

# Diversity of responses to environmental constraints and extreme environmental conditions

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**T**he prevailing environmental conditions in aquatic habitats often allow different fish species to coexist. In certain conditions, however, an environmental factor can change in such a way that it becomes an intolerable constraint that leads to the elimination of most of the species. Some of the species that have developed adaptive solutions to such constraints can nonetheless tolerate extreme conditions, at least within certain limits and/or for a given period that allows them to await the return of more favourable conditions.

Unlike birds and mammals, fish do not regulate their body temperature, but can exhibit great flexibility in their responses to environmental changes and in traits such as growth, age at first reproduction, life span, and other life-history traits. The nature of the responses of organisms to changing environmental conditions is a central problem in biology and the meaning of “adaptation” has been widely discussed (Løvtrup, 1988; Endler & McLellan, 1988).

This chapter is concerned with some of the major environmental constraints to which tropical freshwater fish have become adapted since diversity of conditions enhances biodiversity.

## Temperature

Because of its effect on the velocity of chemical reactions, environmental temperature is perhaps the most pervasive of the abiotic factors. It has major influences on many biological processes, such as maturation and spawning, growth, development rate, metabolism, etc. Fish are faced with a simple choice in responding to temperature changes: either to move to another habitat when possible (a behavioural response), or to adapt their metabolic processes to the new situation (metabolic responses).

## Temperature preferences and thermal tolerance ranges

Changes in temperature occur less abruptly in water than in air, but fish can nevertheless be exposed to large temperature variations.

Adult fish can survive over a limited range of temperatures bounded by the upper and lower incipient lethal temperature (UILT and LILT). The LILT for *Coptodon zillii* which occur in Lake Huleh (Israel), is 6.5°C, and the UILT is 42.5°C, but mortality begins when the temperature exceeds 39.5°C (Philippart & Ruwet, 1982). *O. niloticus* can also tolerate a temperature of 8°C for several hours and an upper tolerance limit of 42°C has been reported. These species, and probably also *O. aureus* and *S. galilaeus* which tolerate a wide range of temperatures, are typically eurythermal species. On the other hand, species such as *T. guineensis* (14°-33°C) and *S. melanotheron* (18°-33°C) which live in a narrower range of temperatures are more stenothermal.

It is not perhaps the thermal tolerance limits which are so important for wild populations, but rather the temperature preferenda at which maximum biological performance can be expected. It is generally accepted, for instance, that tilapias cease growing significantly at temperatures below 20°C, and feeding stops completely around 16°C. On the other hand, maximum swimming performance occurs at 28°C in *C. zillii*, 28-32°C in *O. niloticus* and 32°C in *S. galilaeus* (Fukusho, 1968).

The effect of temperature has an important consequence on the egg stage. At low temperatures, the development time from fertilisation to hatching is extended. For *Heterobranchus longifilis*, the thermal optimum for incubation and egg hatching ranges from 25 to 29°C (Legendre & Teugels, 1991). In contrast, the range of optimal temperatures for egg development is much wider for *Clarias gariepinus*: 19 to 31°C (Bruton, 1979b). This better tolerance of low temperature may be explained by (or may explain) the wider distribution range of this species, which is recorded from South Africa to Israel.

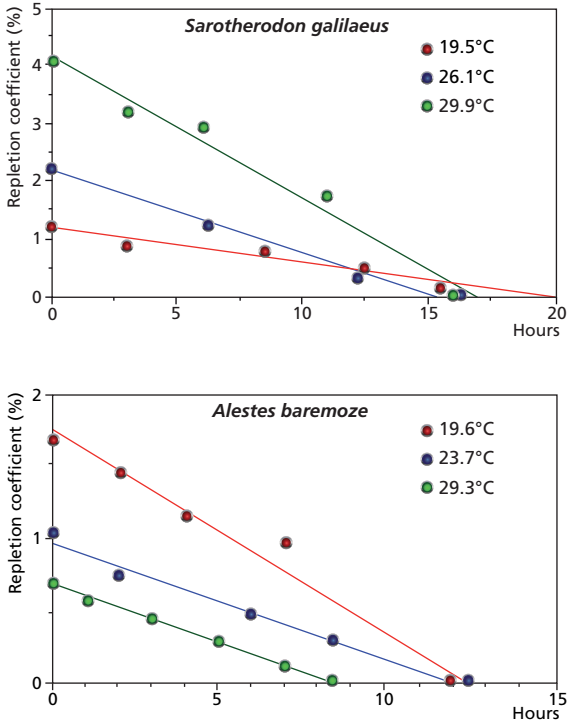
## Temperature and feeding

Temperature affects both the rate of food consumption and the rate of gastric evacuation. At low temperatures the fish may cease to feed, but the rate of consumption increases with increasing temperature.

For *Sarotherodon galilaeus* in Lake Chad, the gut repletion coefficient and rate of gastric evacuation increased with temperature (figure 13.1), but a quite different situation was observed in the same lake with *Alestes baremoze* (figure 13.1). For this latter species gut repletion and gastric evacuation rates were negatively correlated with temperature (Lauzanne, 1969). Lauzanne (1977) tentatively suggested that it could be related to differences in spawning periods, but this explanation is not convincing. What is clear is that the daily food consumption rate (expressed as the ratio of the weight of ingested food to fish weight x 100) decreases with temperature for *Alestes* (1.77% at 19.6°C, 1.43 at 21.6°C, and 1.18 at 30.6°C), whereas it increases for *Sarotherodon* (1.5% at 19.5°C, 3.3 at 26.1°C and 6.1 at 30°C).

**FIGURE 13.1.**

Effect of temperature on gastric evacuation rates for two species from Lake Chad, *Alestes baremoze* and *Sarotherodon galilaeus*. The repletion coefficient is expressed as % of the body weight. (from Lauzanne, 1969 and 1977).



### Behavioural responses to environmental temperature changes

It is usually assumed, but apparently not really tested with quantitative data, that fish are able to select the temperature regime in which they would maximize their lifetime production of offspring (Wootton, 1990).

When juveniles of *O. niloticus* and *C. rendalli* are submitted experimentally to a thermal gradient in tanks from 24 to 40°C, they respond positively to the warm water and swim actively towards water which is only slightly cooler than their lethal temperature tolerance (Caulton, 1977, 1982). In tilapias living in lakes, the juveniles, and above all the alevins, make daily cyclical movements between the shallower littoral zones, occupied during the day, and the deeper zones towards the open water, occupied by night. For instance, in Lake Mcllwaine (Zimbabwe), the juveniles move in the morning from the deep homothermal waters where they stay overnight, into shallow coastal waters where the temperature exceeds that of the homothermal waters (28°C at midday). Large schools of juveniles are eventually found in warm waters at midday. In the late afternoon, a reverse movement is observed, and the juveniles move back into the deeper, homothermal water. The ecological significance and the survival value of these daily migrations have been much discussed. They may be a tactic for avoiding predators present in deep water during the day, or for reducing food competition by the successive exploitation of different habitats in the course of the day. An elegant explanation based on careful energy budgets was proposed by Caulton (1982) who claimed that thermal oscillations were

beneficial to the growth of juvenile cichlids. The offshore-inshore migration tends to maximize growth: faster growth rates are achieved when fish move into warm inshore areas during the day (faster feeding and digestion rates), while when they retreat to cool deeper areas at night, the energy demands are less than if the fish remained at constant temperature.

Temperature creates distinct boundaries which may act as physical barriers to fish movement. Details of thermal structure contribute to defining the amount of suitable habitat available at a given time. Knowledge of the thermal structure of a waterbody is therefore important for understanding fish distribution and abundance.

## Adaptations to the lack of oxygen

With few exceptions, fish essentially have aquatic respiration. The poor solubility of oxygen in water means that the quantity of oxygen available to fishes is always very limited and may still decrease considerably (in which case there is hypoxia) as a result of various factors: water warming, pollution, water stratification, etc. In particular, it is not rare for oxygen content to be a limiting factor in stagnant waters, particularly when they contain much organic matter whose decomposition generally consumes large amounts of oxygen.

When oxygen availability decreases, fish increase their gill ventilation rate. Depending on their choices or available options, fish can either attempt to move to better-oxygenated zones or use physiological, behavioural, or morphological adaptations to face this deoxygenation. In the worst case, the fish will die of asphyxiation.

### Morphological and physiological adaptations

Some fishes are able to use oxygen in the air when its concentration in water becomes critically low. Most of them have organs that are adapted to these two modes of respiration. *Protopterus* spp and *Polypterus* spp possess a true lung, whereas *Gymnarchus*, *Heterotis*, *Papyrocranus*, *Phractolaemus*, have a modified swim bladder (air bladder) that allows them to use aerial respiration when needed. There is an arborescent breathing organ in the gill cavity of *Clarias*, and a labyrinth organ in *Ctenopoma* (Anabantidae).

Aerial respiration occasionally represents 90 to 95% of normal respiration in *Protopterus aethiopicus* even in well-oxygenated waters (Lenfant & Johansen, 1968), whereas this is only a compensatory mechanism when gill respiration is insufficient in *Clarias gariepinus* and *Polypterus senegalus* (Babiker, 1979 ; 1984). The *Protopterus* spp breathe through the mouth, swallowing air into the mouth cavity to send it to the lung. In water, *Protopterus* breathes every five to seven minutes, whereas in air it breathes every one to three minutes.

Generally speaking, Tilapias are resistant to low oxygen content, which explains why some species can live and reproduce in swamps or shallow lakes that may become temporarily anoxic. According to Bénech & Lek (1981) for instance, *O. niloticus*, which is capable of extracting oxygen in poorly oxygenated waters,

**ADAPTATIONS  
TO AERIAL RESPIRATION**

**Adaptation of the gill or pharyngeal cavity**

- gill modifications: Synbranchidae (*Monopterus*); Mastacembelidae (*Mastacembelus*)
- vascularised epithelium in a suprabranchial chamber: Channidae (*Parachanna*)
- labyrinth organ: Anabantidae (*Ctenopoma*)
- arborescent organ: Clariidae (*Clarias*)

**Modified swim bladders**

- Arapaimidae: *Heterotis niloticus*
- Notopteridae: *Papyrocranus afer*
- Gymnarchidae: *Gymnarchus niloticus*
- Phractolaemidae: *Phractolaemus ansorgii*

**True lungs**

- Polypteridae: *Polypterus senegalus*, *Erpetoichthys calabaricus*
- Protopteridae: *Protopterus*

can survive for a few hours in very hypoxic conditions (less than 0.5 mg l<sup>-1</sup>), but their behaviour changes and the fish becomes lethargic. Once it is placed in favourable oxygenation conditions, it quickly reverts to its normal behaviour.

**Behavioural responses  
to reduced oxygen availability**

Some fishes living in poorly oxygenated physical systems have developed behaviours that allow them to face periods of hypoxia and await improved conditions.

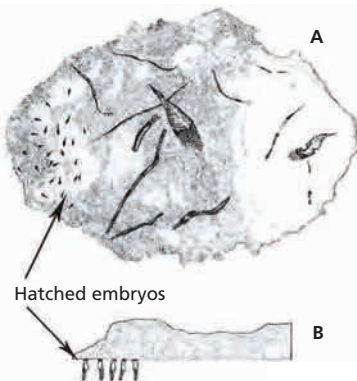
For instance, certain species living in swampy habitats use the superficial layer of water which is comparatively richer in oxygen than the rest of the water column, because of exchanges with the atmosphere. This appears to be the case with *Synodontis membranaceus* and *Synodontis batensoda* (Green, 1977), as well as for *Sarotherodon* spp. (Bénech & Lek, 1981). Use of the superficial layer is undoubtedly facilitated by head shape and the location of the mouth (Kramer, 1983). Thus, Cyprinodontiformes with their flat heads and an upturned mouth are also adapted to this kind of behaviour.

In addition to using the superficial water layer, other species also take water bubbles into their mouth, as in *Synodontis membranaceus* (Roberts, 1975) and *Brevimyrus niger* (Bénech & Lek, 1981).

Another adaptation to hypoxic systems consists of laying eggs in floating nests. *Hepsetus odoe* deposits its eggs at the air-water interface, in a floating foam nest, and the young larvae possess structures that allow them to remain attached to the nest (figure 13.2) (see also chapter *Reproduction*). *Ctenopoma damesi* also

**FIGURE 13.2.**

Foam nest of *Hepsetus odoe*, with hatched embryos. Newly hatched embryos are suspended below the nest via a cement gland (B). Top view (A) and cross section (B) from Merron *et al.*, 1990.



lays eggs in floating foam nests guarded by the male, who ensures the eggs remain oxygenated, while *C. muriei* produces floating eggs.

## Adaptations to salinity

Many fishes live in fresh or salt water, but numerous so-called amphihaline (or euryhaline) species can move from fresh to salt water and back. The internal fluids of freshwater fish are more concentrated than freshwater, so they have a tendency to lose ions ( $\text{Na}^+$ ,  $\text{Mg}^{++}$ ,  $\text{Cl}^-$  in particular) and acquire water through all permeable surfaces such as gills or oral mucosa. Conversely, in salt water, they tend to acquire ions and lose water. Osmoregulation is the phenomenon that allows animals to regulate plasma concentrations of ions and water, and to maintain a constant osmotic pressure in their internal fluids despite variations in ambient conditions.

Gill epithelium is subjected to an uninterrupted flow of water, and the transfer of salts primarily occurs here. For example, in *O. mossambicus* the exchange rate increases nearly two hundred fold when the species is transferred directly from fresh to salt water. But the physiological mechanisms that allow adaptation to salinity are still poorly understood (Prunet & Bornancin, 1989). Nonetheless, we know that adaptation to salinity can be modulated by numerous environmental factors. Very early exposure to high salinities is believed to increase adult resistance to salinity (Watanabe *et al.*, 1985).

Fish species that can live in continental salt waters are rare, and many belong to the Cichlidae of marine origin which may explain their great euryhalinity. Several Tilapias such as *Tilapia guineensis* and *Sarotherodon melanotheron* live and reproduce in the coastal waters of West Africa, in salinities of up to 30‰. In Casamance, Albaret (1987) even observed populations of *Sarotherodon melanotheron* and *Tilapia guineensis*, in 90‰ waters during a period of drought. East African species such as *Oreochromis mossambicus*, *O. urolepis*, and *O. placidus* also have high tolerance for salinity. *O. mossambicus* has been observed to reproduce in waters with a salinity of 69‰, twice that of sea water.

A few Tilapia species are well-adapted to the high salinities found in some lakes. This is the case for *Oreochromis amphimelas* in Lake Manyara (58‰), *Alcolapia grahami* endemic to Lake Magadi (40‰), and *A. alcalica* in Lake Natron (30 to 40‰) (see also chapter *Fish communities in small aquatic ecosystems: caves, gueltas, crater and salt lakes*). *Coptodon zillii* which usually lives in fresh water reproduces in Lake Quarun, in Egypt, where salinity varies from 10 to 26‰, and can survive in waters with a salinity of up to 44‰.

Among the Cyprinodontidae, *Aphanius fasciatus* lives in waters reaching a salinity of 40‰ in North Africa. Mormyridae, meanwhile, are strict freshwater fishes that cannot tolerate even low salinities. Thus, in Lake Chad, Mormyridae are confined to waters whose conductivity remains below  $400\mu\text{S cm}^{-1}$  (Bénech *et al.*, 1983). Mormyridae are also not found in Lake Turkana where conductivity is around  $3500\mu\text{S cm}^{-1}$ , even though the rest of the ichthyofauna has strong

nilotic affinity (Lévêque *et al.*, 1991). It is also believed (Lowe-McConnell, 1987) that the existence of a single species of Mormyridae in Lake Tanganyika may be the result of past events marked by an increase in water salinity that led to the elimination of other species of the same family.

## Adaptations to drought

Africa has numerous temporary aquatic physical systems that dry up seasonally. In general, there is a seasonal cycle related to rainfall and flooding, but in some extreme cases, water is supplied much more sporadically. Meanwhile, in wet tropical areas, small puddles such as those found in the footprints of elephants or cattle can appear and disappear several times a year (see chapter *Life-history strategies*).

A small number of species have adapted to survive total desiccation. The West African lungfish (*Protopterus annectens*) has long been known to survive long periods of desiccation of its habitat (Johnels & Svensson, 1954).

### THE LUNGFISH

When the water level decreases, the West African lungfish (*Protopterus annectens*) digs a vertical burrow in the soft mud as well as a round chamber in which it secretes copious quantities of mucous. When the mud dries up, the mucous also becomes dehydrated, forming a cocoon around the fish which thus becomes dormant. The fish remains immobile, folded upon itself, breathing air through a small opening at the top of the cocoon (figure 13.3).

In nature, *Protopterus annectens* can aestivate for seven to eight months, depending on the length of the dry season. In aestivating *Protopterus aethiopicus*, the rate of oxygen consumption decreases progressively to 10% of an active fish's consumption, and the heart rate decreases to around three beats per minute (Beadle, 1981).

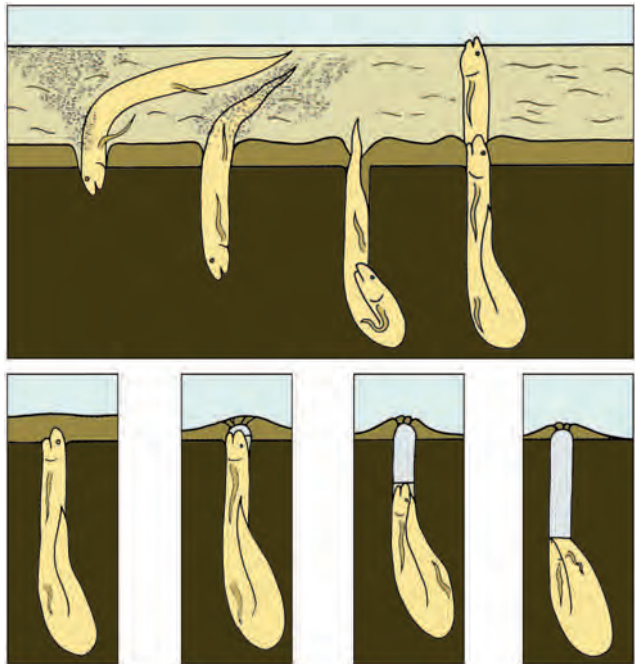


FIGURE 13.3.

Schematic views of aestivating and cocooned *Protopterus annectens* (redrawn from Johnels & Svensson, 1954).



Catfish of the genus *Clarias* are also known to survive in sand or wet mud, but not in fully dried up areas (Bruton, 1979b). Their capacity to recolonize recently flooded areas probably comes from the fact that they are able to travel several hundred metres in wet prairies.

Fishes of the Cyprinodontiformes order are particularly well-adapted to life in temporary habitats, and certain species of the genera *Nothobranchius* and *Aphyosemion* live in the temporary ponds of tropical Africa. Adults only live there for a few months, that is, during the high water period, and the reproductive cycle must be completed during this period. Resistance to drought in this case takes the form of eggs enclosed in a thick membrane. They can resist for several years while buried in the ground and develop once the physical system is filled with water again. Growth after hatching is very rapid, and for *Nothobranchius*, sexual maturity can be reached in less than one month (Haas, 1976a). *Nothobranchius rachovii* can thus spawn at the age of 4 weeks and a size of 9 mm (Simpson, 1979), while *N. guentheri* reaches maturity 7 to 8 weeks after hatching (Bailey, 1972).

#### DIAPAUSE IN CYPRINODONTIFORMES

In Cyprinodontiformes living in temporary physical systems, hatching can be delayed by several days; that is, the fry remains in the egg instead of hatching out. In some species of *Aphyosemion* and *Epiplatys*, this period does not exceed several days, whereas it can reach up to 70 days in *Aphyosemion batesii* (Brosset, 1982).

We have also seen that eggs of Cyprinodontiformes can enter

diapause, that is, suspend development at well-defined stages (Wourms, 1972). Pre-incubation diapause has been observed in *Aphyosemion batesii* (Brosset, 1982), and diapause in an embryo that was ready to hatch has been seen in other annual species such as *Fundulopanchax arnoldi*, *F. fallax*, *F. walkeri*.

Genus and species names have been updated from the ones used by Brosset.

## Blind fish

Life in total darkness, as in underground caves, can lead to the regression or disappearance of eyes. It is generally believed that these “troglolobionts” evolved from surface species with eyes and which, for various reasons, were trapped underground. This resulted in loss of pigmentation, a slower metabolism, and a decrease in eye size that is increasingly pronounced with the duration of the cave colonization (see also chapter *Fish communities in small aquatic ecosystems: caves, gueltas, crater and salt lakes*).

There are few known blind fish species in Africa (see chapter *Fish communities in small aquatic ecosystems: caves, gueltas, crater and salt lakes*). In a large group of caves in the region of Thysville in DRC, belonging to the Kouilou system, scientists discovered *Caecobarbus geertsii*, *Chanallabes apus* and *Dolichallabes microphthalmus* (Heuts, 1951 ; Heuts & Leleup, 1954). *Barbopsis*

*devecchi* and *Uegtiglanis zammaranoi* were captured in wells in Somalia and Ethiopia. Two fully blind species of cave-dwelling Eleotridae were discovered in Madagascar, in karst formations in the south-western part of the island (Kiener, 1963).

Blind fishes have also been found in rapids, and a hypothesis worth verifying is that the loss of eyes and pigmentation could be due to the fact that they spend their lives under rocks. This is the case of *Platyallabes tihoni* (figure 12.3) and *Mastacembelus brichardi*, two species from Stanley Pool living under rocks or in cracks.

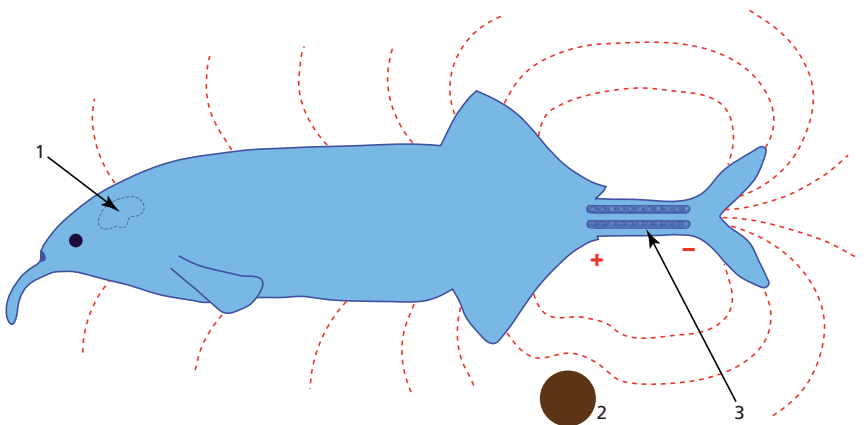
A new blind fish species (*Glossogobius anakaranensis* Banister, 1994) was discovered in an underground river of the Ankarana massif in the north of Madagascar. It is the third blind fish species recorded in the "Grand Île"; the other two were Eleotridae discovered in the southwest of Madagascar.

## Light attenuation and darkness

African river waters are generally turbid and fish cannot use their sight to orient themselves. They have thus developed adaptations that allow them to communicate while in motion.

In electric fish, discharges create an instantaneous electric field around the fish (figure 13.4). The presence of an object in the immediate surroundings of the fish concentrates or disperses the lines of the field, depending on its electric conductivity compared with water. Disturbance of the field owing to the presence of the object is sensed by the fish, whose cerebellum processes messages transmitted by its electroreceptors. Various experiments carried out with *Gymnarchus* in particular have proven that the fish are able to use this detection system to avoid obstacles, but it is only effective within a radius of about 10 centimetres in Mormyridae. The adaptive value of this system is obvious for fish living in murky waters and which are often nocturnal. It allows them to orient themselves and to find prey to feed upon.

**FIGURE 13.4.**  
Principle of electrolocation in a mormyrid fish. The electric organ (3) which is monitored by electroreceptors (1) found in pores of the anterior surface, produces electric discharges. The dotted lines give the current flow associated with electric organ discharge. Each object (2) with conductivity different from that of the surrounding water distorts the current pattern and thus modifies the fish information.



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# The Inland Water Fishes of Africa

*Diversity, Ecology and Human Use*



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