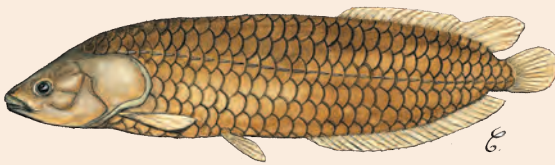# Diversity
# of fish habitats

CHRISTIAN
LÉVÊQUE

Habitat is the place where a species lives and its surrounding biotic and abiotic environment. Ecologists seeking to develop explanatory and forecast models have long wondered about this fundamental question: how can the presence of an individual at a given place and time be explained? Indeed, the different fish species are not distributed at random in aquatic systems, but according to their biological and ecological requirements. The knowledge of factors governing the distribution of species could also improve our understanding of the structure of populations.

Habitat concept

When considering the many parameters that can characterize habitat, one must keep in mind that a fish, at each stage of its existence, is faced with three fundamental requirements (Lévêque, 1995):

• to protect itself from the limits set by the environment (current, oxygen, temperature, etc.) as well as predators and any competitors in order to ensure its survival;

• to feed in the best possible conditions to ensure its growth and maturity, given that nutritional requirements will vary as the fish develops;

• to reproduce once it reaches the adult state, in the most favourable conditions, in order to ensure survival of the species. The fish may thus need to move (migration) and potentially develop means of protecting its eggs (parental care).

Aquatic systems, particularly lotic ones, are characterized by high spatial and temporal variability because of fluctuations in water flow and level that considerably modify the nature and extent of the volumes that fishes can use. In reality, in such a highly variable environment, we can hypothesize that fishes will constantly seek compromises to address the three abovementioned requirements in the most optimal way. For instance, such compromises may take the form of leaving a shelter and risk exposure to predators in order to feed, or to migrate to areas that have poor food resources but are more suitable for egg and larva development. One of the major problems facing every fish is thus figuring out how to allocate its time and energy for feeding and/or reproducing in a way that maximizes its reproductive success. By minimizing the energy needed to find and capture prey, the fish will have more energy to devote to growth and metabolism (Hart, 1986). This quest for compromise aims to optimize "fitness", or the relative contribution of an individual to future generations. Faced with the different options in the natural environment, animals do not choose at random, but carry out activities that ensure higher reproductive success (Pulliam, 1989). These options may lead an individual to behave in ways that seem to require high levels of energy expenditure initially, but that pay off in the longer term for the survival of their young. This is the case of species that undertake long migrations to reproduce.

Throughout its life, and depending on its daily or seasonal activities, the same species may thus successively and temporarily occupy several types of biotope. Habitat, by definition the geographic physical system specific to an animal or plant species, shall thus be defined here as the set of biotopes necessary for the completion of a fish's biological cycle. It has a spatial and temporal dimension, partly related to the variability of the system and the biological and ecological needs of species.

Spatial and temporal scales and the hierarchical system concept

Aquatic environments are complex systems whose different abiotic and biotic components have highly varied spatial and temporal dynamics. In an attempt to untangle these complexities, ecologists often refer to concepts of scale, to better account for temporal variability and spatial heterogeneity in order to derive general laws that can help predict the evolution of ecosystems.

With regard to temporal scales, one generation for a bacterium (several hours) is very different from that of a planktonic crustacean (1 month), and that of a fish (1 to 10 years) is often much longer than for invertebrates. In terms of population dynamics, reaction times to disturbances vary according to the organisms in question. Environments that have been newly created or have just undergone a major upheaval will be colonized more rapidly by organisms with short generation times than by those with long ones.

Certain phenomena can also be present over shorter or longer periods. Hence long-term climatic trends can be superimposed on seasonal variations, in such

a way that the slow evolution of a system may escape our notice as the phenomenon is difficult to identify in the absence of a long series of observations. The expression "invisible present" (Magnuson *et al.*, 1983) has been used to qualify these changes that are only identifiable with long observation series (table 16.I). On the scale of a decade, for example, a river slope may appear stable whereas on the millennial scale it is probably variable.

Years	Scale	Physical events (examples)	Biological phenomena (examples)
100 000	100 millenniums	orogeny; glaciations	evolution of species
10 000	10 millenniums	climate changes; drought-pluvial	species extinction; refuge zones
1 000	millennium	river catches	exchanges between watersheds
100	century	100-year flood	community changes
10	decade	anthropogenic impacts	fish lifetimes
1	year	flood cycle	reproduction cycle; migratory activity
0.1	'month'	lunar cycle	activity cycle
0.01	'day'	diel cycle	circadian cycle; feeding cycle
0.001	'hour'	accidental disturbances	physiological process

TABLE 16.I.

Theoretical relationships between time scales, physical events and biological phenomena (from Magnuson, 1990).

Similar problems crop up for spatial scales. For instance, fish species diversity in a drainage basin is a function of the surface under consideration (see chapter *Species richness of fish communities*). Moreover, many species have discontinuous distributions, and the probability of observing them depends on the scale at which one is working. Finally, given the variability and the heterogeneity of the environment, species can disappear in certain regions and thrive in others depending on the favourability of ecological conditions over time. As we can see in the previous example, there are obviously close interactions between the temporal and spatial scales. The presence of species in a region far removed from its current area of distribution is sometimes the heritage of an historical situation during which the species was much more widely distributed than today (see chapter *Biogeography and past history of the ichthyological faunas*).

The structure and composition of a fish community at a given time and spatial scale are thus the result of a set of phenomena that interact at different spatial and temporal scales for each of the populations that comprise the community. To better understand such situations, scientists often use the concept of hierarchic structure: in heterogeneous systems, it is possible to consider that the area under study is composed of sub-units that in turn can sometimes be broken down into even smaller units. An illustration of this notion of hierarchy in lotic systems was proposed by Frissell *et al.*, 1986 (figure 16.1) as a series of overlapping spatio-temporal scales. The principle behind these hierarchic organizations is that higher levels have slower dynamics and impose restrictions on the lower levels. As such, a watershed will be located in a biogeographical area, which explains the species composition of communities, and several watersheds may belong to an ecoregion whose abiotic characteristics are relatively homogeneous. Likewise, a river may contain different reaches that in turn have several types of microhabitats.
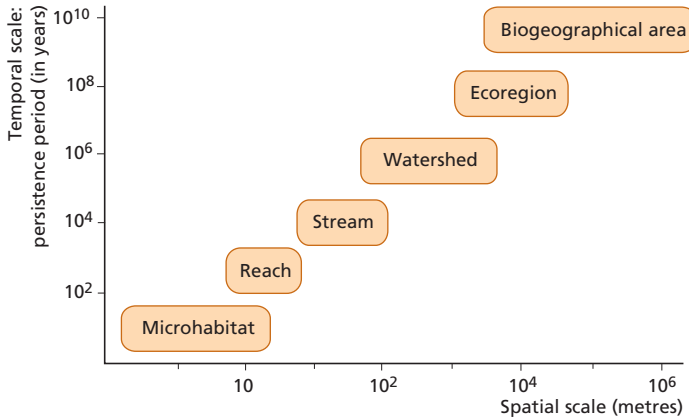
A fundamental question is tied to these notions of scales and hierarchy. Problems that we can consider resolving depend on the scale at which research is focused. Questions of biogeography cannot be tackled by considering a single watershed, nor can we work on migrations if we are only studying one reach. In reality, it is difficult to extrapolate results obtained at a given spatio-temporal scale to other hierarchic levels, given that parameters that are relevant at one level are not necessarily so in others. While biogeography can explain why a given species exists in a given basin, hydrology or the nature of the substrate will explain the presence of the species in a given reach. Much is at stake for environmental research in this question of changes of scale, as it is necessary to know the constraints posed by higher levels before scientists can accurately interpret observations made at a lower level.

Protect itself and rest: the microhabitat

In a river, the distribution of species according to different biotopes does not happen at random. Knowledge of the physical parameters of a biotope as well as the species pool, allows scientists to determine a species' preferences in terms of ecological factors. Microhabitat is defined as the site where a fish finds the most favourable temperature, current, depth, substrate, shelter, etc. conditions that minimize its current energy expenditure and allow it to rest while remaining as well-protected as possible from predators. Habitat changes during development are linked to changes in a fish's performance in terms of physical and physiological capacity. Microhabitat data are thus collected for specific stages of development by collecting enough information to describe the ecological preferences of a given stage.

In rivers, a distinction is usually made between rheophilic species that seek out running water and species that prefer still waters. These preferences should be viewed in relation to the more or less developed swimming capacities of different species, as well as physiological requirements, for instance in terms of the water's oxygen content. In line with this, preferential habitat curves have

been created for several fish species in the Sabie River, a tributary of the Limpopo in Kruger Park (Gore *et al*., 1992). Juvenile *Serranochromis meridianus* and *Barbus viviparus* inhabit stagnant ponds but *B. viviparus* is slightly tolerant to low velocities (up to 60 cm s^{-1}). Both species prefer relatively deep ponds (up to 2.5 m) with gravel or sandy bottoms. Meanwhile, *Chiloglanis swierstrai* prefer rapids in shallow waters (< 50 cm) with shingle bottoms, and water current velocities between 35 and 150 cm s^{-1} (figure 16.2).
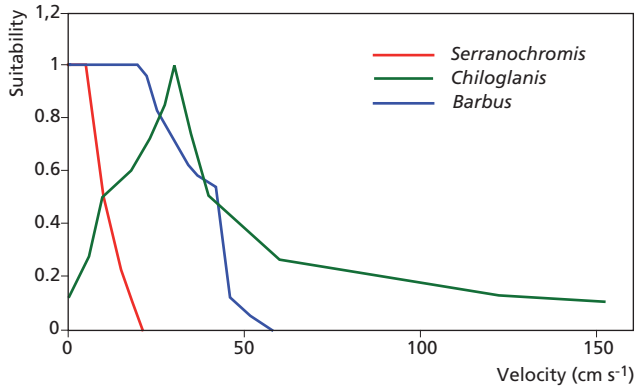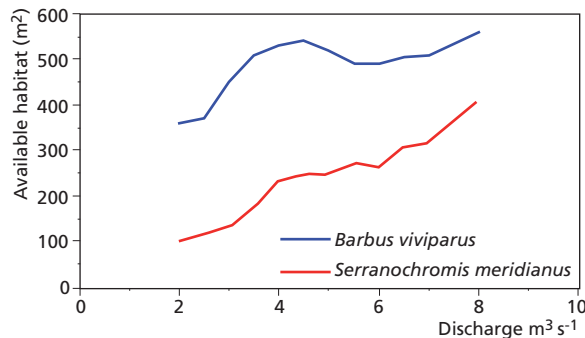
By considering habitat preferences in terms of current velocity, it is possible to predict the surface available for a species for different river discharges. Thus for a 300 m reach of the Sabie River, when the discharge increases from 2 to 8 m^{3}s^{-1}, the available surface for *C. swierstrai* and *S. meridianus* increases considerably (figure 16.3) whereas it remains constant beyond 3.5 m^3 s^{-1} for *B. viviparus*.

Pouilly (1993) also studied the organization of fish communities in three small watercourses in Guinea during the dry season, by identifying the ecological profile of species – that is, their preferences in terms of ecological factors such as current, depth, substrate type, etc.

A connection should also be made between the selection of certain habitat types and the need to find shelter from predators. In many African rivers, flooded zones are thought to provide juveniles of many species that reproduce during the flood

with shelter from large fish-eating predators that have difficulty moving in heavily vegetated areas. It is true that such zones are also particularly favourable to the development of plankton species that meet the nutritional requirements of these juveniles.

In the East African great lakes, many endemic cichlid species sometimes have very specific requirements in terms of microhabitat. In particular, many species that are confined to rocky areas use crevices as both refuge and microhabitat. Other original microhabitats in Lake Tanganyika are the beds of empty gastropod shells that cover large surfaces at depths between 10 and 35 m on a sandy bottom, where the slope is gentle. Many cichlid species, mainly Lamprologines, use these shells as shelter but also as reproductive sites (Ribbink, 1991). The juvenile forms of *Chrysichthys* and *Mastacembelus* also find refuge in these empty shells.

Foraging

An essential reason for a fish to frequent certain types of physical systems is the opportunity of finding food that is adapted to its size and physiological requirements. This relationship between size-diet-ecological conditions is an important parameter for understanding why a species occupies a particular place.

Ontogenetic changes of the diet and habitat

In their lifetime, the size and the weight of fishes change considerably and it is customary to distinguish different periods of development (Balon, 1985, 1990):

• the embryonic period, which begins with fertilization and is characterized by purely endogenous nutrition from the egg yolk;

• the larval period begins with the progressive but rapid transition from endogenous to exogenous feeding. This larval period is characterized by the presence of temporary larval organs;

• the juvenile period begins when the fins are well-differentiated and all temporary organs have been replaced by permanent organs. It ends with the maturation of the first gametes. It is generally a period of rapid growth, sometimes characterized by a specific colour pattern;

• the adult period begins with the maturation of the first gametes. It is characterized by a decrease in the somatic growth rate.

The different phases of development correspond to different dietary requirements, feeding behaviours, and ecological, physiological, and biological needs, which implies in many cases the occupation of different biotopes (Lauzanne, 1975; Winemiller, 1989). Small-sized and poorly vagile juveniles are limited to using small-sized particles as well, such as phyto- or zooplankton. As fish size and vagility increase, the size and nature of prey also changes. In adult ichthyophagous fishes, morphological changes associated with greater specialization are accompanied by changes in prey size and type.
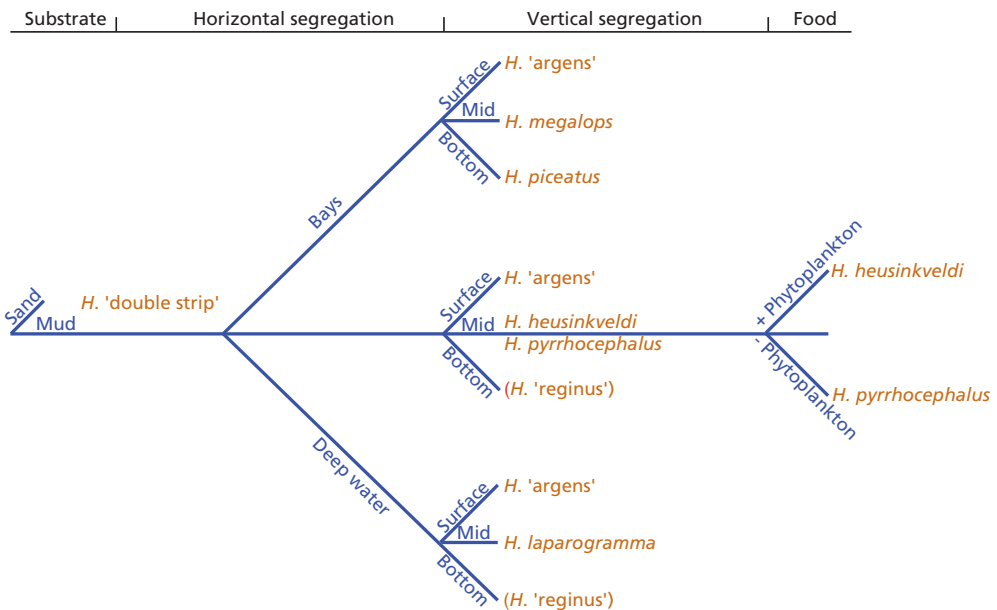
The consequences are significant in terms of habitat. Preys are not distributed at random in aquatic systems, and their availability can vary over the year. In riverine systems, for example, planktonic preys are essentially abundant in calm waters, that is, in riverine annexes where juveniles of many species find favourable conditions, both in terms of nutrition and in the physical conditions of the habitat. The existence and extent of these systems are highly dependent on hydrology, particularly water level. There thus needs to be good synchronization between the appearance of larvae and the existence of favourable prey in the corresponding habitat ("match-mismatch" hypothesis by Cushing, 1982).
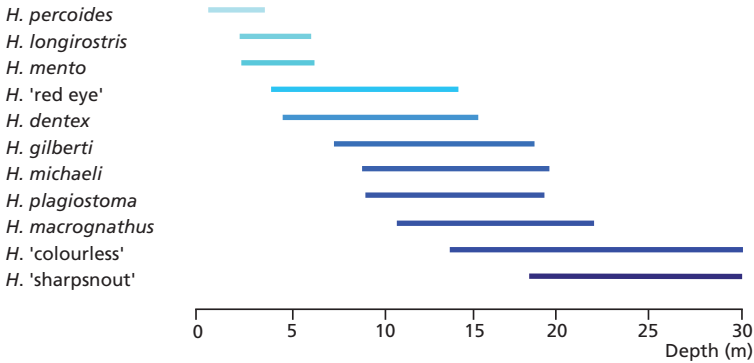
Strategies of research and sharing of food, and spatial segregation of species

Food strategies can be viewed as decision-making systems to address questions such as: where should the individual feed, or what sort of prey should it seek out? (Cézilly *et al.*, 1991). The fish must decide when it will feed, where, for how long, the most suitable prey (in terms of size and nutritional value), the manner in which it will seek out and capture such prey, and so forth. It needs to be efficient in responding to environmental constraints such as competition, food scarcity, and unpredictable variations in the resource.

A fundamental axiom is that feeding strategies were shaped during natural selection, and that every decision tends to optimize certain variables such as the energy assimilation rate which is ultimately correlated to the concept of "fitness" (Pyke, 1984). But a number of results indicate that fishes also have the possibility of learning and engaging in alternative behaviours that allow them to seek out prey more effectively and live longer (Hart, 1986).

FIGURE 16.4.

Schematical representation of expected ecological segregation among zooplanktivore haplochromines in Lake Victoria (from Goldschmidt *et al.*, 1990).

In environments inhabited by numerous species belonging to the same trophic group and with relatively similar diets, strategies may be to occupy spatially different habitats in order to decrease interspecies competition. This is the case in Lake Victoria where spatial segregation phenomena were found among zooplanktophagic haplochromines, thus permitting the ecological isolation of species (Goldschmidt *et al.*, 1990). In addition to a horizontal distribution that is often well-differentiated for each of the species in the Gulf of Mwanza, the type of bottom, wind exposure, and depth of the water column are also important factors contributing to the segregation of species (figure 16.4). Most zooplanktivore juveniles are only seen in shallow waters (less than 9 m) where they find shelter from predators. For species with broad overlaps in their geographic areas of distribution, depth influences the manner in which they segregate themselves, sometimes taking into account the vertical migrations that follow different circadian rhythms.

While piscivorous haplochromines are present in all major habitat types in Lake Victoria, many of them have a distribution that is limited to certain types of substrates (van Oijen, 1981). Compared to their parents, juveniles are generally in shallower, less exposed zones. A few species only occupy sandy bottoms whose depth does not exceed 6 m. Moreover, adults of many species in the Gulf of Mwanza have a different depth distribution. Some are found only in the surface, while others in the deep (figure 16.5).

Trophic migrations

The search for feeding-friendly areas pushes species to engage in short-distance migrations to feed. In the deep lakes, species carry out nycthemeral migrations, spending most of the day in the depths and then swimming up close to the surface at night to feed. In Lake Malawi, the vertical distribution of species in pelagic systems depends on the daily cycle. During the day, most of the fishes are found at different depths: *Diplotaxodon* "big eye" and *Synodontis njassae* at the limit of the oxycline at around 200-220 m; *Diplotaxodon* "elongate" and *Rhamphochromis ferox* between 50 and 200 m; *Copadichromis quadrimaculatus*, *Engraulicypris sardella* and *Rhamphochromis longiceps* in the first 100 m. Most of these species migrate towards the surface at night. Species such as *S. njassae* and *Diplotaxodon* "big eye" carry out migrations of 200 m (Thompson *et al.*, 1995).

Reproduction strategies and breeding sites

The reproduction strategy of a fish species in a given environment is a set of biological traits such as age at first reproduction, the relationship between size (or age) and fecundity, parental behaviour, reproductive season, gamete size, and so forth. An individual may also develop tactics which are in fact variations of the typical reproduction schema to respond successfully to changes in environmental factors. It is thus an adaptive behaviour to specific ecological conditions and whose purpose is to ensure survival of the species.

Defining the habitat of a species requires taking into account the reproductive behaviour of that species and its need to find conditions that allow it to spawn in the best possible conditions. In particular, spawning generally occurs at a period when environmental conditions are, in theory, most favourable to the survival of eggs and larvae, and many species have a seasonal reproductive cycle. In large tropical rivers, the hydrological regime (that is, the set of climatic conditions prevailing at the start of the flood) appears to be the main regulator of reproduction. For many species, spawning coincides with the flood (see chapters *Variability of climate and hydrological systems* and *Life-history strategies*).

Balon (1985, 1990) distinguishes two broad types of ontogenic trajectories in biological cycle models.

In the indirect model, the eggs are generally small and produced in large numbers. They yield small, underdeveloped young larvae with only a small volume of yolk that is insufficient for producing the final phenotype. These young larvae must feed rapidly on small particles to complete their development and are highly vulnerable during this period.

In the direct development model, fishes produce a limited number of large eggs with a large amount of yolk, which allows the embryo to develop to an advanced stage. This shortens or eliminates the larval period, and juveniles are already well-formed and thus less vulnerable when they start shifting to an external diet. *Labeotropheus*, a cichlid mouth-brooder from Lake Malawi, is a good example of this type of fish that releases a large juvenile (14% of adult size) only 31 days after fertilization (Balon, 1977).

We thus have two main strategy types: indirect development consists of producing a large number of eggs that will suffer a high mortality rate, but which frees up the parents for other activities right after spawning, whereas direct development requires effort to be placed in the survival of a low number of individuals, which means parents must invest energy for a long period. In one case (direct development) fishes will have a sedentary and perhaps territorial behaviour. In the other case (indirect development), there will be nomad species who may cover large distances to reproduce.

Direct development and territorial behaviour

An example of highly sedentary behaviour connected to direct development is that of different cichlid species endemic to the East African great lakes. Fryer (1959) had already highlighted the fact that many littoral species were so

confined to rocky zones that they had never been observed more than a metre from these systems. Mature individuals live, feed, and reproduce throughout the year within the strict limits of their habitat. Moreover, large yolk-rich eggs yield young that are large enough to use the same food as the parents, which means that there is no need for a pelagic planktonic stage such as that observed in coral fish (Lowe-McConnell, 1987), and the species can thus spend its entire life in the same biotope. The sedentary nature of these cichlids has been demonstrated experimentally by marking. Some species have an area of distribution limited to a few thousand m^2 (Ribbink *et al.*, 1983). In addition, species transferred from one area of the lake to another remain in the vicinity of the point of introduction and reproduce at that site.

As a general rule, direct development is most often accompanied by parental care, that is, assistance provided by parents to ensure better survival of the egg after its formation. This assistance may range from nest construction to guarding of eggs and fry. The practice of parental care is rather widespread in fishes, particularly in the Cichlidae family (Keenleyside, 1991) (see chapter *Diversity of responses to environmental constraints and extreme environmental conditions*). Its main function is to protect the young from predators. It has been suggested that the practice of parental care developed in fishes occupying physical systems characterized by their spatial and temporal unpredictability (Wootton, 1990), in order to limit the dangers inherent to the latter. Nonetheless, it would do well for this theory to be verified by observations.

The practice of parental care can be accompanied by territorial behaviour linked to competition and the defence of a reproductive site. The territory in this case becomes an indispensable resource for spawning, and one whose availability may be limited. For 12 species of substrate-laying Cichlidae in Lake Tanganyika belonging to the genus *Lamprologus,* and which are very closely related to each other, Gashagaza (1991) has shown that they use the physical system in different ways to spawn and protect their young. Some spawn on block surfaces; others in crevices; still others in holes. This diversity of reproductive behaviour in a system where space is limited given the population density has the advantage of limiting interspecies competition for habitat use.
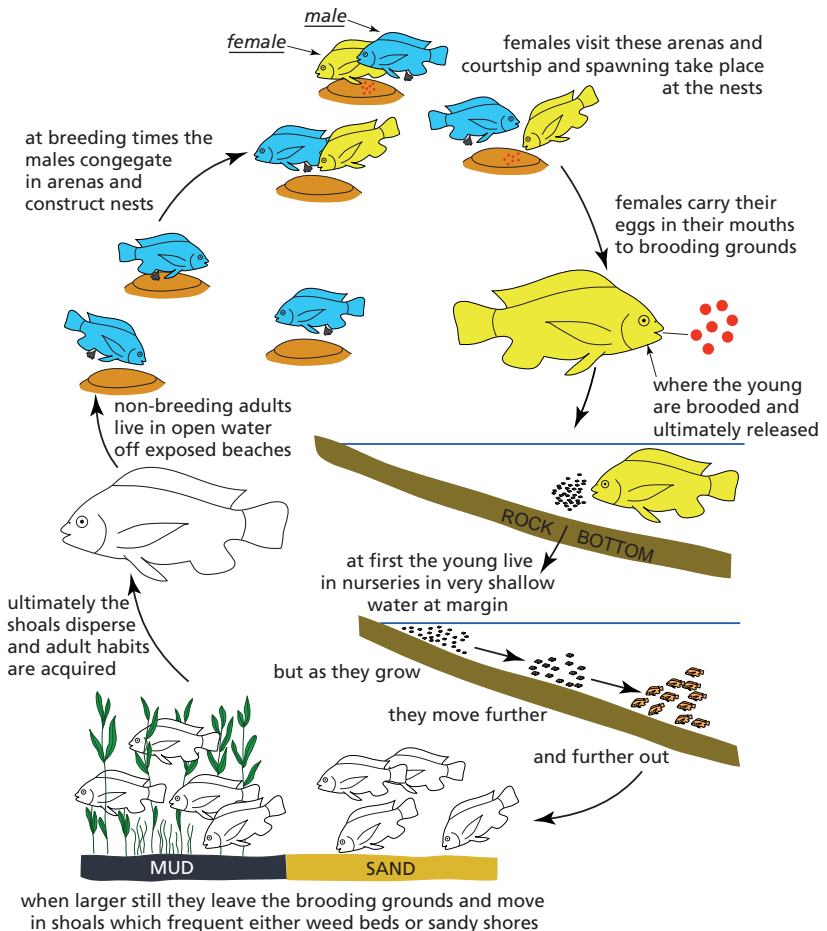
Territorial competition is often expressed in the defence of a territory from conspecific and heterospecific individuals (see chapter *Ethology*). By studying the behaviour of 6 herbivorous cichlid species that are maternal mouth-brooders, Kohda (1995) highlighted the existence of two types of territory:

• the males of six species studied have a restricted territory around the nest (20 to 40 cm in diameter) that they guard ferociously against intruders that are most often potential egg eaters. This nesting territory is used by the females who lay their eggs in the nest, after which they take the eggs in their mouth and leave the zone;

• there is also a larger territory of a few m^2 around the nest, where the males patrol at around 50 cm and 1 m from the bottom and where they feed. When a female enters this zone, the male courts her then brings her into the nest. On the other hand, a male will attack conspecific males and sexually inactive females that enter the zone.

The practice of mouth-brooding is more specialized and is more recent in origin. Its adaptive advantage is to shelter embryos from predators and limit competition for reproductive sites. It can also be viewed as a means of eliminating dependence on a substrate to reproduce when the available benthic space is in high demand (Balon, 1978). In substrate layers that practice mouth-brooding, the biotope occupation cycle can be relatively complex. Fryer & Iles (1972) so describe the reproductive cycle of *Oreochromis variabilis* in Lake Victoria (figure 16.6). On sandy bottoms, males build nests in which females spawn. The latter then take the eggs in their mouth and transport them to incubation areas where the young are released once the eggs have hatched. They first live in shoals in very shallow waters with rocky bottoms, and as they grow, they move to deeper areas. When they are bigger, they move in shoals to sandy shores or weed beds. They gradually acquire adult behaviour as they grow, living in the open water of exposed beaches. The males then build nests in their turn on sandy shores, and the cycle begins again.

FIGURE 16.6.

The life cycle of *Oreochromis variabilis* in Lake Victoria. This diagram shows the different phases of the environment occupation in relation with ontogeny (redrawn from Fryer & Iles, 1972).

male

female

females visit these arenas and courtship and spawning take place at the nests

at breeding times the males congegate in arenas and construct nests

females carry their eggs in their mouths to brooding grounds

where the young are brooded and ultimately released

non-breeding adults live in open water off exposed beaches

ROCK BOTTOM

at first the young live in nurseries in very shallow water at margin

ultimately the shoals disperse and adult habits are acquired

but as they grow

they move further

and further out

MUD   SAND

when larger still they leave the brooding grounds and move in shoals which frequent either weed beds or sandy shores

Indirect development and breeding migrations

In fishes with indirect development, the need to use distinct biotopes for the different stages of development, and in particular the search for sites that are suited to spawning, and then to good development of juveniles, forces the species to carry out migrations that may cover long distances. According to Northcote (1979), a migration is a transfer from one habitat to another that occurs regularly throughout the individual's lifetime, and which involves a large portion of the population.

TYPES OF MIGRATION

A distinction is usually made between diadromous migrations between the sea and continental aquatic zones, and potamodromous migrations which occur wholly within fresh water (Mc Dowall, 1987). Tropical river fishes that carry out long migrations to reproduce are thus potamodromous species.
Among the diadromous species, we can distinguish:
• anadromous fish that spend most of their life in the sea and migrate to fresh water to reproduce;

• catadromous fish that spend most of their life in fresh water and migrate to the sea to reproduce.
The classic example is the eel;
• amphidromous species which divide their time between marine and continental waters, without these migrations being necessarily linked to reproduction.
More simply, we sometimes make a distinction between euryhaline fishes that move freely between fresh and sea water, and amphihaline species that only do so at certain stages of their life.

Fishes making anadromous or catadromous migrations are rare in tropical Africa, whereas plenty of potamodromous fishes can be found there. This type of migration provides an adaptive advantage in that its purpose is to reach sites that favour reproduction or feeding. Some authors believe that it is a mechanism that protects the young from predators, and Fryer (1965) considers it a means of ensuring the dispersion of young throughout the riverine system. The two hypotheses are probably complementary. Spawning in the tributaries of the upper courses allow larvae to be carried by floodwaters to all biotopes, over hundreds of kilometres downstream from the spawning site. Upstream or downstream migrations whose purpose is to bring parents close to floodplains so they can spawn there once water enters these systems also have the goal of allowing larvae to reach floodplains as rapidly as possible so they can find food and shelter there.

The sites most favourable to spawning are not necessarily the best ones for feeding, and some species must therefore migrate over long distances between the two. Daget (1960) and later Welcomme (1985) made the distinction between longitudinal migrations, often stimulated by reproduction and which occur in the riverbed, and lateral migrations, when fishes leave the main riverbed to go to the different habitats of the river flood bed. These lateral migrations are triggered both by the search for food and by reproduction.

MIGRATIONS OF 'TINÉNIS' IN THE NIGER RIVER
(SOURCE: DAGET, 1952)

Even the least-informed observer would agree that the phenomenon is absolutely spectacular.
These fishes (*Brycinus leuciscus*, Alestidae) go up the minor bed in successive waves related to lunar phases.
They all move in the same direction a few centimetres from each other, and parade for several hours with great regularity. Should a predator or fisherman disturb them, they scatter momentarily in all directions before reforming the school and moving on.

The average speed of the migration is not high – somewhere around 1 to 1.5 km per hour.
The extent of the displacement can nonetheless be significant, as Daget has estimated that some schools can cover, over several months, distances of close to 400 km. Generally, the main school itself is precedent beforehand by what local fishermen call "the head of tinénis" formed by a group of smaller individuals.

The migration of the "tinénis" begins when they leave the floodplains to join the minor bed. That said, the actual longitudinal migration only begins when this occurs during a full moon phase.
In the absence of the latter (the last few days of the lunar month), schools stop or disperse, only to reform in the early days of the new moon.

When they are prevented in their progress by a dam such as the Markala dam (Delta Central region of the Niger in Mali),

the schools break up quite rapidly, and its elements then go downstream. This essential fact shows that while the upstream phase is always done in tight groups, the opposite is carried out in a dispersed way, individually or in very small groups.
This school dispersion phase always corresponds to the darkness associated with the end of the lunar month.

In brief, let us revisit what Jacques Daget wrote: "To explain it, we believe there is reason to posit a group effect, as *Alestes* (henceforth *Brycinus*) *leuciscus* are only stimulated to go against the current when they are present in large numbers and packed against each other (…).
There is also probably a constant antagonism between the following phenomena: congregation on moonlit nights; scattering during dark nights. At the end of the lunar month, scattering was predominant; schools stop and and break apart, whereas in the early days of the month, congregation takes precedence, leading to the formation of schools that keep moving owing to the group effect as long as the presence of moonlight prevents scattering from taking over."

The moon's influence is nonetheless not general and should be considered secondary compared with hydrology and the nycthemer for instance, and affecting only a few species in a stable, repeated manner (Bénech & Quensière, 1983).

The mechanisms that trigger migrations are still poorly known, especially for those that require movement over long distances. To the extent that species have different behaviours, there are probably several mechanisms that come into play, some of which are associated with the start of the flood (Welcomme, 1985). Scientists have also not yet identified the signals by which adult fishes know before the youngs that the time has come to leave the floodplains. It is true that these signals are not always very efficient and that large numbers of fishes are blocked every year in residual ponds that dry up during periods of low water flow. The depth and/or water oxygen concentration may be deciding factors.

BREEDING MIGRATIONS IN LAKE CHAD

In the Chad basin, several species carry out breeding migrations (Bénech & Quensière, 1989). In particular, many lacustrine species use the North Cameroon floodplain (Yaéré) as a nursery.

Some species carry out long-distance migrations when they are about to breed. These are primarily pelagic species – many of which are zooplanktivores – in Lake Chad, such as *Alestes baremoze*, *Synodontis batensoda*, *Schilbe intermedius*, *S. uranoscopus*, *S. mystus*, *Synodontis schall* or *Hyperopisus bebe*.

A large part of lacustrine populations go up the Chari before the flood and reproduce close to the North Cameroon floodplain (Yaéré) in August and September, some 150 to 200 km upstream from the lake. Eggs and larvae are dispersed in flooded zones and spend several months there before joining the lake via the Chari or the El Beid, a major drainage channel that connects the Yaéré to Lake Chad during the flood.

Alestes dentex appears to migrate for reproduction to other flood areas located even higher upstream (at least 250 to 300 km from the lake). This is also the case for other species such as *Synodontis membranaceus* and *Labeo senegalensis*. Other species such as *Polypterus bichir*, *Distichodus rostratus*, *Marcusenius cyprinoides*, also seem to possess characteristics of major migrators, but data collected thus far are insufficient to confirm this hypothesis.

Other species carry out shorter migrations. The lacustrine populations of *Hydrocynus forskalii* migrate in the Chari delta and lower reaches to reproduce when the flood subsides, from November to March, as well as at the start of the flood in July-August. *Bagrus bajad* also reproduces in the delta in May-June.

Finally, more or less sedentary species migrate from the main bed to flooded areas to find better feeding conditions, shelters, and conditions favouring reproduction. These species include *Brevimyrus niger*, *Petrocephalus bovei*, *Gymnarchus niloticus*, *Heterotis niloticus*, *Ichthyborus besse*, *Clarias gariepinus* and *Siluranodon auritus*.

The return migration of young fish to Lake Chad is an important phase in general migration patterns. A detailed study of downstream migrations of juveniles when the flood begins to subside was carried out in the El Beid, which connects the Yaéré in North Cameroon to the southern zone of Lake Chad (Durand, 1971; Bénech & Quensière, 1982 and 1983).

A first group of juveniles composed of *Hyperopisus bebe*, *Marcusenius cyprinoides*, *Alestes dentex,* and *Labeo senegalensis* move in large numbers from mid-November to mid-December. It also includes other species such as *Alestes baremoze*, *Polypterus bichir*, *Hydrocynus brevis* and *Lates niloticus* which appear in early November, and *Heterotis niloticus*, *Distichodus rostratus*, and *Oreochromis aureus* which are present until January.

Mormyrus rume, *Pollimyrus isidori,* and *Distichodus brevipinnis* are also present during the first two months of the flow.

A second group of species is found in large numbers in late January: *Sarotherodon galilaeus*, *Brevimyrus niger*, *Clarias* spp., *Barbus* spp., as well as *Oreochromis niloticus* and *Labeo coubie*. Finally, a third group can be observed at the very start of the El Beid flood.

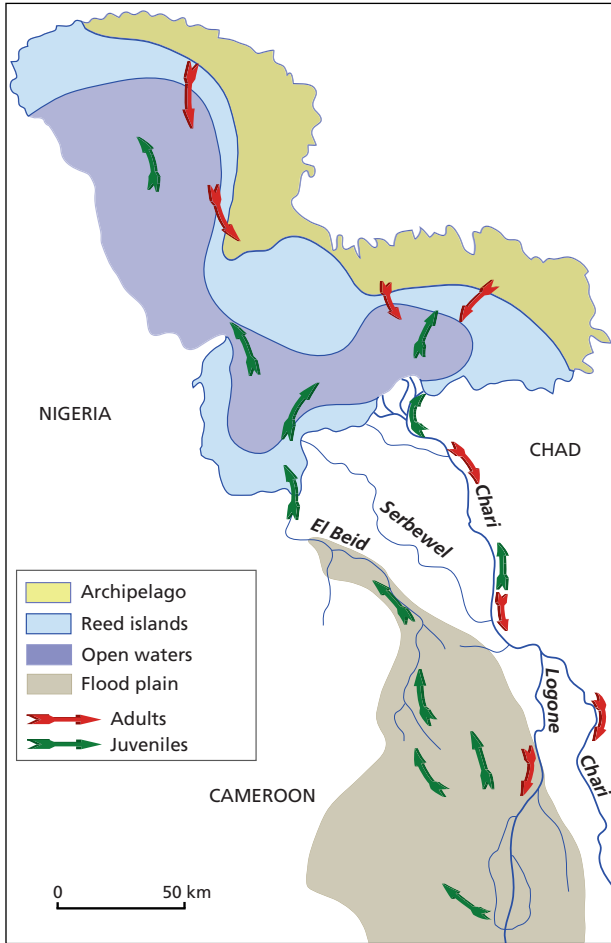The fishes then disappear before coming back again in abundance in February: *Ichthyborus besse*, *Siluranodon auritus*, *Schilbe uranoscopus*, *Synodontis schall,* and *Synodontis nigrita*.

The second and third group migrate to Lake Chad with the drainage of floodplain waters.

Migrations have been the subject of numerous investigations, most of which are nonetheless imprecise given the difficulty of tracking the movement of fishes in aquatic systems during the flood. In Nilo-Sudanian systems, research carried out in the Chad basin have highlighted very varied behaviours (see box "Breeding migrations in Lake Chad") (Bénech *et al.*, 1983; Bénech & Quensière, 1989) (figure 16.7). Similar groups of migrators have been observed in the Senegal River (Reizer, 1974).

NIGERIA

CHAD

Chari

Serbewel

El Beid

Archipelago
Reed islands
Open waters
Flood plain
Adults
Juveniles

Logone

Chari

CAMEROON

0   50 km

In the East African great lakes, many lacustrine species still carry out breeding migrations in the tributaries. In Lake Turkana for example, *Alestes baremoze*, *Citharinus citharus, Distichodus niloticus,* and *Barbus bynni* migrate in the Omo River, while *Brycinus nurse, Labeo horie, Clarias gariepinus,* and *Synodontis schall* migrate in small temporary tributaries (Hopson, 1982).

In Lake Victoria, Whitehead (1959) also identified major migrators such as *Barbus altianalis* that migrate 80 km in rivers, and migrators that cover shorter distances such as *Labeo victorianus* and *Schilbe mystus* that migrate up to 25 km upstream or in flooded zones along the banks to breed. Small Mormyridae (*Marcusenius victoriae, Gnathonemus longibarbis, Hippopotamyrus grahami, Pollimyrus nigricans, Petrocephalus catostoma*) go upstream on Lake Victoria's north tributaries. Mature fishes remain near the river mouths until the flood, then migrate upstream at night, with peaks at dawn and dusk (Okedi, 1969, 1970). They spawn in ponds located 8-24 km from the mouth, and the youngs stay for three to seven months in these ponds.

Generalisation of the habitat concept

Habitat is a notion that is essentially dynamic and involves spatial and temporal scales.

The habitat, consequence of a phylogenetic heritage and adaptive strategies

The place in which a species lives – its physical, chemical, and biological environment – is the result of a compromise between different constraints that, to a large extent, are related to the inheritance of vital traits selected by evolution. This, for instance, is the case for reproductive behaviour, for ecological or physiological requirements, for feeding habits and specializations. Phylogenetic heritage thus imposes a number of abiotic, biological, and behavioural constraints on a species that will determine its needs in terms of habitat.

Genome variability nonetheless allows species to develop tactics, which are adaptive responses to changes in the physical system inhabited by the fish. This flexibility can be vital for the survival of the species which can develop alternative behaviours, depending on the environmental conditions to which it is subjected.

Finally, research is beginning to uncover the possibility of a learning process which would expand the possibilities for fishes to occupy new environments.

This has important consequences in terms of habitat. If phylogenetic heritage limits the fish to a type of physical system, genetic variability would allow certain individuals to push the boundaries of the limits that the species can tolerate. Natural selection could then favour these genotypes and thereby modify species behaviour with regard to habitat.

Ontogenetic niche and its involvements

The species can only complete its biological cycle if the individual finds the conditions necessary for survival and growth at each stage of its development. The ontogenic niche is thus the set of habitats and resources that are needed for the smooth progress of the biological cycle. For species with indirect development in particular, there has to be excellent synchronization over time between ontogenesis and changes in the milieu. In other words, fishes have to be in the right place at the right time. This is the case for example of fishes in large tropical rivers that have flood zones, and which have different stages of reproduction and development that are closely bound to the cycle of hydrological events and the diverse habitat types that are associated with them (figure 16.8).

One of the practical applications of the ontogenic niche concept for the management of species and aquatic systems is that one has to consider all of the environments that the species may need during its development. It is not enough to preserve the biotopes required by adults to ensure the long-term survival of a species. The species must also be able to find conditions favourable to breeding and larval growth.

FIGURE 16.8. The seasonal cycle of events in a floodplain river and their involvements towards the biology and ecology of fish (redrawn from Lowe-McConnell, 1985).
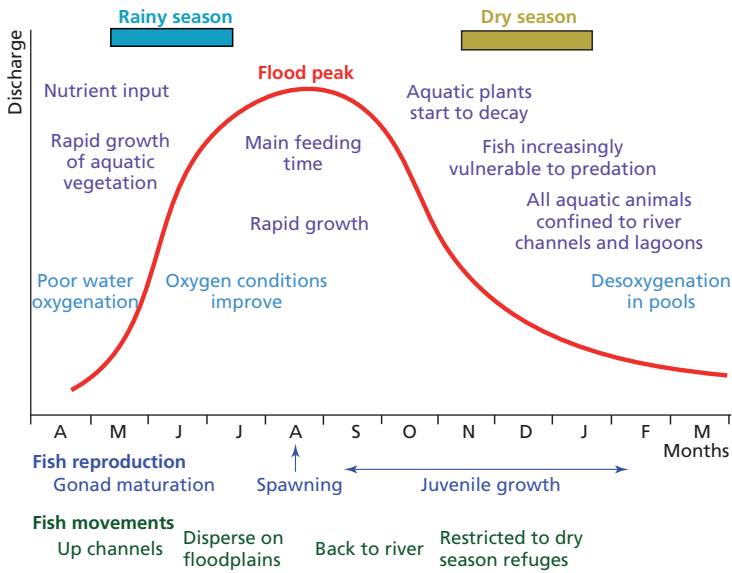
Typology of habitats

For practical and operational reasons, the need to identify a typology of habitats has led some authors to propose a conceptual framework based on physical and geomorphological characteristics (Frissell *et al.*, 1986). This hierarchic approach can serve as a reference for the study of fish communities at different spatial and temporal scales (Bayley & Li, 1992). Climate-related factors generally dominate at a large scale, whereas at the local scale biotic factors such as predation or competition can have a major influence. This classification has the disadvantage, however, of not putting enough emphasis on fish requirements in terms of habitat.

It can indeed prove useful in this space-time continuum to identify some entities of biological significance. Bayley & Li (1992) opened the way by distinguishing four main types of spatio-temporal organization. According to these authors, the microhabitat corresponds to the zone of daily activity: feeding, selection of the best abiotic conditions, social behaviour (gregariousness, territoriality). At the month-long scale, the area of activity covers the river (home range), whereas at the seasonal scale it can also include the drainage basin if the species carries out long-distance migrations. Finally, the regional scale covers evolution (speciation) and the establishment of fauna under the influence of climatic and geological events (extinction, colonization).

This typology proposed by Bayley & Li (1992) is worth noting for its emphasis on the relationship between the use of space and biological behaviour. This effort to provide a better definition of habitats based on the behaviour and needs of the fish nevertheless needs to be pursued, as the definition of the categories selected remains somewhat unclear. For this reason, Lévêque (1995) recognizes four main sets (figure 16.9):

• the resting area is the smallest scale at which a fish tackles a more or less complex set of biotic and abiotic stimuli. Most prevalent is the search for shelter
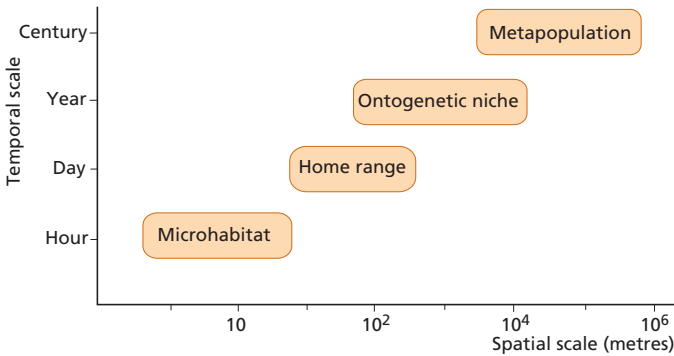
in relation to environmental conditions and/or predators. By staying in this resting area, the fish minimizes its energy use;

• the home range, within which biological and behavioural rhythms are conditioned by nycthemeral or lunar cycles. For territorial fishes, the territory can be the spatial scale of reference for this category. For others, it is the set of refuge or resting areas as well as the areas where the species will feed, which implies short migrations.

With the exception of accidents that compel them to move, many fish species complete their biological cycle in the spatio-temporal context of the activity area. This activity area can nevertheless change when the aquatic environment is modified;

• the ontogenic niche scale corresponds to the set of physical systems needed by a species to complete its biological cycle. The spatial limits are the geographic limits of different habitats occupied by the stages of development, including the spawning areas to which a species can migrate, sometimes over long distances, during reproduction. While the previous scales essentially concerned the individual, the ontogenic niche concerns the population as a whole;

• the regional scale, that of the metapopulation, corresponds to the different drainage basins in which the species is present. These basins are geographically isolated, except during periods that are exceptional from a geological perspective.

The four sets identified above correspond to a growing complexification in terms of the use of space for biological functions (figure 16.10).
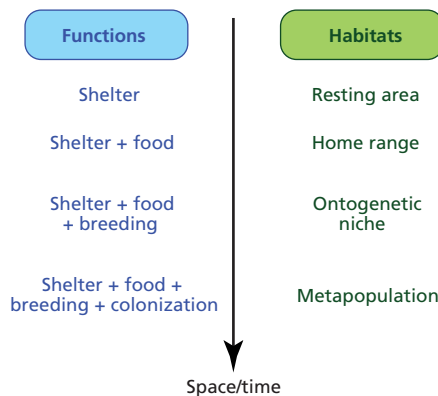
The Inland Water Fishes of Africa

Diversity, Ecology and Human Use

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