Fish communities in shallow lakes

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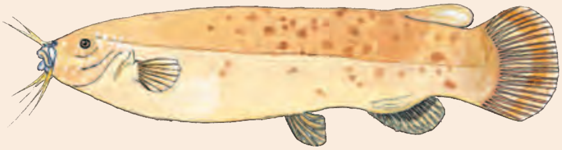


While there is an intuitive understanding of what "shallow lake" means, it is more difficult to provide a precise definition of the term. For our purposes, we could include in this category lakes with a depth not exceeding 10 m and with no permanent stratification of the water column (Lévêque & Quensière, 1988). Shallow lakes are thus lakes in which the coastal area and bankside vegetation play an important role in the function of the system, in contrast to deep lakes where the pelagic zone is particularly well-developed.

Shallow lakes generally occupy depressions in areas with moderate reliefs. Despite their diversity, they all share certain characteristics:

- **There is significant development of grassy zones that can occupy large surfaces.**
- **Macrophytes develop on the shoals and produce a large amount of organic matter;**
- **Fluctuations in the water balance (summation of water inputs and outputs) manifest as large fluctuations in water level and surface, owing to the basin's lack of relief.**
- **The water balance depends greatly on the local climate as well as the climate of the basin feeding the tributaries, and on the shape of the lake basin;**
- **The absence of permanent thermal stratification favours the rapid recycling of nutritive elements as well as the development of benthic fauna that helps increase the productivity of these physical systems.**

Elements for a physicochemical typology of shallow lakes

Different types of shallow lakes can be distinguished based on their hydrological function and physiochemical characteristics.

First, while many lakes are *open,* with one or more superficial outflows that allow the emptying of excessive water inputs, other types of lakes, called *endorheic* lakes, are closed basins with no outflows. These endorheic lakes are areas for the spread and evaporation of water, responding to fluctuations in water inputs by more marked variations in surface. Lake Chad, fed by the Chari, and Lake Ngami, fed by the Okavango, are examples of endorheic lakes in Africa.

We can also distinguish several major types of shallow lakes based on the characteristics of the water balance:

- **pluvial,** dominated by the precipitation-evaporation cycle. Lake Victoria, which receives 83% of its inputs from rainfall and loses the equivalent through evaporation, is a good example. This type is characteristic of many water bodies in semi-arid zones, including in temporary systems such as swamps. These lakes, which depend essentially on rainfall for input, are very sensitive to seasonal and inter-annual variations in rainfall;

- **riverine,** in which inputs and outputs arrive mainly by surface effluents and tributaries. Many shallow lakes are fed thus by floods in the fluvial system, as shown by the lakes of the Central Niger Delta or Lake Chad (83% of inputs from the Chari). Fluctuations in the level of these lakes are generally less pronounced than for lakes whose water input comes from the atmosphere, and fauna that are mostly of fluvial origin can find refuge in watercourses when there is a severe drop in water level.

- **evaporative** lakes for which groundwater inputs are important. These are often endorheic systems that function like evaporation basins. This is the case of Lake Assal (Djibouti), Lake Bogoria (Kenya), and the lakes of the Kanem region (Chad), whose waters contain high salt levels. Fish fauna is poor in this type of system, with a few rare species that have adapted to conditions of extreme salinity.

Endorheic shallow lakes

In an endorheic lake with no surface effluents, all water coming from rivers or precipitation either evaporates or seeps into the groundwater. For several riverine-type endorheic lakes in Africa, including Lakes Chad, Naivasha, Chilwa, and Ngami, water remains fresh. Meanwhile, for other types of evaporative lakes such as Lakes Nakuru, Magadi, and Turkana to a certain extent, waters are salty.

Evaporative type lakes

Only a few species are able to survive in the extreme conditions prevailing in lakes with salinities even higher than that of sea water. The Cichlidae *Alcolapia grahami* is endemic to Lake Magadi where it lives in pools fed by warm and salty water sources (Coe, 1966). Fishes are essentially concentrated in the upper 50 cm where oxygen content is higher.

Alcolapia alcalica lives in Lake Natron whose waters have a salinity between 30 and 40‰ while related species *Oreochromis amphimelas* lives in Lake Manyara where it has been found in waters reaching 58‰ salinity (Trewavas, 1983).

Alcolapia grahami was introduced into Lake Nakuru, where it flourished (Vareschi, 1979). Fishes are not evenly distributed over the entire area of the lake, and a distribution gradient from the banks to open water has been shown, with the smallest fishes concentrated near the former and the largest ones found in the latter. The average number of individuals by m² decreases, from 20 at 50 m from the shore, 18 at 150 m, 9 at 400 m, and 8 at 1,000 m. Meanwhile, biomass goes from 2.5 gm^{-2} (dry weight) at 50 m, to 5.25 at 250-400 m, and 4.2 at 600-1,000 m. In 1972, the average biomass of *Alcolapia grahami* was estimated at 80 kg ha^{-1}, and reached 425 kg ha^{-1} in 1973. In 1976 the average biomass stabilised at 300-400 kg ha^{-1} (Vareschi, 1979).

Riverine type lakes

In these freshwater lakes, the richness of fish fauna mirrors the species richness of the drainage basin and the environmental conditions available to fishes. These may vary over the season or from one year to another.

A familiar case is that of Lake Chad, found in a vast sedimentary basin in the centre of Africa. The lake covered an area of 25,000 km^2 in the 1960s, but in the 1970s, after several years of drought, it only covered 5,000 km^2 in the southern part of the basin directly supplied by the Chari (Carmouze *et al.*, 1983). The ecology of fish populations was studied between 1966 and 1978, including a period of relative stability from 1966 to 1972 and referred to as "normal Chad", and a drought period after 1972 called "small Chad" (Carmouze *et al.*, 1983).

During the "normal Chad" period, species distribution in the lake was strongly influenced by two factors: distance from the riverine system, and the types of aquatic facies (archipelago or open water) (Bénech *et al.*, 1983 ; Bénech & Quensière, 1989). In the southern basin, fauna was more diverse, with three characteristic species captured exclusively in the vicinity of the Chari delta on the lake's east coast: *Ichthyborus besse, Siluranodon auritus* and *Polypterus senegalus*. *Tetraodon lineatus* was also common in this zone, as well as juveniles of *Schilbe uranoscopus* and *Hyperopisus bebe* which were not found in other parts of the lake. In the open water area, *Labeo coubie, Citharinops distichodoides* and *Synodontis clarias* were abundant, as well as large *Synodontis membranaceus*, but no species were present exclusively in this type of environment. On the other hand, several species found in the archipelagic environments were absent from the open waters: *Oreochromis niloticus, O. aureus, Sarotherodon galilaeus, Coptodon zillii*, *Alestes baremoze, A. dentex, Brycinus macrolepidotus*, *Marcusenius cyprinoides, Petrocephalus bane*, *Heterotis niloticus*.

In the northern basin, fauna becomes poorer as one moves farther from the Chari delta. In the northern part, there is an absence of Mormyridae which could be due to the increase in salinity. But *Schilbe uranoscopus* also disappears, and *Hydrocinus brevis* and *Synodontis batensoda* become scarce.

The Sahel drought that began in 1972 triggered a fall in the lake's level and a significant reduction in its area. Environmental conditions underwent profound changes in the drying-out phase (1972-1974 period), with a shift from a lacustrine system to a marshy or swampy system during the so-called "small Chad" period. This change was followed in 1975 by the complete drying out of the northern basin of the lake, which thus shrunk to only the southern basin fed by the floods of the Chari.

This change in hydrology and reduction in lake surface had various consequences and led to serious disturbances in fish communities:

• an increase in the concentration of fishes in a smaller volume, leading to greater interspecies competition and increased vulnerability to fishing gear;

• the lacustrine landscape was overhauled with the lower depth: near-disappearance of vegetation-free open water and development of marshy biotopes encumbered by macrophytes colonizing the shoals;

• owing to the decreased depth, thunderstorms and strong winds stir up waters and sediments more easily, increasing turbidity and decreasing the oxygen content. These water deoxygenation phenomena were responsible for massive fish mortality (Bénech *et al.*, 1976);

• exundation of shoals led to isolation of parts of the lake, obstructing fish movement and the entry of floodwaters.

During the drying-out period, only those species that were adapted to the new ecological conditions prevailing in an increasingly swampy environment were able to survive. The evolution of captures through gillnet fishing in the lake's SE archipelago (table 20.I and figure 20.1) clearly illustrates these changes in terms of species presence.

The lowest level was reached in 1973, and the South-East archipelago was isolated from the rest of the lake in April 1973 as a result of the exposure of the shoals. Several species disappeared from July to September, at the time of the lowest waters, and before the arrival of the flood: *Hydrocynus forskalii, Citharinus citharus, Synodontis membranaceus, Lates niloticus, Alestes dentex* and *Labeo senegalensis*. Storms in June-July, in triggering anoxic conditions by stirring up waters, probably played a role in the disappearance of these species. But the decrease in depth also compromised the free movement of fishes and exchanges between the archipelago and the rest of the lake.

The 1974 flood allowed water to reach near-normal levels in the southern basin. However, before reaching the SE archipelago, this floodwater submerged a

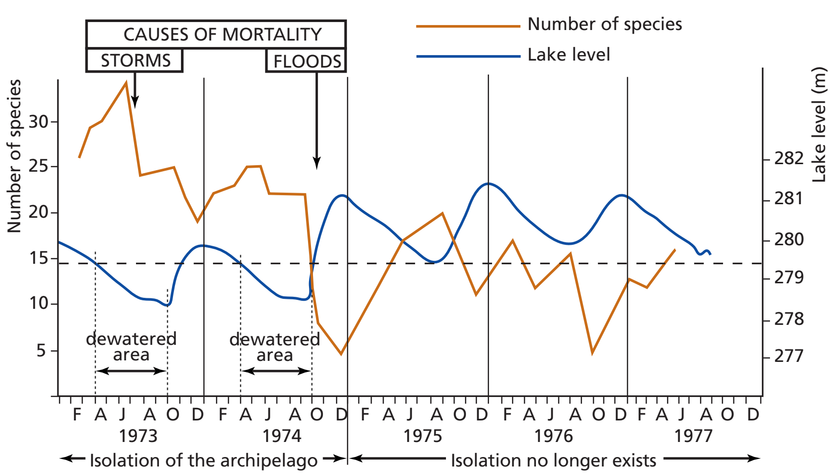


FIGURE 20.1.
Changes in water level and number of fish species caught with experimental gillnets in the South-East archipelago of Lake Chad during the drought period (from Bénech & Quensière, 1989).

TABLE 20.I.

Change in fish species composition in the Lake Chad South-East archipelago during a period of drought (from Bénech & Quensière, 1989).

M: large scale migratory fishes; R: aerial respiration; J-J: January-June; A-D: August-December; J-S: January-September; O-D: October-December.

	Species	1971		1972		1973		1974		1975	1976	1977
		J-J	A-D	J-J	A-D	J-J	A-D	J-S	O-D			
M	*Mormyrus rume*	●	●	●	●	●	●					
	Mormyrops anguilloides	●	●	●	●	●						
	Hippopotamyru ssp.	●	●	●	●	●	●					
	Bagrus bajad	●	●	●	●	●	●					
	Chrysichthys auratus	●	●	●	●	●						
	Labeo coubie	●	●	●		●						
	Brycinus macrolepidotus	●	●	●		●						
M	*Hydrocynus brevis*	●	●	●	●	●						
	Hydrocynus forskalii	●	●	●	●	●	●	●				
M	*Citharinus citharus*	●	●	●	●	●						
M	*Synodontis membranaceus*	●	●	●	●	●	●					
	Lates niloticus	●	●	●	●	●		●				
M	*Hyperopisus bebe*	●	●	●	●	●	●	●				
M	*Marcusenius cyprinoides*	●	●	●	●	●	●	●				
M	*Petrocephalus bane*	●	●	●	●	●	●	●				
M	*Pollimyrus isidori*	●	●	●	●	●	●	●				
M	*Labeo senegalensis*	●	●	●	●	●	●	●				
M	*Schilbe mystus*	●	●	●	●	●	●	●				
	Synodontis clarias	●	●	●	●	●	●	●				
MR	*Polypterus bichir*	●	●	●	●	●	●	●				
R	*Polypterus endlicheri*	●	●	●	●	●	●		●	●		
	Auchenoglanis spp.	●	●	●	●		●	●		●		
M	*Schilbe uranoscopus*	●	●	●	●	●	●	●		●	●	
M	*Synodontis batensoda*	●	●	●	●	●	●	●	●	●	●	
	Synodontis frontosus	●	●	●	●	●	●	●		●	●	
M	*Synodontis schall*	●	●	●	●	●	●	●		●	●	●
M	*Alestes dentex*	●	●	●	●	●	●	●		●	●	●
M	*Alestes baremoze*	●	●	●	●	●	●	●		●	●	●
	Brycinus nurse	●	●	●	●	●	●	●	●	●	●	●
M	*Distichodus rostratus*	●	●	●	●	●	●	●	●	●	●	●
R	*Gymnarchus niloticus*	●	●	●	●	●	●	●	●	●	●	●
R	*Clarias* spp.	●		●	●		●	●	●	●	●	●
	Coptodon zillii	●	●	●	●	●	●	●		●	●	●
	Sarotherodon galilaeus	●	●	●	●	●	●	●		●	●	●
	Oreochromis niloticus	●	●	●	●	●	●	●	●	●	●	●
	Oreochromis aureus		●	●		●	●	●		●	●	●
R	*Polypterus senegalus*			●	●	●	●	●	●	●	●	●
	Schilbe intermedius			●		●	●	●		●	●	●
R	*Heterotis niloticus*	●					●	●		●	●	●
R	*Brevimyrus niger*	●					●	●	●	●	●	●
	Siluranodon auritus						●	●		●	●	●

large quantity of decomposing plants, which led to an oxygen deficit lasting at least 3 months. Most of the common species that had survived up to that time thus disappeared due to the hypoxic conditions: *Labeo senegalensis, Schilbe mystus, Lates niloticus, Polypterus bichir, Synodontis clarias, Marcusenius cyprinoides, Hyperopisus bebe, Petrocephalus bane, Pollimyrus isidori.* The Mochokidae which accounted for 45% of captures a month earlier disappeared in a few days, and the number of species fell sharply in experimental gillnet captures, from 23 in September to 8 in October. In December 1974, only fishes with accessory respiratory organs could be found (table 20.I) such as *Polypterus senegalus, Brevimyrus niger* and *Gymnarchus niloticus*, along with a few individuals from other species with good resistance to hypoxia: *Distichodus rostratus, Oreochromis niloticus, Synodontis batensoda* (Bénech & Lek, 1981).

The persistence of a connection with the southern basin in 1975 allowed recolonization by a few species: *Sarotherodon galilaeus, Oreochromis* spp.*, Schilbe mystus, Siluranodon auritus, Distichodus rostratus*, as well as pelagic species such as *Alestes baremoze* and *Alestes dentex* that rapidly recolonized the archipelago. The fish community during the 1975-1977 period remained stable, despite the disappearance of 3 species that had survived up to that point: *Schilbe uranoscopus, Synodontis batensoda, Synodontis frontosus.* There were fewer than 20 species after 1975, compared with 34 in 1973. The species richness of the SE archipelago shows a seasonal cycle, with a sharp decline at the onset of the flood, followed by an increase until the end of the next water outflow period.

Despite the speed of changes in the environment, the fish community has adapted to the succession of different lake facies, as manifested by the appearance and disappearance of species depending on environmental conditions. The prevalence of hypoxic conditions at certain periods favoured species with respiratory adaptations, and the annual flood, by restoring connections with the southern basin, allowed recolonization by the fluvio-lacustrine stock which more or less acted as a refuge zone.

In the open waters of the southern basin, the connection with the Chari was not interrupted, and after 1974 the system reacquired a lacustrine facies with areas of open water surrounded by thick belts of vegetation.

The northern basin evolved differently. In mid-1973 it was isolated from the Chari's floods owing to the exposure of a shoal area known as "Grand barrière". Only the water brought by the Yobe River, which emptied into the northern portion of the lake, compensated in part for losses by evaporation, but by November 1975 the northern basin of the lake had dried up. The concentration of fishes during this period attracted many fishers, and *Heterotis niloticus, Hydrocynus brevis, Citharinus citharus, Mormyrus rume, Pollimyrus isidori* and *Tetraodon lineatus* progressively disappeared in the second half of 1974. Massive mortalities as a result of storms were also observed (Bénech *et al.*, 1976). The abundance of species such as *Polypterus senegalus* increased in the captures, as did *Sarotherodon galilaeus, Oreochromis aureus* and *O. niloticus*. After 1975, the northern basin was partially flooded each year and a swamp community containing numerous Clariidae colonized this marshy zone.

These fluctuations in the environment and fish communities explain why there are no endemic species in Lake Chad, and all the species present there have also been observed in the Chari. It has even been suggested that Lake Chad is simply an extension of the fluvial system whose species can recolonize the lake after periods of dryness.

Lake Chilwa, southeast of Lake Malawi, is another example of an endorheic lake showing significant fluctuations in area. It is formed primarily by a vast zone of open water surrounded by large marshy areas dominated by *Typha domingensis*. Unlike Lake Chad, Lake Chilwa is only fed by small tributaries, but it has also run into periods of drying out. In 1968 for example, the lake had its lowest recorded level since 1920 and almost completely dried out (Kalk *et al.*, 1979). These variations in level were accompanied by changes in salinity, with high values (16,720 µS) in 1968.

Approximately 30 species are known in the Lake Chilwa basin, but many have only been observed in tributary watercourses. In high water periods, only 3 species constitute the bulk of captures: *Clarias gariepinus, Barbus paludinosus, Oreochromis shiranus*. During the dry season and in periods of low water levels, these species migrate to neighbouring pools where they find waters that are less saline and less turbid. They recolonize the lake when water levels rise. Meanwhile, marshes and tributaries are inhabited by much richer fish fauna that colonize the open waters during floods: *Petrocephalus catostoma, Marcusenius macrolepidotus, Brycinus imberi, Labeo cylindricus, Barbus trimaculatus, Coptodon rendalli, Pseudocrenilabrus philander,* etc. (Kirk, 1967 ; Furse *et al.*, 1979).

Lake Baringo in the Rift valley in Kenya is also endorheic, supplied by two small rivers. Fish fauna is poor, composed essentially of one Cichlidae (*Oreochromis niloticus*), a Clariidae (*Clarias gariepinus*), and two Cyprinidae (*Labeo intermedius* and *L. cylindricus*) (Worthington & Ricardo, 1936).

The fish fauna of Lake Naivasha is almost exclusively composed of introduced species: *Micropterus salmoides* was introduced in 1925, *Oreochromis leucostictus* and *Coptodon zillii* in 1956. *O. leucostictus* preferably inhabits *Papyrus* grass patches, as does *M. salmoides*. Meanwhile *C. zillii* prefers *Nymphea* patches and feeds on macrophytes. The lake's endemic species, *Aplocheilichthys antinorii*, still recorded in 1962, probably disappeared as the result of predation by *Micropterus* (Elder *et al.,* 1971).

Lake Turkana is currently an endorheic lake supplied by the Omo River, whose slightly saline waters have a conductivity of up to 3500 µS (Kolding, 1992). Strictly speaking, it is not a shallow lake, but its average depth is low for most of its area and the lake is not stratified. In the past it was connected to the Nile basin which explains why most of its fish fauna tends to the nilotic.

Of 48 fish species known in the basin, 36 are regularly found in the lake and 12 have a distribution limited to the Omo River delta (Hopson, 1982 ; Lévêque *et al.*, 1991). Some species, such as *Lates niloticus, Synodontis schall, Barbus bynni bynni, Neobola stellae* have a rather wide distribution, but most of the others are limited to specific habitats. Three types of communities have been identified in the lake itself:

• the *coastal community*, limited to a belt covering the edge of the lake and a depth of 4 m. This community contains especially *Oreochromis niloticus* and *Clarias gariepinus,* as well as *Coptodon zillii* and *Raiamas senegalensis* in the rocky bottoms or *Sarotherodon galilaeus*, *Brycinus nurse*, *Micralestes acutidens* and *Chelaethiops bibie* in the mobile bottoms;

• the *demersal community*, comprising benthic species living near the banks between depths of 4 to 10-15 m. The characteristic species are *Labeo horie*, *Citharinus citharus*, *Distichodus niloticus* and *Bagrus docmak*. In deeper zones, the species are *Bagrus bajad*, *Enteromius turkanae*, and *Haplochromis macconneli* which live close to the bottom;

• the *pelagic community*, which includes species such as *Hydrocynus forskalii* and *Alestes baremoze* that are more numerous in the upper layers, and *Brycinus minutus*, *B. ferox*, *Lates longispinis,* and *Schilbe uranoscopus* in open waters.

A large proportion of species carry out seasonal migrations in the Omo River to breed. Among the species breeding in the lake, some have demersal eggs (*Bagrus* spp.), or pelagic eggs (*Lates* spp. and *Brycinus* spp.), while other species provide parental care (*Oreochromis, Sarotherodon, Haplochromis, Tilapia, Heterotis*).

Experimental fishing carried out in 1986-1987 were compared with results obtained during campaigns done in 1972-1975 (Bayley, 1977; Hopson, 1982). There were no significant changes for demersal communities, while for pelagic communities, the populations of *Hydrocynus forskalii, Alestes baremoze* and *Schilbe uranoscopus* declined by about 70% compared with the 1972-75 results (Kolding, 1992). It appears that the pelagic community, whose production is based on the use of zooplankton, was most sensitive to the drop in the lake's levels over a decade or so.

Open shallow lakes

In open lakes, there is a permanent or seasonal connection with a river. These lakes are periodically recolonized by fluvial species, so species richness is generally rather high.

Lake George (Uganda), which has an average depth of 2.4 m, has been the target of numerous limnological investigations. Most of its waters come from the Rwenzori and it has an effluent, the Kazinga River, which empties into Lake Edward (Viner & Smith, 1973). This in turn is connected to Lake Albert via the Semliki River. Lake George's watershed was isolated from Lake Victoria's owing to tectonic movements.

Lake George in its current form is relatively young, at around 4,000 years. Its formation took place after a period of volcanic activity that occurred some 8 to 10,000 years ago and which proved fatal to many species living in Lake Edward (Beadle, 1981). The presence of waterfalls and rapids that were difficult to navigate apparently prevented reinvasion from Lake Albert, and current fauna originated from the fauna of the lake's small tributary rivers as well as the fish fauna of Lake Edward itself.

Two fish groups were identified based on their distribution in the lake (Gwahaba, 1975). The first group includes species captured near the banks and in the open: *Protopterus aethiopicus, Haplochromis nigripinnis, H. pappenheimi, H. angustifrons, Lacustricola vitschumbaensis.* For some species such as *Bagrus docmak, Clarias gariepinus, Haplochromis squamipinnis, Oreochromis niloticus* and *O. leucostictus*, a gradient of diminishing abundance from the banks to the open was observed. In fact, the abundance of juvenile forms near the banks may account for this gradient.

The second group includes 15 species captured only near the banks: *Astatoreochromis alluaudi, Enteromius kerstenii, E. neglectus, Ctenopoma muriei, Marcusenius nigricans* and several *Haplochromis* species. This type of distribution may be due to food requirements. *Haplochromis aeneocolor* feeds mainly on macrophyte debris and *Haplochromis limax*, which feeds on periphyton, remains close to emerging vegetation such as *Vossia cuspidata*. *Haplochromis mylodon* consumes the gastropod *Melanoides tuberculata*, *H. taurinus* feeds on eggs and embryos, and *H. petronius* feeds in the coastal rocky substrate.

TABLE 20.II.
Fish species composition in some shallow lakes from Tropical Africa.

Lakes	species number	Mormyridae	Alestidae	Cyprinidae	Clariidae	Mochokidae	Cyprinodontiformes	Cichlidae	Schilbeidae	Polypteridae	*Lates*	Citharinidae	Bagridaeidae/Claroteidae	others	Source
Salt lakes															
Magadi	**1**							1							Coe, 1969
Nakuru	**1**							1							Coe, 1969
Natron	**1**							1							Coe, 1969
Endorheic lakes															
Chad	**137**	16	12	27	5	14	7	11	6	3	1	15	7		Blache *et al.*, 1964
Ngami	**48**	5	3	10	2	4	3	15	1			2	1	2	Skelton *et al.*, 1985
Chilwa	**31**	3	2	12	2	1		5					1	5	Furse *et al.*, 1979
Turkana	**49**	3	9	2	2	3	7	7	1	2	2	2	4	5	Hopson, 1982
Baringo	**4**			2	1			1							Worthington & Ricardo,1936
Open lakes															
Awasa	**3**			1	1			1							Gasse, 1987
Ziway	**8**			7				1							Gasse, 1987
Abaya	**28**	3	1	13	2	4		2	1		1		1		Gasse, 1987
Tana	**20**			16	3			1							Gasse, 1987
Mweru	**114**	16	10	32	11	9		16	3			3	3		De Kimpe, 1964
Albert	**41**	3	6	8	2	2		6	2		2	3	3	4	Hulot, 1956
Ihema	**34**	7	3	8	2	1	1	10	1					1	Plisnier *et al.*,1988
George	**30**	2		3	1			21					1	4	Gwahaba, 1975
Tumba	**86**	23	16	4	11	3	5	9	3	3	1	14	9	?	Matthes, 1964
Liambezi	**43**	3	3	10	3	4	2	15	1					2	van der Waal, 1980

Three species, *Oreochromis niloticus, Haplochromis nigripinnis* and *Haplochromis angustifrons*, make up nearly 80% of the fish biomass (Gwahaba, 1975). The first two (60% of biomass) are herbivorous and consume cyanobacteria. There is a marked gradient in the distribution of biomass which goes as high as 900 kg ha^{-1} near the banks and only 60 kg ha^{-1} in the centre of the lake, with the average for the entire lake at 290 kg ha^{-1}.

Several lakes of the Ethiopian Rift Valley (Galla lakes) are shallow lakes with a relatively poor fish community (Riedel, 1962). In Lake Ziway only a few species of Cyprinidae and one Cichlidae (*Oreochromis niloticus*) can be found. Lake Abijatta and Lake Awasa, located south, are just as species-poor, whereas in Lakes Abaya and Shamo, even further south, species diversity is greater. There are 28 species belonging to different families in Lake Awasa (table 20.II).

Ethiopian lake fauna is impoverished Nilotic fauna. During the wet periods of the quaternary, Lakes Ziway and Abyata, as well as the deeper Lakes Langano and Shala, formed a single lake, Ziway-Shala, which emptied northwards in the Awash River and towards Lake Abbe in Afar.

Lake Tumba is located in the central region of the Congo basin. It has a permanent connection with the Congo River through the Irebu channel in the north. Its fishes were investigated by Matthes (1964). The fauna is diverse (120 species), because of the permanent connections with the river, but also due to the diversity of biotopes found in the lake's banks. In open water, schools – sometimes large ones – of planktivorous fishes (*Barbus, Clupeopetersius, Microthrissa*) as well as predators such as *Odaxothrissa losera, Mormyrops anguilloides, Hydrocynus*, etc. can be found. A group of fin-eating predators (*Belanophago, Phago, Eugnathichthys*) is especially well-represented in Lake Tumba.

The hydrology of Lake Liambezi (Namibia) is complex. It receives water from different sources including the Zambezi which sometimes empties southward (Seaman *et al.*, 1978). The lake's tributary to the Chobe River is intermittent and depends on the lake's level. Depth is less than 5 m and practically constant throughout the extent of the open waters (100 km^2) which are surrounded by a vast marshy zone (200 km^2). About 43 species, including 15 Cichlidae, were captured in the lake itself, and all are also present in the Upper Zambezi where 73 fish species were identified (van der Waal & Skelton, 1984). In the Chobe River and its floodplains, 56 species are known and are also present in the Zambezi. Most of the fishes observed in the lake and marshes are palustrine species, and some of these are highly tolerant to anoxia and can survive in environments that are completely convered by *Salvinia molesta,* an introduced floating plant.

Conclusions

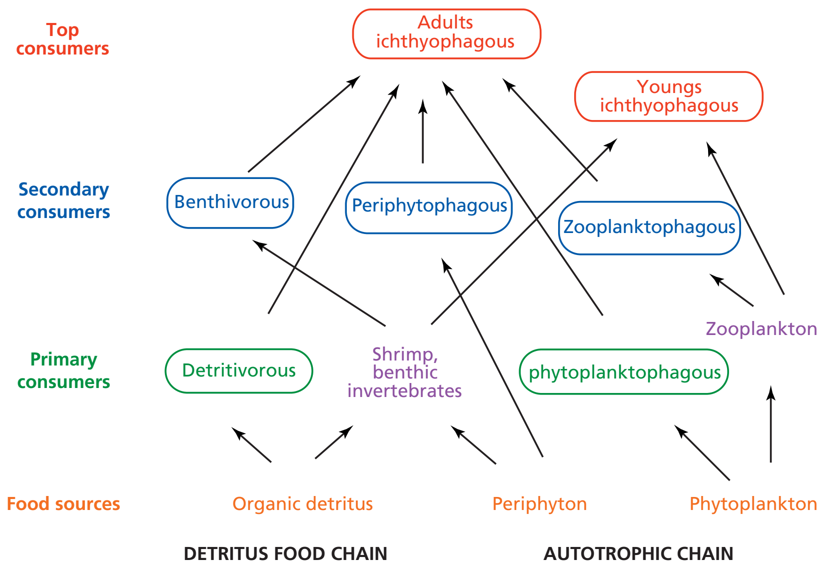
Saltwater lakes fed by groundwater have very poor communities, formed essentially by one Cichlidae species adapted to these extreme East African environments. Many of these salt lakes do not host a single fish species, as can be seen in the many salt lakes of the Kanem region north of Lake Chad.

The fish population of shallow freshwater lakes is highly dependent on that found in the rivers with which the lakes are associated. The biogeographic situation, the area of the drainage basin (see chapter *Biogeography and past history of the ichthyological faunas*) and the basin's climate and geological history (see chapter *Geographical distribution and affinities of African freshwater fishes*) determine the possibilities for lake population. In general, there is a low rate of endemism. Despite its high number of species, Lake Chad does not have a single endemic species. Lake George is an exception, with 16 endemic *Haplochromis* species, that is about half of all species found in it.

Because of their depth, shallow lakes are subject to significant variations in area depending on fluctuations in water supply, which are in turn dependent on climate variations. During periods of water deficit, these fluctuations select species adapted to palustrine conditions that are able to tolerate poor water oxygenation and more or less prolonged periods of anoxia (see chapter *Diversity of responses to extreme environmental conditions*). Meanwhile, during periods with a good supply of water, the area expands, depth increases, and a pelagic system may be established. The latter may nonetheless be strongly influenced by the coastal area and the benthic system, whether in terms of food supply or biogeochemical interactions. Because of the shallowness, significant disturbances can nonetheless occur, such as those triggered by tornadoes which bring sediment particles in suspension in the water, and even lead to massive fish mortalities (see chapter *Diversity of fish habitats*).

Shallow lakes such as Lakes Chad, Chilwa, or Ngami are highly dependent on water supply, which makes them particularly vulnerable to the impact of human activity. In particular, water collection from their tributaries disturbs the water balance, and at present, the water surface of these lakes tends to be going down.

FIGURE 20.2.
Simplified representation of the main components of a food web in a shallow lake with a high specific richness.



The fact that these shallow lakes can more or less be considered vast coastal zones is a factor that favours high productivity in these environments, where fishing is generally active (see chapter *Fisheries*). In species-rich lakes such as Lake Chad or Lake Mweru, trophic networks are organized around two chains: the detritus food chain and the autotrophic chain (figure 20.2). This results in a very complex network of interactions between fish species, given that juveniles of some species compete with adults of other species for the same trophic resources. In reality, though, many species have opportunistic regimes and are probably capable of adapting to available trophic resources.

We must remember that shallow lakes are not closed systems but have important exchanges with the terrestrial environment surrounding them. There are thus many live or dead organisms that fall into the lakes, as well as detritus of terrestrial origin. Stomachs of *Schilbe mystus* captured in open waters, tens of kilometres from the banks of Lake Chad, have been found to be full of orthopteran insects (Lauzanne, 1976). Meanwhile, vertebrates such as birds (see chapter *Role of fish in ecosystem functioning*) and some mammals can take out significant numbers of fishes from the aquatic environment.

Exchanges also take place during migrations of certain fish species in the tributaries. These are often breeding migrations (see chapter *Life-history strategies*) or trophic migrations, but the latter are still poorly documented.

Scientific editors

Didier Paugy Christian Lévêque Olga Otero

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