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Fish Behavior 1

Eco-ethology

Jacques Bruslé
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Preface

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

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

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

Scientists, through observations and experiments published in credible international journals and from whom the authors of this book take their inspiration, bear witness to the surprising abilities of fish. Abilities that are not so far removed from those of other vertebrates, and even humans with similar characteristics because they are derived and inherited from these "fish ancestors".

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

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

Jacques BRUSLÉ
Jean-Pierre QUIGNARD
January 2020

Introduction

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

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

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

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

Acknowledgments

The authors would like to express their sincere thanks to all those who helped them by generously providing the original photos and figures to illustrate this book.

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.

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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/buslé/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.

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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