce as early as 4 weeks of age. Such forms are considered “extremophilic”.

Bibliography: *Freshwat.Biol.*, 2015, DOI:10.1111/fwb.12530

1.3.1.3. *Spawning on the ground and in the air*

Australian species such as *Galaxias truttaceus*, a small galaxid in the southern hemisphere, lay their eggs upstream of estuaries or in streams along seasonally submerged forests, in shoreline vegetation or among plant roots. Eggs develop out of water, but in a moist atmosphere, with their hatching dependent on a seasonal rise in water levels in the floodplain. These spawnings may not be submerged when the embryos have exhausted their energy reserves, but, generally, the arrival of high water in the wet season not only promotes their hatching (after some mechanical agitation), but also ensures the downstream transport of larvae to the sea and their dispersion, with the high turbidity of the water reducing the risk of predation. These “aerophilic” spawners are waiting for the lifesaver rising from the water.

This is also the case for the California grunion, *Leuresthes tenuis*, which lays eggs at low tide in wet beach sediments and whose eggs hatch only when they are covered with water during the high tides of the next tidal cycle*. Similarly, the eggs of the splash tetra, *Copella arnoldi*, develop in the open air, glued on the underside of the leaves of plants bordering the banks of the Amazon, their humidification being ensured by water projections (tailbeats) made by the male.

Bibliography: *Fish Fish.* 2006; **7**: 153-164

1.3.2. *Protecting oneself from congeners and competing species*

Intra- and interspecies competition is an almost normal situation in the living world. It governs social relations and concerns the occupation of habitats, access to food, possession of sexual partners and the use of spawning grounds. It is a permanent competition that often justifies the struggle for life.

1.3.2.1. *Competition for space*

Competition between fish concerns the occupation of habitats that are used for protection (secure niches), food (trophic niches) and reproduction (of courting and mating grounds, nests for spawned eggs). As a result, on coral reefs, the possession of a habitat and the occupation of a territory within the corals are crucial to the survival of individuals, which generally gives rise to very strong intra- and interspecies disputes, with the installation of pelagic larvae on the reefs during recruitment (Volume 2, section 2.14) constituting a vital stage in the life cycle of each of the reef species.

Figure 1.8. *Damselfish in the vicinity of their* Acropora *sp. coral shelters (source: Jomard, C.)*

The damselfish, *Chromis viridis*, of the Red Sea resides among the corals of the *Acropora* genus in accordance with their own morphology – size, branch density, distance from interbranchial spaces – which determines the richness – spatial distribution, abundance – of the stands of these pomacentridae. The *Dascyllus adustus* of the Virgin Islands, which forms dense reef populations, shows a strong territoriality, and each owner must constantly defend their territory, their algal garden (Volume 1, section 1.2.3.4), against the many potential intruders who try to enter it. They know how to recognize the predators, both innately – hereditarily – and through experience acquired, based on visual and olfactory criteria, and are able to discriminate against the apparent dangerousness of these competitors (Volume 1, section 3.8.5) who are herbivores, carnivores, predators or egg eaters so that they adopt an appropriate aggressive behavior, with different degrees of combativeness depending on a scale of threats, avoiding exhausting their defensive energy against undesirable intruders, generally preferring to attack their congeners with the greatest energy, especially if they are smaller than themselves, taking care not to attack large intruders and powerful competitors. The defense of the territory by the males of the Australian damselfish, *Pomatocentrus amboinensis*, requires a visual identification of the intruder congeners reported by the UV reflections of their bodies and fins, which are perceived in high contrast and whose intensity determines the virulence of the attack directed, in particular, against heterospecific males.

Territorial species such as the cichlid, *Amatitlania siquia*, from a Nicaraguan lake are fiercely defending their territory against any intrusion. The cost of such a territorial defense is often high. The presence of natural landmarks in this territory reduces these energy expenditures, as the size of the territories decreases as the size of the territorial landmarks that establish visual boundaries accessible to the resident increases. The shape and size of the territories affect the cost of their defense, with the greatest number of hunting and pursuit movements per square meter involving small, elongated territories that are more easily defensible. With the daffodil cichlid, *Neolamprologus pulcher*, the male defends his territory against any intruder who approaches it, with his degree of aggressiveness being proportional to his plasma concentration in *testosterone 11-KT*, the *androgen* that conditions the virility of the fighter. Such aggressiveness bears no relation to the size of the males engaged in combat, and the most aggressive of them are often small individuals who do not hesitate to confront larger opponents.

Bibliography: *Anim.Behav*., 2004, **68**: 273-282 & DOI:10.1016/j.abehav.2003.11.010, *Behav.Proc.,* 2013, **92** : 47-51 & DOI:10.1016/j.beproc.2012.10.005

1.3.3. *Protecting oneself from predators*

The aquatic world is a dangerous environment given the number and activity of predators, with a considerable threat of predation in most environments. Fish are commonly the victims, with most predators present in their immediate environment and sometimes even within a family – filial cannibalism (Volume 1, section 1.2.3), in addition to intrusions from land (birds: herons, cormorants, eagles; reptiles: snakes; and mammals: otters). More unusual is the capture of small fish of 2–6 cm long, such as mosquitofish, *Gambusia* sp., by semi-aquatic spiders of various species such as fishing spiders (lycosids, water spiders, etc.); these predators do not hesitate to attack prey up to 2.2 times larger than them.

The use of visual signals for the quick and accurate identification of predators is quite common, but all senses are generally alert when there is a potential danger.

Bibliography: *Ethol*. 2017, **123**: 560-570 & DOI:10.1111/eth.12630, *PLoS ONE*, 2014, **9**: e99459 & DOI:10.1371/journal.pone.0099459

1.3.3.1. *Appreciating the dangerousness of an intruder*

Male damselfish, *Stegastes adustus*, have territory in coral reefs that they defend fiercely against intruders, as they are able to discriminate between different intrusive species and to measure their aggressive response – attack distance, intensity and frequency – distinguishing between homospecific and heterospecific individuals; the former are fought with greater virulence as they constitute threats to access to food and breeding, unlike heterospecific herbivorous and invertebrate-consuming species that appear less dangerous. The different levels of aggressiveness are therefore adapted to the degrees of danger they pose to the owner of the territory.

The defense of their territory by resident males of the American pupfish, *Cyprinodon bovinus*, concerns a specific area bordering a sharing zone with neighbors known as "dear enemies", who are less of a target for their aggression than against foreign intruders. Females rarely enter a resident's territory, preferring to meet the largest number of males on their borders and judging the quality of the owner of the premises on the basis of his behavior towards intruders, with his aggressiveness greater in the presence of females than in their absence. Flexible aggressiveness according to the social environment allows females to take advantage of these social interactions to mate with the best males.

The cichlids *Neolamprologus mustax* from Lake Tanganyika, consumers of zoobenthos, prefer to hunt in the territory of a closely related algivorous species *N. moorii*, which mainly contains filamentous algae and is rich in benthic invertebrates*. They are tolerated as long as they do not pose a threat to either the plant reserves or the spawning grounds of the host species. Their presence is a deterrent to algivorous species other than *N. moorii*, which tend to move away from this algal garden. Focusing defenses on truly dangerous species and making friends with non-competing species is a cost-effective strategy.

Bibliography: *Ethol.*, 2006, **112**: 417-423 & DOI:10.1111/j.1439-0310.2006.01166.x, *J.Fish Biol.,* 2007, **71**: 399-410 & DOI:10.1111/j.1095-8649.2007.01493.x

1.3.3.2. *Innate protective reactions*

The usual reaction of prey species to a threat of predation is flight, a flight towards the nearest shelter, which implies a rapid and immediate mobilization of energy resources for swimming, following physiological stress inducing an increase in the availability of blood *glucose* through the hydrolysis of liver and muscle *glycogen*. The amplified swimming abilities then decide the fate of the prey. An immobilization behavior – stop and go or freeze reaction – offers the advantage, firstly, of avoiding detection by the predator and making it possible to analyze the situation such as the presumed dangerousness of the predator, and then to promote, secondly, the fastest possible escape.

Natural mortality of fish is particularly high during the early stages of their development. It is therefore urgent that these young organisms have the ability to detect their predators as quickly as possible in order to improve their chances of survival. Thus, the embryos of the clownfish, *Amphiprion melanopus*, react, by increasing their heart rate, to warning signals or *pheromones** emitted by congeners (Volume 1, section 3.2) and that they perceive through olfaction. They therefore have a potential for the early recognition of future predation risks, which may be useful to them in their close post-embryonic life. Newborns and juveniles of the cichlid, *Amatitlania nigrofasciata*, show a natural phobia of predators such as the rainbow trout, *O. mykiss,* which they retain for the first 3 weeks of their lives. There would be a stronger phobia in the early stages of development, when these juveniles are most vulnerable, and which weakens during development because it is not expressed in the pre-adult phase.

Visual identification of predators is a priority for any prey struggling for survival. This function is used early in larval life for escape purposes, as in the zebrafish, *Danio rerio*, whose larvae have visual abilities that allow them to detect a vague silhouette of a predator in approach movement.

In Nicaragua, the reproductive success of the convict cichlid, *Amatitlania nigrofasciata* ex *Archocentrus nigrofasciatus*, is improved in the presence of predators: cichlids like *Hypsophrys nicaraguensis*. The survival of young in nests located nearby, less than 1 m from the territory of a predator, is higher than that of their congeners born in more distant nests. Would living in the immediate vicinity of danger make a species stronger, unless the predator's aggressiveness is less towards the immediate neighbors considered "dear enemies"?

The visual detection of a predator is necessary for larvae, even if their optical system is still rudimentary. However, their retinal receptors are already able, as in the larvae of the zebrafish, *Danio rerio*, to communicate stimuli to the neurons on their optic roof – the diencephalon – corresponding to the detection of a vague silhouette that immediately triggers a flight reaction. Is it necessary to have a precise picture of the type of danger to know how to try to avoid it?

Knowledge of the danger may even originate at a very early stage, before birth. Rainbow trout, *O. mykiss*, embryos exposed to alarm signals – *alarm pheromones* – during egg incubation express less fear at birth – greater activity and no immobilization reaction or freezing – than untreated controls. The behavioral plasticity of the fear reactions manifested by spawning is modulated by the level of risk perceived by *in ovo* embryos.

Bibliography: *Anim.Behav.,* 2015, **103**: 1-6 & DOI:10.1016/j.anbehav.2015.01.033, 2016, **114**: 37-43 & DOI:10.1016/j.anbehav.2016.01.007, 2017, **133**: 35-45 & DOI:10.1016/j.anbehav.2017.09.013*, Biol.Lett.,* 2008, **4**: 610-612 & DOI:10.1098/rsbl.2008.0378, *Curr.Sci*., 2015, **25**: 1823-1834 & DOI:10.1016/j.cub.2015.06.00, *J.Fish Biol.,* 2006, **68**: 613-617 & DOI:10.1111/ j.1095-8649.2006.00922.x *2*

1.3.3.3. *Have defensive, mechanical or chemical weapons or both*

An effective means of protection for many species is the possession of thorns that play a mechanical role and are often associated with poisonous glands with toxic chemical action that enhance their effectiveness. A defensive “hedgehog” posture is innate in rays, *Amblyraja radiata* and *Raja rondeleti*, which have many long thorns on their backs and tails. Similarly, stingrays, *Dasyatis* sp., armed with one or two barbed wire stingrays on the tail can confront a threat – a diver, for example, by displaying their tails and inflicting very painful injuries.

The possession by the American catfish, *Ictalurus punctatus*, of pectoral spines which, when erect, are twice as long as the body width of the fish, is intended to significantly complicate its ingestion by predators with limited mouth openings. Their articulation – abduction–adduction* – at the pectoral girdle of the fish constitutes a robust and very effective anchoring system, particularly annoying for the predator. Well developed in wild Virginia populations, these thorns are relatively shorter – negative growth allometry* – in large individuals that have become less vulnerable due to their size. They are reduced in breeding individuals who are not subjected to predation pressure, as exposure to 13 weeks of predation threat by a black-bass *Micropterus salmoides* is insufficient to induce an increase in such defensive device in juveniles.

Lionfish of the *Pterois* and *Dendrochirus* genera combine 13 very sharp dorsal spines with venom glands that inoculate the victim with a powerful *neurotoxin** whose effect is particularly devastating. Such a fish that Nature has made almost invulnerable, although such protection has its limits, *P. miles* avoiding the reefs of the Red Sea rich in its predator, the moray eel, *Gymnothorax flavimarginatus*.

Figure 1.9. *Lionfish* Pterois *sp., protected by its poisonous spines linked to toxic glands*

Australian blennies, *Meiacanthus atrodorsalis*, offer the particularity of having, on their lower jaw, very sharp teeth – canines – connected to a venom gland, which flows out through a groove on their anterior side. Consisting of *phospholipases*, *proenkephalin* and *neuropeptide Y* which have negative cardiovascular effects (hypotension), this venom plays a defensive role against predators, individuals amputated of their venom hook becoming edible by them. The deterrent effects of owning such a venomous system are such that blennies-like species such as *Aspidontus tæniatus* have imitated them using a defensive mimicry* process (Volume 2, section 3.8).

Chemical deterrence is sometimes used by itself. This effective protection method has been developed by Red Sea reef gobies, *Gobiodon histrio*, which live in association with *Acropora* corals and which, in addition to their visual camouflage capabilities, produce skin toxins that act as a repellent against their natural predator, the grouper, *Epinephelus fasciatus*. Ingested by the predator, these gobies are immediately spit out before being swallowed. Such ichthyo-crino-toxicity is quite widespread – 50 species belonging to 13 families of teleosts including siluriforms and tetraodontiforms – and proves effective as a post-capture rejection process due to its non-palatability*, with the toxic mucus ingested experimentally by damselfish fish *Chromis viridis* causing them to lose balance within 60–120 sec. The Australian common stinkfish, *Foetorepus calauropomus*, secretes a viscous mucus that gives off a pestilential odor that is a real deterrent to potential predators.

Hagfish, *Myxine* sp., in deep waters have particularly effective mechanical anti-predatory measures. In addition to having soft skin that is resistant to predator bites due to the possession of subcutaneous spaces protecting muscles and viscera from damage by shark teeth, they also expel, in the event of danger, a particularly viscous mucus that is abundant in the form of long filaments of 10–15 cm with a diameter of 1–3 µm. Concentrated in mucous glands, this material literally "explodes" (volume x 10,000 in 100–400 ms) in the predator's mouth and this threatens to clog it and its gills. The predator that is unable to take it out! Were these hagfish not rightly referred to as slime-eels?

Bibliography: *Curr.Biol.*, 2017, **27**: 1-8 & DOI:10.1016/j.cub.2017.02.067, *Env.Biol.Fishes*, 2017, **100**: 745-748 & DOI:10.1007/s10641-017-0600-7, *Evol.,* 2014, **68**: 2102-2107 & DOI:10.1111/evo.12379, *J.Roy.Soc.Interface*, 2017, **14**, 137 & DOI:10.1098/rsif.2017.0765, *Mar.Ecol.*, 2015, **36**: DOI:10.1111/maec.12117, *Mar.Ecol.Prog.Ser.*, 2014, **506**: 243-253 & DOI:103354/meps10789, *Proc.Royal Acad. Sci. B*, 2014, **281**, DOI:10.1098/rspb.2013.3220, *The Royal.Soc.Interface*, 2019, **16**: 150 & DOI:10.1098/rsif.2018.0710

1.3.3.4. *Have swimming potential for rapid escape*

An ability to escape danger as quickly as possible to reach a shelter is a certain safeguard. Fish in dangerous habitats develop a swimming profile that favors a higher escape rate: hydrodynamic profile, developed fins, in particular, the caudal, which, with a muscular caudal peduncle, conditions a rapid start with a swing jump whose effectiveness depends on the intensity of the body curvature in C, with such a *C-start* greatly conditioning the chances of survival.

The availability of energy resources – liver *glycogen* and body *fat* – is a physiological requirement throughout the life of the fish, but especially in the early phase of its development. For example, the larvae of the American sawfly, *Sciænops ocellatus*, are dependent on the fatty acid* (Essential Fatty Acids, EFAs) content of the eggs from which they originate, a potential that they owe to their mother's diet (Volume 2, section 2.13). This does not exempt the larvae themselves from actively seeking to enrich their own diet by consuming planktonic prey rich in *fatty acids* ω^3.

1.3.3.5. *Body shape modification*

A morpho-anatomical response to predation pressure consists of obtaining a greater dorso-ventral height of the prey body that makes it difficult for the predator to ingest them, as occurs in common carp, *Cyprinus carpio*, raised, for several generations, under the threat of black-bass, *Micropterus salmoides*. These carp can be divided into two categories: some active and reluctant to seek shelter and others more passive and in search of protection areas, the former having a higher height/length dimensional ratio than the latter, demonstrating the existence of a clear link between the behavior and the development of adaptive anti-predatory morphologies. Similarly, the presence of pike, *Esox lucius*, in their environment causes young perch, *Perca fluviatilis*, and roaches, *Rutilus rutilus*, to undergo adaptive morphological changes – increased body height, more posterior dorsal fin, more anterior pelvic fins, wider anal fin – that have an anti-predatory purpose and allow improved swimming performance. In contrast, in Finnish lakes with only harmless cyprinids, the perches have a sharper profile with a longer head. In addition, on Australia's northwest coast, the depletion of shark populations due to overfishing results in morphological changes in the various prey fish species with smaller eyes and caudal fins (size in the range of –40 to –45%) than when predator populations were abundant, demonstrating that morphological changes induced by high predation are reversible at the population level.

Bibliography: *Behav*., 2016, **153**: 15-30 & DOI:10.1163/1568539X.00003320, *J.Fish Biol,* 2007, **70**: 155-164 & DOI:10.1111/j.1095-8649.2006.01283.x, 2010, **76**: 787-799 & DOI:10.1111/j.1095-8649.2009.02475.x, 2012, **80**: 49-60, *Mar.Ecol.Prog.Ser*., 2018, **586**: 127-139 & DOI:10.3364/meps12426, *The Amer.Natur*., 2006, **167**: 440-452

1.3.3.6. *Growth acceleration*

In Canadian lakes, the growth potential of yellow perch, *Perca flavescens*, is greater when they are the only available prey of *Sander vitreum* pike-perch for several successive generations, than when alternative prey such as *Coregonus artedi* are also present. They must have access, as quickly as possible, to a size larger than the predators' oral diameter. On the other hand, an acceleration of the growth of common carp, *Cyprinus carpio*, genetically modified by the introduction of a *GH* growth gene, is accompanied by a higher risk of predation, following a relaxation of their anti-predator defense. These transgenic fish* have become more vulnerable, at least until they reach a safe size quickly.

Bibliography: *J.Fish Biol*., 2014, **84**: 1527-1538 & DOI:10.1111/jfb.12381

1.3.4. *Practicing the art of camouflage*

1.3.4.1. *A clever precaution: become cryptic**

Adopting a "camouflage outfit" consists, on the one hand, of blending into the landscape in order to escape the sight of predators – defensive camouflage – and, on the other hand, of avoiding being noticed by prey in order to get as close as possible to them – offensive camouflage – before attacking them. Practicing the art of concealment is a defensive goal for some and an offensive one for others.

1.3.4.2. *Passive camouflage, visual and/or chemical*

Specific and hereditary morphological specializations are intended not to resemble a given type of prey, but rather to resemble structural elements of its habitat – homomorphy* – and, generally, in the adoption of colors identical to those of the habitat – homochromy*; these modalities are acquired during evolution, and the camouflaged individual is merely obeying their genetic heritage.

The tropical monacanthid, *Oxymonacanthus longirostris*, living in reefs where it feeds on coral polyps is a champion of camouflage, combining a certain chromatic invisibility with chemical camouflage that makes it quite invulnerable to predation. Such chemical camouflage is indeed carried out on coral reefs by this coral consumer, who has the ability not to be recognized by certain predators. Such a chemical "camisole" allows this fish not to be smelled.

All seahorse species seek protective habitats such as seaweed and phanerogamous meadows, coral reefs, and hide in microhabitats of tree sponges, branchy corals, whose shapes they adopt – homomorphy* – and colors – homochromy* – in order to go completely unnoticed by predators. The hippocampus-pygmy, *Hippocampus denise*, of Australian coral reefs hides among gorgonians in the midst of which it is difficult to detect due to its small size (<14 mm).

Figure 1.10. *Pygmy seahorse,* Hippocampus denise*, from Australian reefs, hidden in gorgonians whose shape (homomorphy) and color (homochromy) it adopts*

Rapid color changes can also occur in response to changes in habitat color to avoid predators. They consist of blending into the color of the environment, which is more or less light and/or more or less dark, as well as when grouping in shoals in order to avoid being alone by adopting the color of all its congeners in order to dilute the risks of predation, as do guppys, *Pœcilia reticulata*. Whatever the energy cost of these rapid color changes, it is always advantageous for these "chameleon fish" to adopt cryptic behavior*.

An original case concerns the ribbon fish, *Zu cristatus*, which lives at depths of –150 to –400 m and feeds on light-producing prey (stomiid fish), their bioluminescence* resulting from bacterial activity with the production of *luciferin* oxidized by an *enzyme**, *luciferase*. After ingestion, bioluminescent prey continue to emit their biological light for some time so that ribbon fish, fearing that they will be spotted by other predators, hide their gastric content with an opaque black pigment screen made of melanophores* containing *melanin* granules and located on the wall of their stomachs to hide the nature of their prey.

Prey are generally victims of predators who "target" their eyes. While large eyes have the advantage of better detecting the presence of predators, they use this criterion to make their attack more effective. It has been shown that, in populations of river perch, *Perca fluviatilis*, at risk of predation by pike, *Esox lucius*, the selection that occurs naturally leads to a significant reduction in male, but not female, eye size. Such differential phenotypic plasticity implies that females adopt compensatory behaviors. Various reef species such as the butterflyfish, *Chaetodon* sp., camouflage their eyes with black pigmented bands, which confuse predators.

Figure 1.11. *Camouflage of the eye of a butterfly fish of the Chaetodon genus. Associated with an eye patch or "false eye", it has the purpose of protecting against predators*

Bibliography: *Env.Biol.Fish,* 2015, **98**: 1005-1013 & DOI:10.1007/s10641-014-0333-9, *J.Exp.Biol.,* 2015, **218**: 966 & DOI:10.1242/jeb.112110, *J.Fish Biol.,* 2005, **66**; 1489-1492 & DOI:10.1111/j.1095-8649.2005.00680.x, *Proc.Roy.Soc.B*, 2014, DOI:10.1098/rspb.2014.1887, 2019, **286** : 20182625 & DOI.org./10.1098/rspb.2018.2625, *Zool.Stud.,* 2003, **42**: 284-291

1.3.4.3. *Active camouflage*

There are also active camouflage modalities, during which color changes are dynamic and voluntary, with very rapid temporal variations adapted to circumstances and expressing behavioral intentions. The female cichlid *Amatitlania siquia* abandons its *carotenoid*-rich color pattern, with its bright orange belly serving as a sexual signal, when the predation pressure increases and during a specific heterogeneous competition. The Nassau grouper, *Epinephelus striatus*, from the Caribbean shows rapid changes in color pattern and contrast in less than a second when it approaches its prey, crustaceans and fish as discreetly as possible. Such changes require neuroendocrine control of the functioning of its skin chromatophores*.

Flatfish are well known for their remarkable ability to rapidly modify the color and texture of their skin patterns in order to acquire perfect camouflage on the sedimentary substrate that they rest on, following pigmentary movements of dermal melanosomes* within melanocytes or chromatophores*; their dispersion or aggregation is under sympathetic nervous control, with *noradrenaline* produced by the chromaffin tissue* being the neuro-transmitter that regulates the dispersion or concentration of melanosomes. In American plaice, *Pseudopleuronectes americanus*, white dots characterize the color pattern when the fish is placed on a light background, with melanosomes* being concentrated - aggregation. These disperse quickly when the fish is positioned on a dark bottom, causing it to adopt a dark color pattern. These mechanisms involving varying degrees of pigment aggregation and dispersion are induced in response to retinal visual stimuli. If wild juveniles quickly resort to such camouflages, those born in hatcheries and naïve about sediment because they have always lived in uniformly colored hard-bottomed ponds are not very capable of leading a hidden or cryptic existence*. They need more than 2 days to know how to bury themselves quickly in the sedimentary substrate provided that the granulometry < 540 µm of the latter is favorable to them and 90 days to be able to achieve perfect homochromy* with it. They are therefore long exposed to high risks of predation, particularly by visual predators such as birds: they sometimes constitute up to 80% in biomass of the stomach contents of cormorants *Phalacrocorax carbo*.

Different flatfish species have different abilities to hide from predators, resulting in different predation mortality rates. As a result, the English sole, *Parophrys vetulus,* which is quite active, buries itself little in the sediment and adopts a straightened head position that reveals it in the eyes of visual predators. This vulnerability justifies its occupation of turbid estuarine areas rich in mineral particles suspended in the water column in which predation pressure is lower due to the decreased visual acuity of predators.

Figure 1.12. *Camouflage of a flatfish,* Solea solea*, whose color pattern is homochromous* of the sandy sediment on which it is positioned (source: Ruitton, S.)*

Juveniles of the flounder *Platichthys flesus* in the Baltic encounter difficulties on sedimentary floors cluttered with filamentous green algae or enteromorphs, and prefer the bare, clean floors to which they are well adapted in terms of their concealment from predators. Their ancestral natural camouflage is endangered by the eutrophication* of the waters.

Bibliography: *J.Fish Biol.*, 2004, **65** supplt A: 69-87 & DOI:10.1111/j.1095-8649.2004.00529.x, 2008, **72**: 2570-2578 & DOI:10.1111/j.1095-8649.2008.01866.x, **73**: 639-649 & DOI:10.1111/j.1095-8649.2008.01960.x, 2014, **85**: 1634-1649 & DOI:10.1111/jfb.12519, *Mar.Ecol.Prog.Ser.*, 2006, **328**: 267-273

1.3.4.3.1. A backlight that serves as a camouflage

In leiognathid fish ponies along the Indo-Pacific coast, such as *Leiognathus* sp. and *Photoplagios* sp., *Photobacterium leiognathi* bacteria are located in a circum-esophageal lumen organ that is more than 100 times more developed in males than in females during the breeding season, with the light reflected in the ventral direction by the gas bladder, corresponding to camouflage by a counter-illumination process. This bright light is scattered downwards being blocked a predator located below them, with solar illumination from the surface. Such a process is ingenious in order to skillfully erase its contrast in the water mass and not be seen by deeper predators.

Lantern sharks of the *Etmopterus* genus from deep waters at –1,000 m have photophores* in their stomachs consisting of a cupule containing several photocytes (fluorescent vesicles), a pigmented layer (iris) and lens cells. These nine bioluminescent* light devices, which exist early in embryos, would serve to group together between congeners and above all to protect juveniles from predators: cetaceans and unknown fish. Indeed, at hatching, the larvae emit a blue light on more than 80% of the surface of their stomach, which would function, on the principle of a counter-illumination adopted by the ponyfish, as a camouflage system against predators unable to locate them in backlight because they have become "ghost larvae". The mesopelagic* adults of *E. benchleyi* of the Pacific emit a bluish light that allows them to blend into the faint light coming from above, into the ocean depths, and they make themselves invisible from predators below them. Because of their blackish skin, they were called lantern-shark ninjas and considered champions of light camouflage.

Bibliography: *J.Fish Biol.,* 2008, **73**: 1337-1350 & DOI:10.111/j.1095-8649.2008.02006.x, *Mar.Biol.*, 2008, **153**: 1009-1014 & DOI:10.1007/s00227-007-0869-8

1.3.5. *A safe resting phase*

It is during their resting phase that fish, like all animals, are most exposed to predators as they let their guards down. This phase of inactivity, which is "high risk" owing to the considerable food activity of many nocturnal fish-eating predators (sharks, morays), requires them to use reinforced camouflage and concealment in structural shelters (crevices, cavities, caves, algae and phanerogams) in their habitat.

The question of whether some of them have actual sleep periods will be addressed in volume 2 (neurophysiology).

1.3.5.1. *Real night protection*

Parrot fish of the *Scarus* and *Sparisoma* genera stand out because of their protected isolation capacities, following a nightly confinement within coral reefs, in a mucus cocoon made of *glyco-proteins* that they secrete orally each evening and which protects them, chemically and mechanically, from damage by predators, who are unable both to detect their presence in a reef cavity and to pierce the mucous membrane. This "sleeping bag" allows them to ensure that they can rest safely.

Figure 1.13. *A parrot fish in the shell of deciduous mucus cocoon that provides it with nocturnal protection*

1.3.5.2. *Choose the pace of activity*

The search for food, both individually and collectively, is often affected by the risk of predation, as in the case of the minnow, *Phoxinus phoxinus*, which, threatened by trout, *Salmo fario*, stops pursuing its potential prey. A shift in trophic activity time is often a favorable solution, when, for example, the roach, *Rutilus rutilus*, from boreal lakes chooses to feed at night rather than during the day because of diurnal predation risks. The darkness makes them feel comfortable.

Bibliography: *Ethol.*, 2007, **113**: 166-173 & DOI:10.1111/j.1439-0310.2006.01296.x, *J.Fish Biol.*, 2008, **73**: 1407-1418 & DOI:10.1111/j.1095-8649.2008.02020.x

1.3.6. *Owning and defending a territory*

The possession of a favorable habitat offering both the security and availability of food can generate a feeling of “well-being” in its occupant and cause “positive emotions” as evidenced by the absence of stress (*cortisol*) and the presence, in the brain, of *neurohormones* (*dopamine**, *serotonin*, *isotocin*, *oxytocin, etc.*) indicating a certain level of “well-being”.

The choice between various colored habitats has, for example, been tested in the zebrafish, *Danio rerio*, and tilapia, *Oreochromis niloticus*, with a marked preference for some (Conditioned Place Preference, CPP) where they seem happy to live.

The "value" of such habitats fully justifies that the owners of the places are ready to fight to preserve them in the face of the desires of certain rivals.

1.3.6.1. *Early vital acquisition*

Salmonid larvae, in general, and Atlantic salmon, *Salmo salar*, in particular, after a long intra-gravel winter incubation (Volume 2, section 2.1.3), have an exit or emergence phase that is particularly critical in terms of survival. It is a question of finding an installation site as quickly as possible that can serve as a hydraulic shelter, a feeding zone and anti-predator protection, the possession of such a territory significantly affecting the chances of survival. Competition for a post-emergence area is generally very intense, with all larvae having almost simultaneous hatching timing, with a clear advantage for the first hatches born from early egg spawning. This competition can become all the more complicated and serious as newborns born from salmon escaped from farms tend to behave as invaders and seriously compete with wild larvae, as is happening in several rivers in Norway – 198,000 individuals escaped from these farms in 2013. With higher growth capacities, greater aggressiveness, less fear of predators and more risky exploratory behavior, domestic larvae tend to occupy the best early post-emergence habitats and benefit from these competitive advantages. By behaving in a dominant manner, they significantly reduce the survival rates of wild larvae, which is – 30% smolt* a few months later. The quality of a territory, such as the possession of a secure shelter, increases the combativeness of owners' conscious of the value of their property, as with the male mangrove killfish, *Kryptolebias marmoratus*.

1.3.6.2. *Differential use of living space*

The use of the space of its home range* by a fish depends on its ability to defend it, its available energy, therefore its size and mass. As a result, with the African convict cichlid *Amatitlania siquia*, it is the largest individuals who exploit the environment for food and defend the largest areas the hardest, in relation to their greater mobility, which is linked to better swimming performance. A hegemonic behavior of habitat occupation from which subordinates are driven out results, in the most aggressive dominant groups, in a despotic monopolization of the best habitats.

Bibliography: *Anim.Behav.,* 2016, **111**: 79-83 & DOI:10.1016/j.a,behav.2015.10.010, *Behav.Proc.*, 2019, **158** : 163-171 & DOI .10.1016/j.beproc;2018.12.002, *Ethol.*.2015, **121**: 915-921 & DOI:10.1111/eth.12404

1.3.6.3. *Bourgeois males, ardent defenders of the garden necessary for their survival*

In natural environments, habitats are sometimes numerous and varied, and males of nesting territorial species choose the one that offers guarantees of size and especially protection from intruder congeners and potential predators. A territory chosen by the resident male depends on the presence of markers and landmarks, as shown by an experiment using the Nicaraguan convict cichlid, *Amatitlania siquia*, which uses plants as "territorial landmarks". Clear boundaries are needed to better define each field. The owners, called "bourgeois males", have requirements and are in favor of the idea of everyone being in their own home.

The possession of a territory has a value that is so vital for the individual himself (territory of rest, protection, feeding) as well as for his descendants (territory of spawning, breeding and parental care) that it justifies a major effort to preserve it. Since competition can be fierce, its conservation frequently gives rise to fighting, with owners refusing any intrusion by competitors (Volume 1, section 3.10), and owner males having to defend their territory against the lusts of rival males.

In the males of the Caribbean damselfish, *Stegastes leucostictus*, the defensive strategy adopted, especially against egg predators such as the wrasse, *Thalassoma bifasciatum*, is flexible and depends on the quality of the 1–2 m diameter territory that contains their nest. High quality territories – large size, good concealment, structural protection – are more strongly defended, even if at the expense of court activity in regard to females. The priority given to the defense of seemingly insignificant things is lower when males have only a low quality territory that has provided them with less reproductive success and in which there are fewer eggs to protect. They therefore adjust their energy investment (love or war?) according to the cost of aggressiveness and the prospects for the future in terms of new couplings.

The male damselfish, *Stegastes rocasensis*, from an archipelago in the southwest Atlantic is the sole parent and therefore responsible for the care and protection of the eggs laid in its territory (Volume 2, section 2.12.13.4). It cleans the substrate on which the adhesive eggs will be glued and then ventilates them by beating the lids, as well as, above all, defending them against predators. It attacks intruders, being able to identify them and appreciate the danger they represent so that it remains quite indifferent towards herbivorous species and even becomes quite threatening towards omnivorous egg predators. In addition to laying eggs, it defends the garden in which it grows the algae necessary for his food (Volume 1, section 1.2.4).

Female yellowtail damselfish, *Microspathodon chrysurus*, from Barbados leave their territory once every 3 days to lay eggs in other areas, but they stop spawning and generally make frequent returns to avoid too many foreign intrusions near nests built by males and owned by them after their departure. Regular revisits are proving effective.

The males of the zebrafish, *Danio rerio*, a cyprinid native to northeast India, live in groups of 2–30 individuals and are territorial and non-territorial, with their reproductive behavior differing. The former court females through circular swimming rituals (Volume 2, section 1.1.3.1) and obtain their reproductive success through their status as owners of land valued by females concerned about the survival of their offspring, while the latter are forced to pursue females. This behavioral difference depends on the density of males present and the importance of intrasexual competition, with the number of cuckolds increasing with the density of competitors seeking mating, with high paternity rates (92%) among territorial males who monopolize receptive females when male density is low. On the other hand, in the case of high density, territorial males are forced to use part of their energy to aggressively pursue their rivals and renounce courting females. They face a difficult choice between seduction and combat.

Bibliography: *Anim.Behav*., 2006, **71**: 71-78 & DOI:10.1016/j.anbehav.2005.03.028, *Biol.Lett*., 2009, **5**: 188-190 & DOI:10.1098/rsbl.2008.0698, 2014, DOI:10.1098/rsbl.2014.0009, *Ethol.,* 2015, **121**: 785-792 & DOI:10.1111/eth.12393, *Frontiers in Zool*., 2006, **3**: 1-6 & DOI:10.1186/1742-9994-3-5

1.3.6.4. *Promoting the idea of everyone being in their own home by cultivating gardens*

The Chinese mudskipper, *Boleophthalmus pectinorostris*, a goby that lives in intertidal pools, digs tunnels in the sediment and folds back in at high tide to come out at low tide to feed by grazing on the surface of muddy sediments rich in a microbial film – flagellates and cyanobacteria – diatoms and benthic microalgae* which constitute the essential part of its food. Its polygonal territory is limited by sedimentary walls that it has built itself using its pectoral fins. Such a territorial delimitation, which varies in size according to the density of individuals present and which develops during the cold season, has a double function: the promotion of populations of diatoms and microphytobenthos organisms that thrive in their own gardens and a reduction in attacks between neighbors. Everyone is in their own garden and is not interested in that of their neighbors owing to the visual barriers formed by the walls.

Bibliography: *J.Mar.Biol.Ass.UK*, 2007, **87**: 615-619 & DOI:10.1017/S0253154.7058434

1.4. Breeding habitats (Volume 2, section 2.1)

Spawners of all species choose the territory most favorable to the development of the selection behaviors of their sexual partner, wedding celebrations, mating and spawning. These territories, known as spawning grounds, must also promote the survival of eggs and the development of larvae thanks to the most favorable thermal, haline and light conditions in terms of protection and larval feeding, whether the larvae are abandoned in the natural environment or sheltered in nests under the care of parents who provide them with parental care.

Behavior specific to the spawners and then to the parents justifies that their description should preferably be found in the chapters of Volume 2, which will deal with fish reproduction and the related predation risks. The greater their number of congeners, the more rapid their progress.