Fish communities in small aquatic ecosystems: caves, gueltas, crater and salt lakes

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Small aquatic ecosystems generally have several similar physical and biological characteristics. Except for their size, they are, most of the time, extreme ecosystems. For example, soda lakes have very high salinity and/or alkalinity; crater lakes are deep with a low level of oxygen in the deep layers of the water; in gueltas and chotts, the water is perennial in only a few and the temperature is high; in caves, organisms live in permanent darkness. In relation with these severe conditions, fish have developed physiological and behavioural adaptations that allow them to survive and perpetuate. Thus, specific and usually endemic species inhabit these environments. In some cases, small species flocks exist, as can be observed in the Great Lakes of East Africa. Finally, most of these environments are vulnerable to even minor disturbances. Continued vigilance, protective measures and conservation recommendations must be a high priority to protect them from actual or potential local threats.

Strictly speaking, the crater lakes and the graben/horst lakes are different, while they both owe their formation to tectonic events.

A crater lake is a lake that formed in a volcanic crater or a caldera. In Africa, most of the crater lakes are located in dormant or extinct volcanoes, and tend to be freshwater. The water clarity in such lakes can be exceptional due to the lack of inflowing streams and sediment. Crater lakes are well represented in tropical Africa, especially in the Guinean rainforest zone of Cameroon, where there may be 36 or more (McGregor Reid & Gibson, 2011). There are also crater lakes in Eastern Africa, mainly high-mountain crater lakes in Ethiopia (Degefu *et al.*, 2014), but the natural fish richness is generally very low or non-existent.

A graben is the result of a block of land being downthrown, producing a valley with a distinct scarp on each side. Grabens often occur side-by-side with horsts. Horst and graben structures are indicative of tensional forces and crustal stretching. This kind of lake is very present in the eastern arm (Gregory branch) of the African Rift Valley. This Gregory rift valley is most clearly defined in Kenya where classical grabens penetrate the regional domal upwarping. A string of lakes follow its course southward through Kenya and into Tanzania, including Turkana, Baringo, Bogoria, Nakuru, Elmenteita, Naivasha, Magadi, Natron, Eyasi and Manyara.

Lake level is a product of the balance of inputs (precipitation, inflowing streams, groundwater inflows) and outputs (evaporation, outflows, groundwater seepage). The relative importance of these factors will govern the responsiveness of particular basins to changes in climate, and these will be examined in the following section (*Salt and alkaline lakes*).

Salt and alkaline lakes

A salt lake is generally a landlocked body of water whose concentration of salts (typically sodium chloride) and other dissolved minerals is significantly higher than most lakes (often defined as at least three grams of salt per litre). In some cases, salt lakes have a higher concentration of salt than seawater, but such lakes would also be termed hypersaline lakes. That is, for example, the case of Lake Retba in Senegal ("lac Rose" meaning "Pink lake" as it is known by locals) where the salinity is between 80-350 g/l according to the seasons (Sow *et al.*, 2008).

An alkaline lake that has a high carbonate content is sometimes called a soda lake. This type of lake is alkaline with a pH value above 7.5. In addition, many soda lakes also contain high concentrations of sodium chloride and other dissolved salts, making them saline lakes as well. High pH and salinity often coincide.

Salt and soda lakes form when the water flowing into the lake, containing salt or minerals, cannot leave because the lake is endorheic (without outlet). The water then evaporates, leaving behind dissolved salts and thus increasing its salinity, making a salt lake an excellent place for salt production.

The hypersaline and highly alkalic soda lakes are considered some of the most extreme aquatic environments on Earth. In spite of their apparent inhospitableness, soda lakes are often highly productive ecosystems, compared to their (pH-neutral) freshwater counterparts. An important reason for this high productivity is the virtually unlimited availability of dissolved carbon dioxide.

Nevertheless, overly high salinity or alkalinity will also lead to a unique flora and fauna in the lake in question; sometimes, in fact, the result may be an absence or near absence of life near the salt lake. In fact it depends on the tolerance of organisms to the mineral concentrations that exist in the lake. For African fish like cichlids, we generally agree that the highest salinity must not exceed 50-60 g/l (see also chapter *Diversity of responses to extreme environmental conditions*). Thus, some specialized species, like *Alcolapia grahami*, have been introduced with success in Lake Nakuru (Kenya), where salinity can reach 20-25 g/l (Vareschi, 1982). However, authors (Garnier & Gaudant, 1984) have recorded the presence of a tilapia (*Sarotherodon melanotheron*) in Lake Retba (Senegal) where salinity reaches at least 80 g/l but can rise up to 350 g/l during the dry season.

In their paper the authors say "In its North-Eastern part, the lake is extended by an intermittent creek that is supplied in water through inputs from groundwater.

It is in one of these water holes that we have observed many cichlid fish of which one specimen was captured in April 1978". At present these holes no longer exist, but there are still small ponds of brackish water where a dwarf form of *Sarotherodon* still lives. In these ponds as well as the ancient holes, water is less concentrated than in the lake itself, which is really unsustainable for tilapines.

Soda lakes occur naturally throughout the world (see Table 21.I below for African ones), typically in arid and semi-arid areas and in connection to tectonic rifts like the East African Rift Valley. The pH of most freshwater lakes is on the alkaline side of neutrality and many exhibit similar water chemistries to soda lakes, only less extreme.

TABLE 21.I.
Chemical characteristics (pH and salinity) for major African salt lakes.

Name	Country	pH	Salinity (g/l)
Wadi Natrun lakes	Egypt	9.5	50
Malha Crater Lake	Sudan	9.5-10.3	
Lake Abbe	Ethiopia	9.8-11	115
Lake Arenguadi (Green Lake)	Ethiopia	9.5-9.9	2,5
Lake Basaka	Ethiopia	9.6	3
Lake Shala	Ethiopia	9.8	18
Lake Chitu	Ethiopia	10.3	58
Lake Abijatta	Ethiopia	9.9	34
Lake Magadi	Kenya	10	>100
Lake Bogoria	Kenya	10.5	350
Lake Turkana	Kenya/Ethiopia	8.5-9.2	2,5
Lake Nakuru	Kenya	10.5	5-90
Lake Logipi	Kenya	9.5-10.5	20-50
Lake Manyara	Tanzania	9.5-10	40
Lake Natron	Tanzania/Kenya	9-10.5	100
Lake Rukwa	Tanzania	8.5-9.2	
Lake Eyasi	Tanzania	9.3	5

Generally speaking, tilapias *s.l.* have a wide and varied diet and can occupy a large range of habitats, from freshwater to hypersaline conditions; therefore, its distribution is unlikely to be limited by many environmental, physical or chemical conditions. However, the one factor that appears to affect tilapia is its vulnerability to cold temperatures. Tilapia is traditionally viewed as a tropical to warm-temperate species.

Salt concentration may constitute a limiting factor for fish and for other many organisms. Thus, in Africa a marked decrease has been observed in the number of zooplankton and foraminifera species in increasingly confined water (Debenay *et al.*, 1989). Likewise, studies on the Casamance river have shown that fish taxa disappear with increasing salinity and that fish fauna becomes monospecific (*Sarotherodon melanotheron*) above 75‰ (Albaret, 1987). The capacity of *S. melanotheron* to withstand salty environments suggests that this species has the capacity to modify its life-history traits, mainly reproductive and growth ones. The most profound changes are only visible in hypersaline conditions where the species is able to limit its growth, to reduce its size-at-maturity, and to change its fecundity (Panfili *et al.*, 2004b). The main modification in the reproductive traits concerns the change in size at maturity, which decreases in *S. melanotheron* as salinity increases. Conversely, the influence of intermediate or high salinities (35-90‰) don't show any clear significant relationship with fecundity or oocyte size of this species (Panfili *et al.*, 2004b).

Some authors mentioned several species of tilapias isolated in the alkaline lakes of the Great Rift Valley of Africa, living in extreme conditions of temperature, salinity and pH (Reiter *et al.*, 1974). It is true for some of them like *Oreochromis mossambicus* or *Sarotherodon melanotheron*, which may survive for some time in harsh conditions. But, it seems that only one complex of fish species (*Alcolapia*) can actually be found in saline and alkaline lakes and is adapted to very harsh conditions. Much research has been performed on these fish, indicating that the fish have adapted to live in temperatures up to and possibly above 44°C, a pH varying between 5-11 (though the lake naturally ranges from pH 9-11), low oxygen levels in the water (as low as 1.1 mg O_2/L of water), and a salinity concentration of up to 4% (Reiter *et al.*, 1974). These tilapia developed many adaptations to survive in this lake where, due to the lake's extreme conditions, little other non-microbial life exists.

Until recently only one cichlid species (Soda tilapias) was known from the Lake Natron basin, *Alcolapia alcalica*, assumed to be very closely related to *A. grahami* from Lake Magadi, some 20 km to the north of Lake Natron. But today we know that the Lake Natron basin hosts a small species flock of four polymorphic tilapiine cichlids (Seegers & Tichy, 1999). Later, it was found that the Soda tilapias are fairly distant (mitochondrial DNA sequences) compared with related *Oreochromis* species in the area that are closer together. These results, as well as morphological data, confirm that the Soda tilapias must be considered as a new genus, *Alcolapia* (Seegers *et al.*, 1999).

In natural salt lakes like Lake Nakuru and Lake Elmenteita, where no fish at all was present (Kenya), *Alcolapia alcalica* and *A. grahami* were introduced in the early 1960s and naturalized. Conversely, in Lake Bogoria (Kenya), which is alkaline (pH>10) and saline (from 100 to 300 g/l, total dissolved salt), fish life seems impossible, although the lake is highly productive with abundant cyanobacteria and rotifer. But the ecological conditions are too harsh for fish.

Gueltas and chotts: the Sahara fish fauna

These collections of water are other types of harsh biotopes (see box "Some definitions concerning some particular small isolated patches of water"). Their common characteristic is to have very impoverished fauna constituted by

Some definitions concerning some particular small isolated patches of water

NOTE 1
Originally, wadi refers to a dry (ephemeral) riverbed of North Africa that contains water only during times of heavy rain or simply an intermittent stream. Nevertheless, in the Maghreb, the term *wadi* is, most of the time, applied to all rivers including regular ones.

A **guelta** is a pocket of water left in drainage channels or wadis[1] during the dry season in the Sahara (Ramdani *et al.*, 2010). The size and duration will depend on the location and conditions. It may last year-round through the dry season if fed by a source such as a spring. When rivers (wadis) dry up there may remain pockets of water along its course.

A **chott** is ephemeral and usually possesses brackish water (Ramdani *et al.*, 2010). In geology, a chott is a dry (salt) lake in the Saharan area of Africa (mainly in Tunisia, Algeria and Morocco) that stays dry in the summer, but receives some water in the winter. These lakes have changing shores and are dry for much of the year.

A **cave** is an underground natural hollow. Some caves, connected to a dynamic hydrographic system, may include an underground lake or a river.

some resistant fish species belonging to three main families, Cyprinidae, Cichlidae and Clariidae. These species have evolved abilities to survive in extreme conditions (see also chapter *Diversity of responses to extreme environmental conditions)*.

For a long time the Sahara Desert was considered to be an obstacle to dispersals of humans and animals. But nowadays it is evident that the Sahara was not an effective barrier and that both animals and humans had been present during the past humid phases (Drake *et al.*, 2011). Dispersal was facilitated during the Holocene humid period when linked lakes, rivers, and inland deltas were present. Furthermore, the presence of several fish species in more or less perennial collections of water attest to wet conditions in this area during the Holocene. Finally, it was interesting to note that this relict fish fauna is always housed in mountainous massifs from Mauritania to Chad.

Fish communities in gueltas

Here, we exclude the fish fauna in the Atlantic slope and only take into account the southern part of the Maghreb province including the Sahara desert. Most of the perennial water bodies where fishes have survived since the last humid period match with gueltas or wells located in the main Saharian mountains (figure 21.1):

- Ahaggar (Hoggar), Mouydir and Tassili n'Adjer in southern Algeria;
- Adrar in Mauritania;
- Tibest, Ennedi and Borkou in northern Chad.

Gueltas are mainly encountered in mountains because of the soil composition, which is generally rather water impermeable. So, gueltas are fed by rainwater that has accumulated in rocky pools (sandstones, basalts, granites) or in ponds with clay bottoms. If some Chadian gueltas, in Ennedi or Tibesti, may have relatively large dimensions (a few hundred square meters) those of Mauritania are conversely very small and their surface does not exceed one square meter with a depth of 15-20 cm. Nevertheless, such small collections of water may contain more than 50 *Barbus* (Daget, 1968).

FIGURE 21.1.
Saharian mountains (except Tenere) where fishes survive in gueltas or wells.

The presence of fish in the Sahara was reported in the early 20th century (Pellegrin, 1937). Later, the inventory of perennial water bodies was expanded in the 1950s (Monod 1951; 1954; 1955; Daget, 1959a). More recently, systematic revisions and re-examination of collections hosted in different museums have clarified and completed the inventory (Lévêque, 1990). Finally, very recently, a series of surveys were carried out in the Adrar Mountains in Mauritania (Trape, 2009) and in the Tibesti Mountains, the Borkou plateaus and the Ennedi Mountains in northern Chad (Trape, 2013).

Sixteen species of fish belonging to six families were reported in perennial bodies of water in the Sahara desert (table 21.II). Most of them are relict populations of Sudanese fish species, but one of them, *Barbus callensis*, restricted to the Hoggar mountains (Ahaggar and Tassili N'Ajjer) in the Sahara area is a northern colonizer widespread in most of the coastal wadis in the Maghreb province (figure 21.2). *Astatotilapia desfontainii* is one among doubtful fish species occurring in the considered area. This species is native from Algeria and Tunisia (the type locality is Gafsa in central Tunisia, north of Chott El Jerid). In Algeria, its most southern distribution reaches Ouargla and Hassi Massaoud (Schraml, 2010). Unfortunately, no fish collection confirms such an austral extension. Trape (2009 and 2013) also mentions the presence of this species in the Mouydir basin which is an extension of the Tassili n'Ajjer, but none of the cited references provide such information. In the collections housed in different museums, the most austral presence of the species is Biskra. Finally, this species was never reported in the Sahara fish fauna synthesis (Doadrio, 1994). Therefore, at the moment we consider that the presence of *A. desfontainii* in southern Algeria (Hoggar Mountains) seems very doubtful. Trape (2009 and 2013) reports two sub-species of *Sarotherodon galilaeus*, the first *S. g. galilaeus* (Linnaeus, 1758) present in the Adrar Mountains (Mauritania) and the second *S. g. borkuanus* (Pellegrin, 1919) present in the northern Chad desert. But according to Trewavas & Teugels (1991), all subspecies

FIGURE 21.2.
Distribution of the 16 species recorded in the Sahara region.

of *S. galilaeus* must be synonymised. Finally, we must consider some introduced species reported in data collections (Paugy *et al.*, 2014). Trape (2009) specifies that there are no fish in the Aïr massif of Niger, but some specimens of *Oreochromis aureus* have been introduced and apparently naturalized in the Dirkou oasis. In the Fezzan desert, Libya, several species of the poeciliid *Gambusia* (*G. affinis* and *G. holbrooki*) have been introduced. There is no date for the introduction of these species in Libya, but it could have been introduced by the Italians in 1929 (Jawad & Busneina, 2000). Currently the genus is widespread to almost local ponds and wells, frequently at the expense of other (native) species (Hughes & Hughes, 1992).

It appears that the relict fish fauna of the northern Chad area exhibits the highest diversity and this fauna is clearly related to the fauna that exists in Sudanese basins, *i.e.*, Nile and Chad in the region.[2] The Mauritanian fish fauna is also of Sudanese origin, but it is slightly different (*C. gariepinus* substituted by *C. anguillaris*) and only a third as diverse (4 species *versus* 12 in Chad area).

NOTE 2
For the evolution from Mega-Chad to marshy Chad, see also chapter *Variability of the climate and hydrological systems*.

Despite the extreme aridity, it seems that the perennial water bodies in Chad region are more persistent and resistant, particularly in water volume, in this

Families	Species	Adrar Mauritania	Tassili Algeria	Ahaggar Algeria	Ennedi Chad	Tibesti Chad	Borkou Chad)
Polypteridae	*Polypterus senegalus*						*
Cyprinidae	*Barbus apleurogramma*				*		
Cyprinidae	*Barbus callensis*		*	*			
Cyprinidae	*Barbus macrops*	*	*	*	*	*	
Cyprinidae	*Barbus occidentalis*					*	
Cyprinidae	*Barbus pobeguini*	*					
Cyprinidae	*Labeo niloticus*					*	
Cyprinidae	*Labeo parvus*				*	*	
Cyprinidae	*Raiamas senegalensis*					*	
Clariidae	*Clarias anguillaris*	*	*				
Clariidae	*Clarias gariepinus*		*		*	*	
Nothobranchiidae	*Epiplatys spilargyreius*						*
Poeciliidae	*Poropanchax normani*						*
Cichlidae	*Hemichromis bimaculatus*		*				*
Cichlidae	*Sarotherodon galilaeus*	*			*	*	*
Cichlidae	*Coptodon zillii*		*	*	*	*	
Total number of species		**4**	**6**	**3**	**6**	**8**	**5**

TABLE 21.II.
Distribution of the 16 relict fish species in Sahara.

region than in the Mauritanian area. Thus, pools, gueltas or wells prospected in the 1950-60s (Bruneau de Miré and Quézel in 1956; Gillet, Lauzanne and Monod in 1967) are still present and seem in good health. Conversely, with the drought that has lasted nearly forty years, the relict fish fauna in the Adrar region of Mauritania appear to be highly endangered. Thus, of the thirteen sites mentioned in the literature, four are no longer home to fishes, at least on a permanent basis, and one appears to be highly endangered (Trape, 2009). The repetition of severe climatic conditions in this region is perhaps the reason for the poverty of the fish fauna in this region.

In southern Algeria, the fish fauna is also rather poor, with six species. One, *Barbus callensis* is Palaeoarctic while the other five have a Sudanese origin, with an intermediate composition between Mauritanian and Chadian faunas (table 21.III).

Algeria	Mauritania	Chad
Barbus macrops	*	*
Clarias anguillaris	*	
Clarias gariepinus		*
Hemichromis bimaculatus		*
Coptodon zillii		*

TABLE 21.III.
Sudanese faunistic similarity between Algeria on the one hand versus Mauritania and Chad on the other hand.

All species of the relict fauna of the Chadian area are found in Chad and Nile basins, except *B. apleurogramma*. The record of this species in the Ennedi is more surprising as it is nowadays known from the Lake Victoria basin. Knowing that the species no longer occurs in the Chad and the lower Nile, it could well be the relict of a more ancient fish fauna extending northwards, and whose representatives later disappeared from Sudanese river basins. It may well be that *B. apleurogramma* from Ennedi was part of an ancient fauna which was more widely distributed than nowadays, and whose representatives probably disappeared during an arid climatic phase, with relict populations subsisting in particular zones. That could imply that the isolation of *B. apleurogramma* would be older than the last humid period.

Fish communities in chotts

The chotts, vast shallow temporary lakes of saline character, lie along the northern border of the Sahara, in the Sahara/Mediterranean transition zone, and are large salt flats. Some are flooded every winter; others seldom carry surface water. In Algeria, chotts are the major wetlands. Most of the chotts are of importance to wintering and migrating waterfowl, and support large numbers of ducks. Conversely, due to their high salinity and also because water is not generally perennial, most of the chotts are not inhabited by fish.

However, there are some exceptions such as the Chott Djerid and Chott el Fedjadj complex in Tunisia (Doadrio, 1994). The chotts proper are devoid of fish, amphibians, reptiles or mammals. By contrast much more diverse floras and faunas, including fishes, are found in the beds of the oueds that feed the chotts and in the springs around the margins. Several species of fish live in the oases, including *Aphanius fasciatus*, *Barbus callensis*, *Clarias gariepinus*, *Haplochromis desfontainesi* and *Hemichromis bimaculatus* (Doadrio, 1994). *Oreochromis niloticus*, *Poecilia reticulata* and *Gambusia affinis* have been introduced, this last one for mosquito control.

In Egypt, Lake Qarun (or Birket Qarun or Lake Moeris) (figure 21.3) was freshwater in prehistory, but it is a saltwater lake today and could be compared to a chott. Lake Qarun is endorheic and was, in the past, artificially fed by water from the Nile, but now, with modern agricultural practices, it receives only the

FIGURE 21.3.
Lake Qarun is an ancient lake in the northwest of the Faiyum Oasis, 80 km southwest of Cairo, Egypt. It persists in modern times as a smaller lake and the lake's surface is about 45 m below sea level and covers about 200-250 square kilometres. The lake has a mean depth of 4.2 m and a maximum depth of 8.5 m in the western basin. The rate of salinization has increased since the closure of the Aswan dam. Artificial fertilizers are used to replace the nutrients formerly provided by the sediment deposited during the annual flood, and these raise the concentration of salts in the waters entering the lake (© IRD/D. Paugy).

run-off from the irrigated peripheral lands, which enters the lake via two canals at the eastern end. The lake is becoming increasingly saline. At the turn of the 20th century salinity was measured as 13‰, but this had risen to over 34‰ in some parts of the lake by 1976. The most important species of fish are *Liza ramada*, *Mugil cephalus*, *Solea vulgaris* and *Coptodon zillii*. All of these were first introduced in 1928 and are now restocked annually (Hughes & Hughes, 1992). The evolution of the salinity of Lake Qarun has led to modifications in fish composition; its gradual increase led to the gradual disappearance of *O. niloticus* and *O. aureus* and their replacement by *C. zillii* (Fryer & Iles, 1972).

Although in some cases, as in Lake Qarun, there is a rather flourishing fishery, chotts or sebkhas are not suitable ecosystems for the development of fish. Most of the time in these environments, fish populations are very reduced and are restricted to freshwater areas close to springs or in tributaries.

Fish communities of caves

Caves are generally fed by tributaries of larger river basins. The fish fauna show adaptations in relation to a permanent darkness. Some species use caves only occasionally to avoid unfavourable conditions outside. Others live permanently in caves and these fishes are discussed here. According to Parzefall (1993), these true cave-dwellers can be called "troglobionts". Their striking morphological differences in comparison with epigean relatives concern the reduction of the eye and generally uncoloured pigmentation. Most of them are blind, but the degree of eye reduction in different species seems to be connected with phylogenetic age of cave colonization (Parzefall, 1993).

All around the world, there are 87 species of troglomorphic fishes belonging to 18 families (Romero & Paulson, 2001; Sparks & Chakrabarty, 2012). In the teleostean fish of Africa, 9 species belonging to four families have colonized caves successfully (table 21.IV and figure 21.4).

family/species	location	descriptor	year
Cyprinidae			
Barbopsis devecchii	Somalia	Di Caporiacco	1926
Caecobarbus geertsi	DRC	Boulenger	1921
Phreatichthys andruzzii	Somalia	Vinciguerra	1924
Clariidae			
Clarias cavernicola	Namibia	Trewavas	1936
Uegitglanis zammaranoi	Somalia	Gianferrari	1923
Gobiidae			
Glossogobius ankaranensis	Madagascar	Banister	1994
Eleotridae			
Typhleotris madagascariensis	Madagascar	Petit	1933
Typhleotris mararybe	Madagascar	Sparks & Chakrabarty	2012
Typhleotris pauliani	Madagascar	Arnoult	1959

TABLE 21.IV.
Blind fish recorded from caves of Africa. Non-troglomorphic fishes found in caves as well as blind fish not found in caves are not included.

FIGURE 21.4.
Localities of the nine troglomorphic fish species in Africa.

Two others species (*Mastacembelus brichardi* and *Platyallabes tihoni*) are also considered blind fish, but they live in riffles under flagstones in the Stanley Pool, so they cannot be considered as cave-dwellers. Finally, two clariids (*Channallabes apus* and *Dolichallabes microphthalmus*) are sometimes collected in caves near Kanka (ex-Thysville) in DRC, but these species have a larger distribution and are recorded in many epigean watercourses, so they must not be considered as strictly cave-dwellers.

Although the scientific community has known of cavefishes for more than a century, they have not been studied in any detail with regard to their basic biology and/or species diversity, due to the difficulty of access to their habitats. Furthermore, these species are scarce and generally vulnerable or endangered, so it is very difficult to carry out samplings to study their basic biology.

However an exception exists and some important insights in ecology, variation and adaptation were obtained in the 1950s for *Caecobarbus geertsii* (Heuts, 1951) (figure 21.5).

FIGURE 21.5.
A preserved specimen of *Caecobarbus geertsii* from the cave 'Grotte de Lukaku', DRC (© Royal Museum for Central Africa).

Firstly, not all caves of the region are inhabited by *Caecobarbus*, even when they provide ample occasion for the development of aquatic life. Clearly caves have to offer a combination of ecological conditions if they are to be populated by *Caecobarbus*. This combination seems to be achieved only in particular caves of a selected area. According to the conclusions of Heuts (1951), we can summarize the situation as follow. First, a cave inhabited by animals is not just a dark subterranean hole but an ecologically complex and specialized habitat where many factors play a role. Among these factors, the darkness seems to have no more importance than others. All the others – high calcium, bicarbonate and carbon dioxyde concentrations, absence of photoperiodism, scarcity of food, isolation, and the constancy of all these – exert an influence on the inhabitants.

Some caves must be considered as a more or less long subterranean course of an epigean stream. Such caves never contain any blind fish populations. Conversely, all *Caecobarbus* caves are in locations that receive, during the rainy season, an inflow of water through intermittent stream beds. The first important ecological consequence of this periodicity is that the food resources are also subjected to a similar cycle. Examination of the stomach contents of the fishes show that they eat exogenous insects which are brought into the inside of the cave by the rain during the wet season. In other words, food is only supplied for more or less six months of the year. In connection with their periodical inundation, and the consequent instability of certain conditions, other typical cave animals, especially terrestrial insects, are absent in *Caecobarbus* habitats, so that the exogenous fauna is really the only resource for the fish. In conclusion, the species lives under specific ecological characteristics, but due to the heterogeneity and the discontinuity of the entire area, each population may live in different conditions so long as these lie within the limits of the species' requirements.

In addition to diet, two other biological features were studied. But the results are quite disappointing, because the hypotheses issued by the author (Heuts, 1951) seem questionable. According to observations of scale rings, Heuts considers that the maximal longevity varies from 10 to 14 years. This result is very surprising when we know that the maximal length of the species reaches 80 to 90 mm SL, even if the species must have slow growth because of the scarcity of the food availability and the severity of ecological conditions. With regard to reproduction, the author has never found young specimens and all the individuals caught measured more than 40 mm. Two hypotheses have been put forth to explain this feature. First, reproduction takes place with a maximal intensity about every ten years, regularly increasing and falling to zero with the same periodicity. Second, reproduction takes place every year, but the juvenile stages are bound to live in special habitats exhibiting the most ideal cave conditions, and as such, inaccessible to man for investigation. These two explanations are unsatisfactory and only a study of populations during successive years will be able to reveal the real state of the parameters concerning the reproductive cycle in *Caecobarbus geertsii*.

Crater lakes

Worldwide, crater lakes are relatively rare, usually small and specialized freshwater habitats formed in geological depressions. But they are well represented in tropical Africa, especially in the Lower Guinean rainforest zone of Cameroon (figure 21.6), where there may be 36 or more (McGregor Reid & Gibson, 2011). Crater lakes may contain a substantial number of endemic organisms, including fishes. All Cameroonian crater lakes are formed through volcanism and are calderas (deep inverted cones)[3] or maars (shallow cones with a low profile).[4] For example Lake Nyos (see box "Nyos, an extreme example", in the chapter *The diversity of aquatic environments*) is a simple maar lake, but a relatively deep one, whereas Lake Barombi Mbo is formed in a caldera.

NOTE 3

A caldera is a cauldron-like volcanic feature usually formed by the collapse of land following a volcanic eruption. They are sometimes confused with volcanic craters.

NOTE 4

A maar is a broad, low-relief volcanic crater that is caused by a phreatomagmatic (interaction between water and magma) eruption, which is an explosion caused by groundwater coming into contact with hot lava or magma. A maar characteristically fills with water to form a relatively shallow crater lake.

Fish fauna

Fish species from different families had entered lake basins, but that of the family Cichlidae proved to be the most versatile competitors and speciated extensively. The fishes of this family now exploit almost all available resources in these lakes. Among African fishes endemic to craters, small assemblages of species and genera belonging to the Cichlidae have been the most studied. In fact, the craters represent a younger, less complex ecosystem more easily studied than the East African Great Lakes. Such craters provide an opportunity to investigate the stages in ecological colonization from an initially lifeless environment, as well as the processes of population differentiation and speciation. While invariably occupied by invertebrates, not all western African crater lakes contain fishes and shrimp (Schliewen 2005).

Based initially on Lake Victoria results, the general eastern African hypothesis is that cichlid taxa evolved into lacustrine species flocks through a process of allopatric speciation, that is, one involving periodic geographical separation of populations. It was suggested that a regular rise and fall of waters created satellite lakes to isolate cichlid populations, which then differentiated ecologically, morphologically, behaviourally and genetically into distinct species. These isolates supposedly later returned to the main lake during high water levels, but by that time did not interbreed with their congeners.

An alternative model is that species can arise as monophyletic flocks within the lake itself without such total isolation, that is, through a process of sympatric

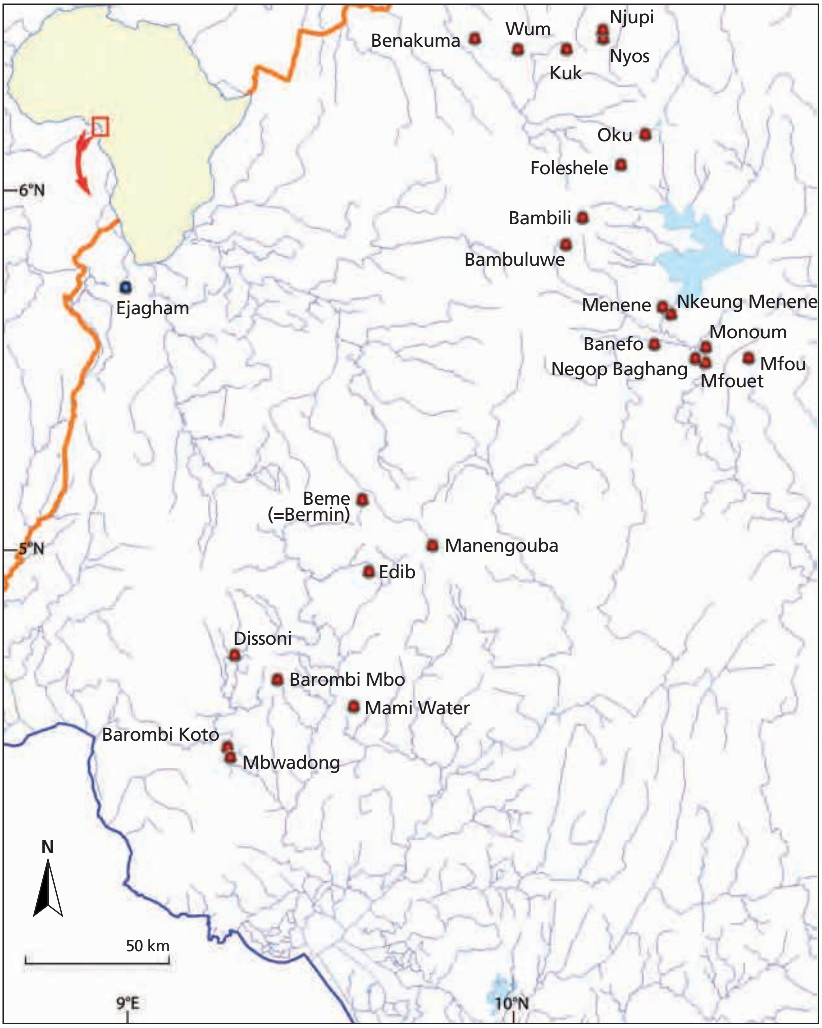

FIGURE 21.6.
Main crater lakes in the Lower Guinean rainforest zone of Cameroon (source: "Faunafri" and "GeoNames"). Lake Ejagham (blue point) is a special case because it is not a volcanic crater lake but it is geomorphologically and ecologically very similar to the other crater lakes.

speciation. Comparisons with a closely related riverine outgroup of cichlids from Lake Ejagham suggest that synapotypic colouration and 'differential ecological adaptations in combination with assortative mating could easily lead to speciation in sympatry' (Schliewen *et al.*, 2001). Comparable empirical research on post-colonization cichlids in a young crater lake in Nicaragua also supports the idea that sympatric endemic '*morphs*' of individual cichlid species may diversify rapidly (say, within a hundred years or generations) in ecology, morphology and genetics and this can be interpreted as 'incipient speciation' (Elmer *et al.*, 2010).

Barombi Mbo is the best known of the high-endemism lakes. The roughly circular lake basin has a diameter of 2.15 km and a maximum depth of 111 m. The area used by fishes is limited to the upper layers of the permanently stratified lake because below 40 m no oxygen is detectable (Schliewen, 2005). At present, fifteen fish species have been found in the lake, twelve of which are endemic, and except for the clariid catfish (*Clarias maclareni*), all endemics are tilapiine cichlid fishes. Four of the five tilapiine genera are endemic: *Konia* (two species), *Stomatepia* (three species), *Pungu* (one species), and *Myaka* (one species) (figure 21.7).

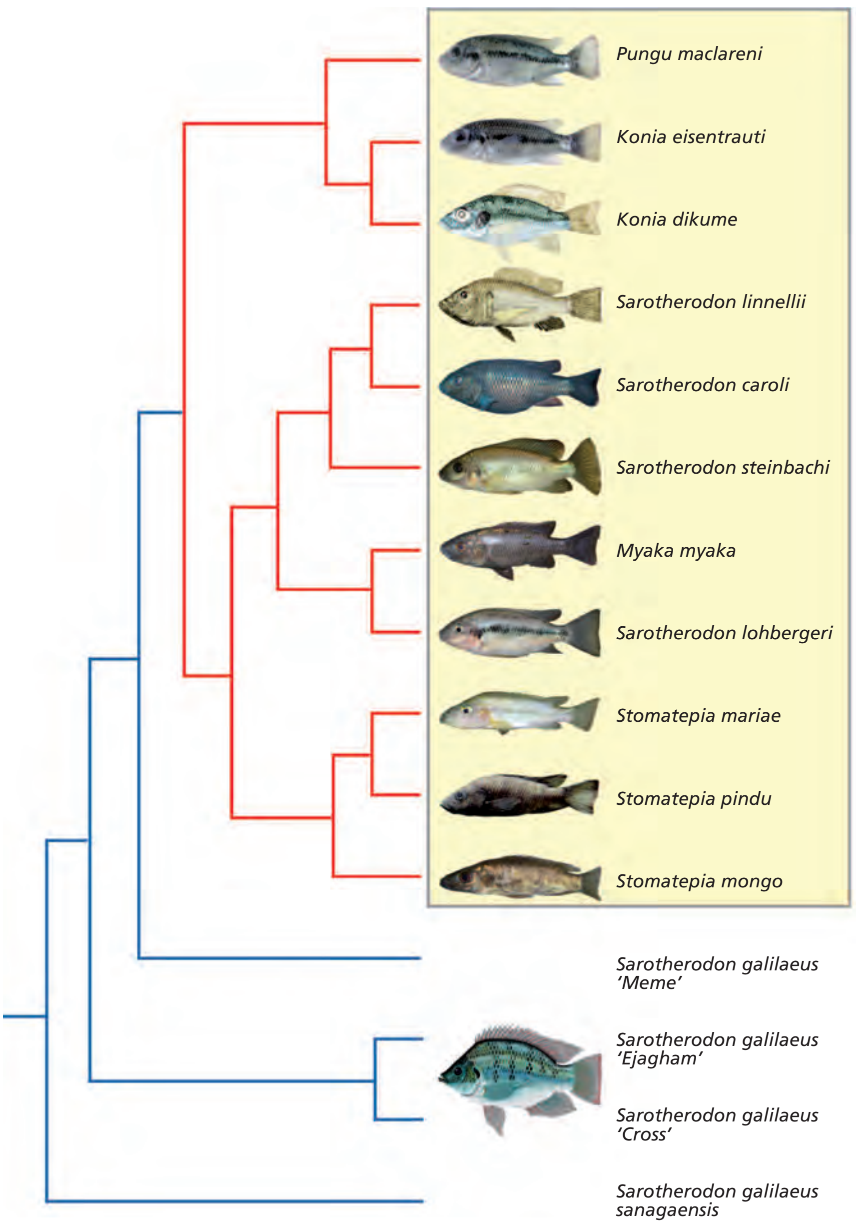

FIGURE 21.7.
Sympatric speciation of cichlids in Lake Barombi Mbo, Cameroon (redrawn from Schliewen *et al.*, 1994).

Some Barombi Mbo cichlids exhibit unique ecological and morphological specializations. For example, *Pungu maclareni* is a sponge-feeder that uses its very strong jaw musculature and specialized teeth to crush sponge spicules (Dominey 1987). Similarly, *Konia dikume* temporarily enters deep waters with extremely low oxygen concentrations to feed on *Chaoborus* larvae. This unique fish can spend short amounts of time in deoxygenated water because a high hemoglobin concentration allows storage of large amounts of oxygen in its blood (Green & Corbet 1973).

Lake Bermin (figure 21.6), with a diameter of only approximately 700 m and a maximum depth of approximately 16 m, is much smaller than Lake Barombi Mbo. It is home to nine endemic cichlid species, which all belong to the tilapiine subgenus *Coptodon*. No exact determination of the crater's age exists, although the degree of erosion of the crater rim suggests an age of much less than a million years (Schliewen, 2005). This finding seems to be corroborated by the lesser degree of morphological specialization in comparison with the Barombi Mbo cichlids. However, several species exhibit striking features. For example *Coptodon spongotroktis* feeds predominantly on the freshwater sponge of Lake Bermin. Another species, *C. snyderae*, is approximately 5.5 cm long, making it the smallest known tilapiine cichlid fish.

Lake Ejagham (figure 21.6) is a special case because it is not a volcanic crater lake but is ecologically and geomorphologically very similar to the other crater lakes. The lake's outlet is isolated from the nearby Munaya River by a waterfall that is insurmountable for cichlid fishes. Its oval-shaped lake basin (approximately 1,050 x 700 m) has a maximum depth of 18 m. In contrast to Barombi Mbo and Bermin lakes, this lake was colonized both by *Coptodon* and *Sarotherodon* tilapias (Schliewen *et al.*, 2001). The *Coptodon* gave rise to four different species (Dunz & Scliewen, 2010), whereas the *Sarotherodon* split into two.

On the basis of the analysis of mitochondrial DNA, these different studies have shown that cichlid species in each of these lakes are monophyletic flocks that have evolved within the body of the lake from a single colonizing species. Given the size and the shape of these lakes, it is unlikely that geographical micro-barriers have facilitated a micro-allopatric speciation. Because the lakes are isolated from nearby river systems, are conical in shape, and geomorphologically homogenous, the results implied that speciation had taken place entirely within the limits of these lakes and therefore in full sympatry. Finally, the authors of these studies suggest that the diversification of trophic behaviour, and resulting ecological behaviour, has been the main factor of this sympatric speciation in each of these lakes.

Several other lakes do not harbour endemic cichlids but support endemic fishes from other groups. For example, Lake Dissoni harbors one endemic poeciliid (*Procatopus lacustris*) and probably one endemic *Barbus* and *Clarias* (Schliewen 2005).

The impact (meteoritic) crater Lake Bosumtwi (Ghana) is dominated by cichlids, while the non-cichlids predominate in the riverine situations. More than 37 streams drain into the lake, but only five of these are permanent and the main

FIGURE 21.8.
Only wooden planks ('*padua*') can be used for fishing in Lake Bosumtwi (© IRD/C. Lévêque).

source of water entering Lake Bosumtwi is rainwater flowing inwards from the crater rim (Whyte, 1975). Unlike the crater lakes of Cameroon, no endemic species and species flock can be found in this lake. Due to its age (± 1.07 million years ago) and the isolation of this lake, it is strange that no endemic species had developed, as observed in Cameroon. Perhaps the geological history and the climate alternation in the region are the main reasons. Locals consider this a sacred lake where souls of the dead come to bid farewell to the god Twi. Due to local beliefs, fishing here is only allowed from wooden planks (*padua*) (figure 21.8) – it is taboo to touch the water with iron.

Conservation

Despite the high levels of endemicity and the unique behaviours of the fish that live in these lakes, conservation efforts to protect the lakes' ecosystems are poor. Such unique lake environments and endemic species are clearly of national and international importance. The small size of the lakes renders them extremely vulnerable to even minor disturbances. In particular, the most diverse and famous lake, Barombi Mbo, is under immediate threat. Partial deforestation of the interior crater rim has already taken place because of increased demand for agricultural land by the local Barombi people and by people from nearby Kumba town. This is likely to cause increased erosion and consequently increased sediment input into the oligotrophic lake system. Water extraction has also temporarily caused lake level alterations, which have changed breeding habitat needs for some of the endemic cichlid species, especially *Sarotherdon linnellii* (Schliewen, 2005). The use of modern gillnets has supposedly decreased populations of target fish species, although all fish species are still present in the lake (Schliewen, 2005). Water pollution from insecticide use in small farms within the crater rim and from increased waste-water inflow from the small Barombi village is also likely to affect the lake's ecosystem. Last but not least, the introduction of exotic fish species most likely would have disastrous results. Although no direct action has been planned, the mere chance that either molluscivorous fish species for bilharzia control or nonindigenous tilapias for increased fishery revenue would be introduced is a serious threat (Schliewen, 2005). These threats to Barombi Mbo also largely apply to the other lakes.

Among conservation recommendations that have been proposed, the following summary can be given (McGregor Reid & Gibson, 2011):

• Red List threat assessments;

• formal designation of lakes as legally and practically protected aquatic nature reserves of national and international importance;

• *ex situ* programmes for the conservation breeding of species at risk, with the prospect of eventual reintroduction in appropriate circumstances.

Despite the persistent threats outlined above, a survey of Lake Barombi Mbo in 2002 found all fish species to still be present (Schliewen 2005). However, many of the species present are threatened (even Critically Endangered *sensu* IUCN), but there have been no recorded fish or invertebrate population declines to the point of extinction in any of the crater lakes. Nevertheless, continued vigilance, conservation monitoring, threat assessment, mitigation and protective measures certainly remain highly appropriate.

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