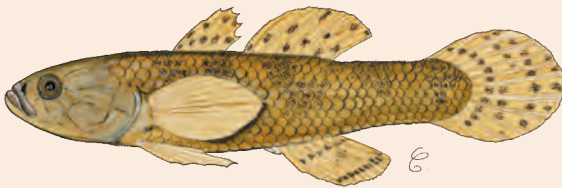


Fish communities in East African rift lakes



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The Great Lakes of East Africa are unique systems in various ways. The region has been subject to much tectonic activity. Hence, some of the deepest lakes of the world can be found in the area, most of them stretched in a north-south direction in the western branch of the Rift Valley (figure 19.1). The elongated and deep lakes Tanganyika and Malawi, together with the saucer-shaped, relatively shallow Lake Victoria form the three largest freshwater bodies in the region. All three figure amongst the top ten largest lakes in the world in terms of surface and volume. Other large lakes in the region include Kivu, Edward (with George), Albert, Turkana, Mweru and Rukwa.

However, what really makes these lakes unique is their biodiversity and especially their fishes. Nowhere else in the world can one find a larger number of fish species than in these lakes. Not only is the sheer number of species exceptional, but most of these fishes are also endemic to a certain lake. Remarkably, the largest compound of the fish fauna, over 95% for the three large lakes, belongs to only one family, the Cichlidae. These cichlids represent the largest radiation of vertebrates in the world. Hence these lakes are considered natural laboratories for the study of evolution and speciation.

While the fishes in these lakes represent an unparalleled biodiversity treasure, one should not forget that they are of prime importance as the largest source of animal protein for the riparian human population (Snoeks, 2001). It is clear that the exploitation and the conservation of these fishes give rise to conflicts. Increasing human activities in the region undeniably have a direct (fisheries) or indirect impact on the lake's fish communities. This is likely to increase and the sustainable management of the ecosystems of the large African lakes will become a huge challenge. In this respect, one should also not forget that most of these lakes have relatively long to very long flushing times, which makes them highly vulnerable to pollution.

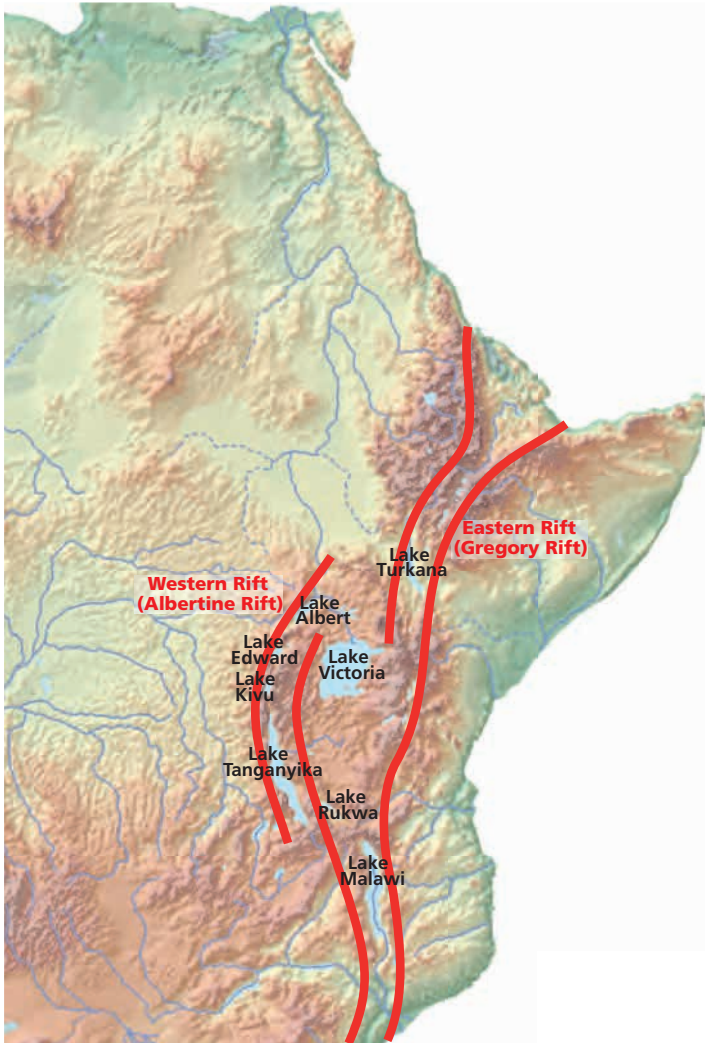


FIGURE 19.1.

Major lakes of the East African Rift system.

What determines the overall structure of the fish communities in these lakes is principally depth and substrate type. Depth distribution of fishes is limited by the oxycline. Therefore in the deeper lakes (Tanganyika, Malawi, Kivu), fish only occupy a small part of the lake's volume, *i.e.*, the upper oxygenated layer, the depth of which differs from lake to lake. In lakes Tanganyika and Malawi, the fish composition clearly changes with depth and both lakes harbour a typical deep-water benthic fish fauna. Pelagic species can effect daily vertical migrations in search of food.

Substrate type determines largely the horizontal component of the differences in fish community structure. Indeed, in most lakes, fish communities differ largely between muddy, sandy, rocky and intermediary habitats.

One of the most, if not the most important extrinsic factor in the evolutionary history of the endemic cichlids, is lake level change. During their history the lakes faced many periods of aridity resulting in a dramatic decrease in lake level volume, followed by an increase during wetter periods in which large stretches of new shorelines became available to invade. Small-sized lake level changes resulting in a split or admixis of populations could act as species pumps (Rossiter, 1995).

Many cichlid species are intrinsically linked to a particular habitat and are called stenotopes; others occur in various habitats and are eurytopes. Fish preferring rocky habitats are called lithophylic; those typical for sandy habitats psammophylic.

Other important aspects determining the fish community structure in the great lakes are migrations, either for reproduction or for food.

Communities in Lake Tanganyika.

Lake Tanganyika is the third largest lake in the world in volume, and the second in length and depth (Cohen *et al.*, 1993b). While its age is often set at between 9-12 million years (Cohen *et al.*, 1993b), other sources place the origin of the lake in its present form at 5.5 million years ago (Weiss *et al.*, 2015), still making it the oldest of the East African rift valley lakes.

Lake Tanganyika harbours the most phylogenetically diverse and ancient flock of endemic cichlids and has been regarded as an evolutionary reservoir for the endemic species flocks in the other lakes in the region (Nishida, 1991). It currently harbours some 219 cichlid species (Konings, 2015) and several tens are still to be described. It is not the species-richest lake in the region, but certainly the most diverse in terms of phylogeny, ethology, morphology, etc.

Lake Tanganyika is also special in having endemic assemblages of non-cichlid taxa, including radiations of *Synodontis*, *Mastacembelus*, Claroteinae and *Luciolates*. There are several endemic species in other groups as well. This non-cichlid endemism is linked to the ancient origin of the lake. The number of non-cichlid species for the Tanganyika basin exceeds 150, and new species are still being discovered (Banyankimbona *et al.*, 2012).

Much of our current knowledge on Lake Tanganyika fish communities is based upon the results of the 18-month Belgian Expedition in 1946-1947, which were written down by Max Poll in two classical monumental books on the non-cichlids and the cichlids (Poll, 1953 and 1956). Much of what we know since then about the cichlid fish communities is based on the observations of two pioneering aquarists and naturalists who summarised their knowledge in various books (e.g. Brichard, 1978 and 1989; Konings, 1988 and 2015). For many years, Japanese scientists have studied the ecology and ethology of the Tanganyika cichlids (summarised in Kawanabe *et al.*, 1997). Observations on the various ecosystems and fisheries were discussed in Coulter's classic book (1991).

In comparison to the other East African lakes, the fauna of Lake Tanganyika is unique in several aspects:

- the existence of various endemic radiations in non-cichlids (see above);
- the existence of a pelagic community comprised of two Clupeid endemics and their predators;
- the existence of a radiation of substrate-spawning cichlids (other than tilapias), the Lamprologini;
- the absence of *Chaoborus* larvae (lake flies, also absent in lakes Kivu and Turkana), which in the other lakes form an important part of the food chain.

Fish in Lake Tanganyika belong to four large communities: those inhabiting the rivers, the littoral and sublittoral, the benthic and bathypelagic, and the pelagic zone.

It is interesting to see that the occupation of the main habitats is somehow linked to the cichlids' phylogeny (Meyer *et al.*, 2015). Basal tribes such as the Bathybatini, Trematocarini, together with Cyprichromini, Cyphotilapiini and Limnochromini generally frequent the open-water column or deep water habitats, while the species-rich tribes of the so-called H-lineage (Eretmodini, Ectodini and Haplochromini), together with the major part of the Lamprologini occupy the coastal areas.

The pelagic community

The pelagic community is mainly composed of six endemic non-cichlid species. Two clupeid species, *Stolothrissa tanganicae* and *Limnothrissa miodon*, live in large schools feeding on phyto- and zooplankton (figure 19.2). Though belonging to different genera, they are sister taxa (Wilson *et al.*, 2008). They constitute a key element of the pelagic food chain as important food sources for piscivorous fish, notable the four *Lates* predators of the endemic subgenus *Luciolates*. These predator-prey relationships are a crucial element in the sustainability of the industrialized fisheries in the basin.

These clupeids, in their juvenile stages, have a more littoral lifestyle. As adults, *S. tanganicae* is the more specialized to a pelagic life of the two (Coulter, 1991). The larger-sized *Limnothrissa miodon* has a more generalized diet and preys upon *S. tanganicae*. Also young individuals of three of the *Lates* predators, *Lates mariae*, *L. angustifrons* and *L. microlepis*, live merely in littoral, weedy habitats. The former two have a mixed benthic-pelagic life, preying upon the sardines during daytime, while the latter remains in the pelagic zone as an adult. *Lates stappersii*, in contrast, spends its entire life in the pelagic habitat.

The predator-prey relationship between *Lates stappersii* and *S. tanganicae* traditionally have been regarded as crucial in explaining fluctuating patterns of the distribution of both taxa within the lake. However, planktonic abundance and physico-chemical parameters may be important drivers as well (Plisnier *et al.*, 2009).

While various other taxa occasionally venture into the pelagic zone, one other species, a small Cyprinid (*Chelaethiops minutus*), with a maximum standard length of slightly over 10 cm also occurs in this zone. While the young live in

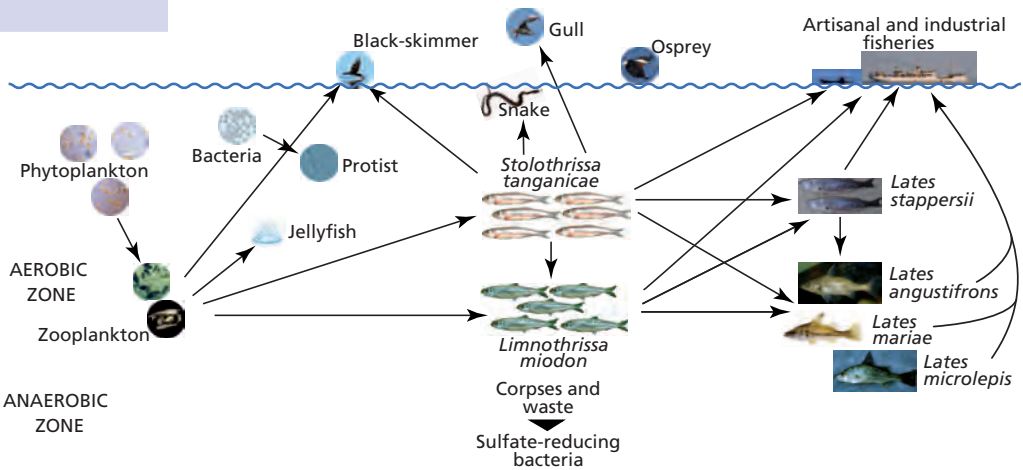


FIGURE 19.2.

Simplified trophic network of the pelagic community of Lake Tanganyika, illustrating the main types of food preferences.

the littoral, adults migrate towards the open water, but do not form schools, as the sardines do (Coulter, 1991). Interestingly, in all three large lakes, an endemic pelagic Cyprinid species occurs. While in lakes Victoria and Malawi these belong each to an endemic, monospecific genus, in Lake Tanganyika, the species belongs to a more widespread genus.

The littoral and sub-littoral communities

Generally, the littoral and sub-littoral communities are those living in the coastal stretch to a depth of about 40 m (Coulter, 1991). These communities are very species-rich with complex interactions and are dominated by cichlids. The major part of the littoral zone consists of rocky areas, often on a steep slope that reflects the sharp terrestrial gradient. These areas are interrupted by sandy or pebble-stone beaches, or muddy areas often associated with the mouth of affluent rivers. These disconnections can form ecological barriers for various stenotopic, lithophylic cichlid species. Many of these lithophylic species have narrow ranges of depth and substrate preferences (figure 19.3).

In the littoral and sublittoral environment plentiful species of other fish families occur. While some of them are clearly linked to the lake environment, for others it is difficult to assess whether they are merely riverine, occasionally frequenting the lake.

The largest catfish family are the Claroteidae with 16 species ranging from relatively small species within the endemic genera *Lophiobagrus* and *Phyllonemus* to the large non-endemic *Auchenoglanis occidentalis* of over 85 cm TL. The latter species is involved in a uncommon case of alloparental care; it can act as a host parent for the eggs and young of *Dinotopterus cunningtoni*, an endemic Clariid catfish. The brood of the latter species benefits from the parental care of the host species, but larger young are also observed to feed on the host brood (Ochi *et al.*, 2001).

Most of the claroteid catfish in the lake are rock dwellers (Hardman, 2008). Though they are quite diverse in shape, they form a monophyletic flock, except for *Chrysichthys brachynema* (Peart *et al.*, 2014). This species is also a Lake

Tanganyika endemic, differing however clearly in morphology from the other larger endemic *Chrysichthys* clade (Risch, 1986). While various species have a lake-wide distribution, some are restricted to the northern part of the lake while others to the southern part (Hardman, 2008). Circum-lacustrine species appear to be living in shallow waters, whilst restricted species are found in deeper waters, perhaps reflecting a more specialized life history. As such, it is difficult to assess whether their distribution is restricted due to habitat availability, or whether the pattern observed is the result of a sampling artefact.

Mochokidae is the second largest catfish family, with 13 species of *Synodontis*, all of which except one, *i.e.*, *S. victoriae*, are endemic. However, the latter does not occur in the lake itself. While one would expect this lineage to have a Congo basin ancestry, the affinities of this flock are with Eastern African lineages within a larger Eastern African/Congo/Southern African clade (Pinton *et al.*, 2013; Day *et al.*, 2013) and genetically distant from the main Congo clade. Worth mentioning is the cuckoo behaviour of *S. multipunctatus*. During reproduction, a couple of these catfish disturb the mating cycle of certain mouthbrooding cichlids and lay their eggs on the mating spot of the cichlids. When these come back to continue mating, the cichlid female will take up the catfish eggs in the mouth as she does with her own eggs and guard them in her mouth. The catfish young develop more quickly than the cichlids and will feed upon the cichlid fry inside the female's mouth. At the end of the brooding cycle, the female cichlid will release the catfish young from her mouth and even then will still take care of the cuckoo young for several days.

Most Mastacembelidae or spiny eels live in rocky habitats, where the larger species such as *Mastacembelus moorii* are important predators. Smaller species can be caught on sandy habitats as well. Most species are nocturnal, while some are active during the day (Ochi *et al.*, 1999). Some species may be obligate egg feeders following a lunar cycle (Ochi *et al.*, 1999). Two species, *M. micropectus* and *M. apectoralis*, are special in respectively their reduction and loss of the pectoral fins, probably as an adaptation to the highly complex rocky habitat they live in (Brown *et al.*, 2011).

A parallel with the genus *Synodontis* appears in *Mastacembelus*. Fifteen species of this genus occur in the basin, all endemic, except *M. frenatus*, which does not occur in the lake itself. This species again is shared with the Lake Victoria basin, but in contrast to *S. victoriae*, has a much wider distribution (Van Steenberge *et al.*, 2014). Also in this case, the Tanganyika clade (not including *M. frenatus*) is part of a larger Eastern African/Congo/Southern African clade (Brown *et al.*, 2010). However, in this study the number of Congo basin species was very limited and interestingly the sister group of the Tanganyika clade was an undescribed species from an affluent of Lake Mweru (upper Congo).

The seemingly most abundant non-cichlid in the littoral is the endemic Tanganyika poeciliid *Lamprichthys tanganicanus*, which occurs over every rocky shore area in large numbers, but occasionally also ventures in more pelagic waters (Brichard, 1989). This species has been introduced in Lake Kivu, where it showed up in commercial catches from 2006 onwards (Muderhwa & Matabaro, 2010).

Within the Cichlidae, the lamprologines are most abundant in terms of species (± 80 described species) and individuals in the littoral and sub-littoral habitats. These are substrate brooders that are more dominant in rocky habitats than on sand; they lack a clear sexual dimorphism in colour pattern, as is known for most of the mouthbrooding cichlid lineages. Lamprologines form a very diverse clade in terms of shape, ecology and behaviour. While most form pairs, others form harems. In at least eight species, lunar synchronization of spawning was observed, the adaptive significance of which still has to be assessed (Nakai *et al.*, 1990). In several species cooperative breeding has developed (Taborsky, 1984; Heg & Bachar, 2007). A unique component of the lamprologine benthic community are the shell-breeding cichlids. Large shell beds occur on gentle slopes between 10 and 35 m, often at the lower limits of the rocky habitat. At least 9 species are obligate shell brooders (Yanagisawa *et al.*, 1997), most of which are small. However in some species such as *Neolamprologus callipterus*, there is a strong sexual size dimorphism. Females are much smaller than regular males, which cannot enter the shells; however, much smaller, parasitic males can sneak fertilization at the entrance of or inside the shell (Sato *et al.*, 2004).

The periphyton is an important food source in the rocky habitat. Though species of many other tribes feed on the algae or the organisms associated (together known as "aufwuchs"), it is within the tribe of the Tropheini that we find most specialists feeding on the rocks. A commensalistic behaviour exists even between *Petrochromis polyodon* and *Tropheus sp.* 'black' (mentioned as *Tropheus moorii*), with the latter clearly preferring patches of algae that first had been combed by *P. polyodon* (Takamura, 1997).

Fishes from the littoral communities are not only preyed upon by other fishes, but also by other vertebrates; these include crocodiles, several bird species such as cormorants, otters and also the aquatic cobra, *Naja (Boulengerina) annulata*, a species with a venom deadly to humans. It is often encountered while diving or snorkelling in the lake; fortunately, it is not aggressive under water.

Densities of species and individuals are very high in the rocky habitat. Censuses of quadrats of 20 x 20 m in various parts of the lake, revealed 2,600 to 6,600 individuals belonging to more than 40 species (Hori, 1997). Long-term monitoring and removal experiments demonstrated that the littoral communities are very stable. Such densities obviously are accompanied by a large number of intraspecific and interspecific interactions, associated with commensalism and exploitative mutualism that are assumed to increase species richness (Hori, 1997).

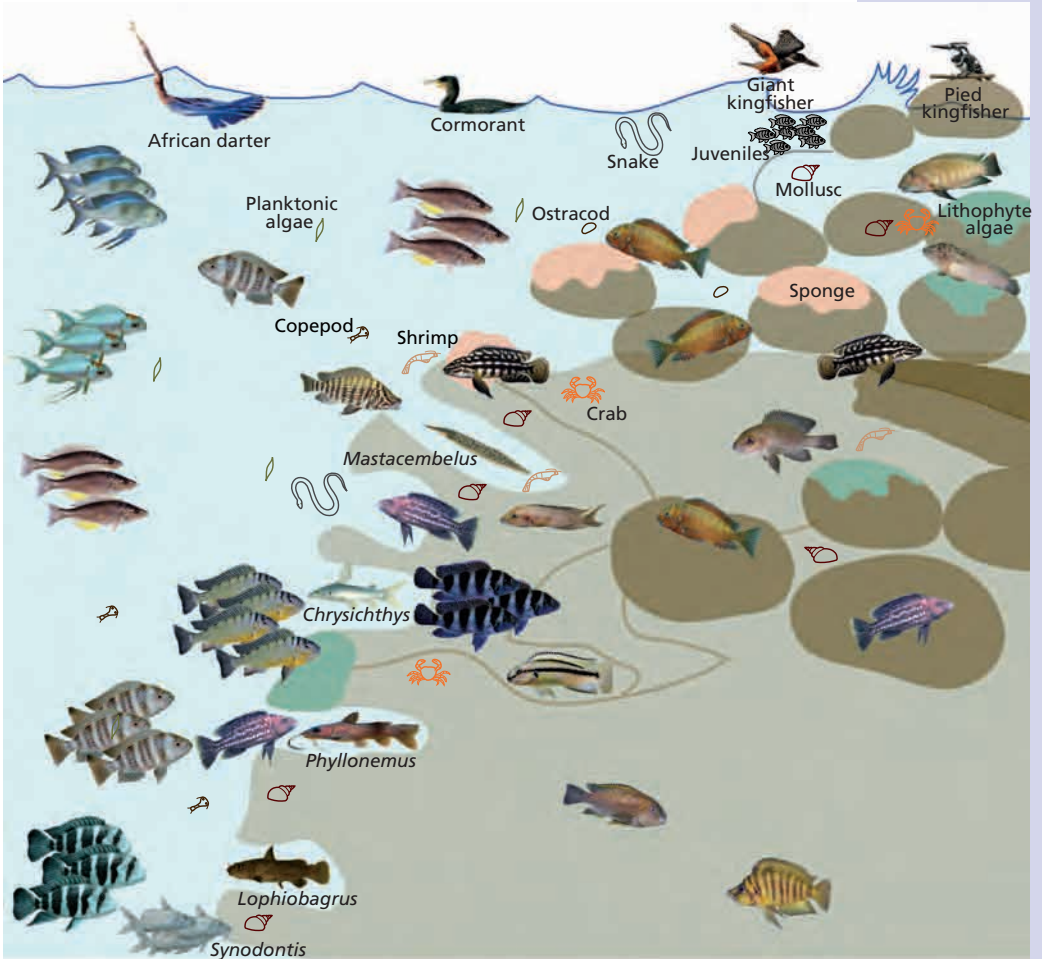
One tribe of cichlids is typical for the surge zone where they eat algae and small invertebrates: the Eretmodini or goby cichlids.

The communities of the sandy and marshy habitats are less diverse and but also less well known. They are however more under threat because of the increasing pressure of beach seining, even with mosquito nets.

This is the domain of various Ectodini taxa, such as *Callochromis*, *Xenotilapia*, *Cardiopharynx*, *Lestradea*, *Ectodus* and *Grammatotria* and a few Lamprologini

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Altamprologus compressiceps



Lepidilamprologus elongatus



Neolamprologus furcifer



Neolamprologus toae



Neolamprologus tetrocephalus



Julidochromis marlieri



Cyatopharynx furcifer



Ophthalmotilapia sp.



Cyprichromis sp.



Cyphotilapia frontosa



Loboichilotes labiatus



Plecodus sp.



Petrochromis sp.



Spathodus sp.



Limnotilapia sp.



Eretmodus cyanotictus



Telmatochromis sp.



Tropheus moorii

FIGURE 19.3.

Schematic presentation of the occupation of the rocky habitat in Lake Tanganyika by various fish species.

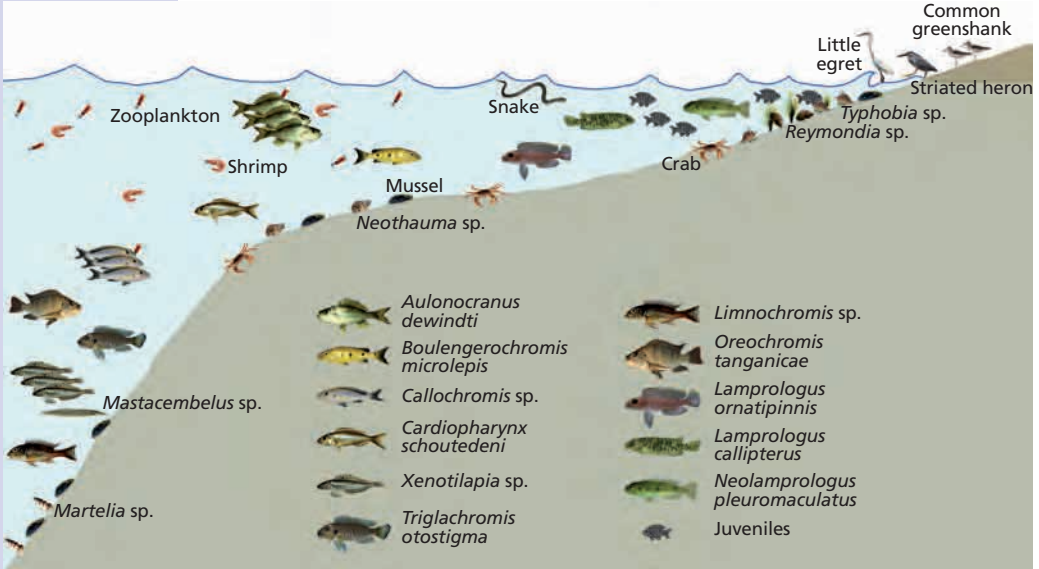


FIGURE 19.4.

Schematic presentation of the occupation of the soft bottom littoral habitat in Lake Tanganyika by various fish species.

(Konings, 2015), but also of *Boulengerochromis microlepis* (figure 19.4). This fish is supposed to be the largest cichlid on earth and has a high economic importance. The intermediate zone or the areas closer to the rocky habitat are frequented by various other cichlids and non-cichlids. In these areas one can find substrate brooding couples of *B. microlepis* vigorously defending their thousands of eggs or young in a shallow nest in the sand against the continuous attacks of all kinds of predators, as well as the leks of many Ectodini. Marshy areas are mostly associated with river mouths. They typically harbour a mixture of a few true lacustrine species and riverine species.

Deep-water communities

The deep-water communities are also dominated by cichlids. Coulter (1991) considered the benthic and bathypelagic communities to live from ± 40 m downwards to the oxycline. The oxygen concentration is the major factor limiting the depth distribution of these fishes. The oxycline is deepest at the southern end (about 200 m vs. 80 m in the north) and varies between seasons (Plisnier *et al.*, 1999). This zone is the most stable habitat, almost uninfluenced by wave actions and shifts in water level. However large seasonal oscillations do occur in the lake that may impact these communities. While they are not as species-rich as the littoral and sublittoral, still some 80 species have been recorded (Coulter, 1991). One of the more important guilds of the shallow waters, the algae eaters, are not present in this area, which is devoid of light. Typical tribes are the predatory Bathybathini and the Trematocarini that have large sensory canal pores on their head that probably aid in prey detection. Also the Limnochromini and the scale-eating Perissodini are well represented. Non-cichlids are represented by *Lates mariae* and *L. angustifrons*, several *Chrysichthys* and *Synodontis* species, and the endemic clariid *Dinotopterus cunniingtonii*.

The shelf areas are dependent on the rain of organic material from the pelagic zone. While cichlids are large in number, non-cichlids may represent the highest biomass. Most probably, fish are much less stenotypic here than in the shallower zones of the lake. The communities of the rocky slopes represent an extension of the rocky littoral habitat with many small-sized cichlids (Coulter, 1991). The *Trematocara* species living here appear to ascend the slopes into the littoral at night for feeding. The bathypelagic community living above the deeper bottoms is difficult to demarcate and consists of some ten relatively small zooplanktivorous cichlid species (Coulter, 1991).

The marshy areas and tributaries of the lake are dominated by the non-cichlids. Here occur 103 of the 145 species of non-cichlids present in the basin (De Vos & Snoeks, 1994). Most of them are known from the Malagarasi River, the largest affluent of the lake. The majority of the species belong to the Cyprinidae (by far the largest group), the Mormyridae, the Characidae and the Mochokidae. Most of these species are only exceptionally found in other habitats of the lake.

The communities of Lake Malawi

Lake Malawi is the fish species-richest lake on earth harbouring some 800, or even 1,000 cichlid species, only fewer than 400 of which are described. In addition, the basin, taken as the lake itself, its affluents and the associated Lake Malombe and the Upper and Middle Shire upstream of the Murchison cataracts, contains some 62 native non-cichlids belonging to 11 families (Snoeks, 2004b).

When Lake Malawi appeared in its present form is not clear. The minimum age of the rift basin currently including the lake, is about 8.6 Ma, but deep water conditions were only reached by 4.5 Ma (Delvaux, 1995). Like the other large lakes in the region, Lake Malawi went through periods of severe aridity. During the last mega-droughts between 160 000 and 60 000 BP, the water level dropped several times to about 550 m below the current level resulting in a small palaeo-lake with a 97% reduction of the current volume (Lyons *et al.*, 2011). Such mega-events but also smaller lake level changes must have had a profound impact on its fish fauna. The lake is anoxic below 170-200 m.

Roughly, the Lake Malawi cichlids can be divided in two groups of mouth-brooding haplochromines, the *mbuna* and the *non-mbuna*. The former is a morphological and ecological entity, encompassing a group of beautifully coloured, small to medium-sized, mainly rock-dwelling fishes. The *non-mbuna* include all other haplochromines. In addition there are some tilapiine cichlids, some of which are endemic, and a group of 62 non-cichlids (Snoeks, 2004b).

Non-mbuna cichlids can phylogenetically but also ecologically roughly be divided in a *Rhamphochromis* and a *Diplotaxodon/Pallidochromis* group, most species of which live in pelagic or deeper benthic habitats, and the remaining *non-mbuna* split up in a shallow-water and a deep-water component. For a long time the deep-benthic *non-mbuna* ended up in a clade not with the shallow

water *non-mbuna* but with the rock-dwelling *mbuna* (Moran *et al.*, 1994), making the *mbuna* a non-monophyletic assemblage. However, recent molecular analyses (Genner & Turner, 2012) confirmed the common sense feeling (Snoeks 2000) that, based on morphology and ecology, there should be a closer relationship between the two *non-mbuna* communities.

Over 99% of the cichlids are endemic to the lake (Snoeks, 2000). Exceptions found in the lake are *Astatotilapia calliptera* [possibly the species represents a complex of species (Seehausen *et al.*, 2003)] and the two tilapias, *Coptodon rendalli* (Boulenger, 1896) and *Oreochromis shiranus* Boulenger, 1896. Of the latter, there is an endemic subspecies *Oreochromis shiranus shiranus* restricted to the Lake Malawi basin. Also the former *Serranochromis robustus robustus* (Günther, 1864) is restricted to the basin, but it should be considered as a valid species (Snoeks & Hanssens, 2004a). The non-endemic *Pseudocrenilabrus philander* (Weber, 1897) and *Tilapia sparmanni* (Smith, 1840) have not been found in the lake itself but are present in the associated lagoons and rivers (Snoeks & Hanssens, 2004a).

Several cichlid taxa were revised and earlier work on the Lake Malawi fauna reviewed by Trewavas at various instances during her career (e.g. Trewavas, 1931; 1935 and 1941) resulting in a new classification scheme of the *non-mbuna* cichlids (Eccles & Trewavas, 1989) that also included a synopsis on the distribution and ecology of the species.

Ecological research on the tilapias (local name *chambo*) started with the studies of Lowe-McConnell (e.g. Lowe, 1952 and 1953). Work on the *mbuna* was headed by Fryer (1959) and a special group of zooplanktivorous *non-mbuna*, the *utaka* by Iles (1960). Both joined forces in writing a classical volume on the biology and evolution of the cichlids of the great African lakes (Fryer & Iles, 1972). In the late seventies, a detailed programme started on the *mbuna* of the Malawi part of the lake (Ribbink *et al.*, 1983) that set the scene for a decades-long scientific exploration of this group.

Lake Malawi supports what probably is the world's richest multispecies fresh-water fishery. In a twenty-minute shallow-water trawl, up to 72 species can be found (Snoeks & Hanssens, 2004b) and more than 200 species have been recorded from single fishing localities during recent surveys of the artisanal and industrial fisheries in southern Lake Malawi (Weyl *et al.*, 2010).

The pelagic community

The pelagic community for a long time was considered to be underexploited by fish with only shoals of the Cyprinid *Engraulicypris sardella* (locally known as *usipa*) occurring in large numbers but unable, due to their small size, to feed on the rather large lakefly (*Chaoborus*) larvae. Several projects, from the early 1990s onwards, have contributed largely to the current knowledge of the pelagic fish communities, which are much more important than previously thought. The off-shore zone is characterized by the genera *Rhamphochromis* (locally known as *ncheni*), and *Diplotaxodon* (*ndunduma*), but not all of the species of these genera live only in the pelagic (Turner *et al.*, 2004). These genera contain mainly zooplanktivorous and piscivorous fish and taxa comprise

more than 80% of the biomass of the pelagic fish communities (Turner *et al.*, 2002). Many of the species aggregate in large numbers on the benthic shelves in breeding areas or leks. *Diploaxodon* seem to be more active during the night while *Rhamphochromis* are caught more in daylight-set gillnets (Thompson *et al.*, 1995). The similarity between the elongated predatory *Rhamphochromis* from Lake Malawi and *Bathybates* from Lake Tanganyika is one of the classic examples of morphological convergence in cichlids of the African Great Lakes (Kocher *et al.*, 1993).

One species of the *utaka* group (see below) appears to be common in the pelagic zone, *Copadichromis quadrimaculatus*. In addition to this cichlid community, two non-cichlid taxa are common: the cyprinid *Engraulicypris sardella* and the mochokid catfish *Synodontis nyassae*. The complex diversity of true pelagic cichlids is a unique feature of Lake Malawi (Turner *et al.*, 2001).

Pelagic fish live in the oxygenated zone between 0 and 200 m. They all seem to have a lake-wide distribution (Turner *et al.*, 2002). The food taken by the pelagic cichlids differs according to their life stage. Small individuals feed on crustacean zooplankton, *Chaoborus* larvae and pupae, and juveniles of *E. sardella*. Larger individuals prey on fish, mainly *E. sardella* and small pelagic cichlids (Allison *et al.*, 1996; Turner *et al.*, 2002). Contrary to earlier reports, the lakefly biomass is efficiently utilised by the lake fish community (Darwall *et al.*, 2010).

The littoral communities

In general topography, the lake resembles Lake Tanganyika. However, for the littoral communities, one of the greater differences is that only about one-third of the shoreline is rocky habitat, while roughly two-thirds is sand (Weyl *et al.*, 2010), while in Lake Tanganyika, the major part of the littoral zone is rocky.

The rocky habitat is occupied by both *mbuna* and *non-mbuna*, while *non-mbuna* dominate the sandy habitats. Genner & Turner (2005) report about 400 species occurring on the rocky shores, and fewer than 200 on the sandy shores.

About 325 species of phylopatric and stenotopic *mbuna* live in the rocky habitat (Konings, 2007). Many *mbuna* species have not been scientifically described, but their general habitus and colour pattern, and their distribution, habitat preference and behaviour are often documented in the scientific, and even more so in the aquarium literature (e.g. Ribbink *et al.*, 1983; Konings, 2007). *Mbuna* display a high level of intra-lacustrine endemism, unmatched in any other vertebrate group. Many species are limited to one or a few islands or reefs or to small parts of the mainland (Ribbink *et al.*, 1983; Konings, 2007). Consequently, the rocky habitat community can be quite different from one area to another. In addition to community structure along this geographic spatial axis, *mbuna* communities also differ along a habitat-related axis. Konings (2007) distinguishes the communities of the upper surge zone, the sediment-free and the sediment-rich rocky habitat.

A gillnet survey on the rocky habitat in various parts of the lake revealed a strong decline in *mbuna* species numbers between 20 m and 30 m depth (Hanssens & Snoeks, 2004). Down to depths of 20 m, on average 10-11 species were found

in the nets, while at 30 m, only six were found, decreasing to an average of four at 50 m. A few typical rock-dwelling *mbuna* were still present in a net set at 55 m. The species-richest catches were made at islands and reefs (Mbenji, Likwandje, Likoma), and the nearby mainland of the latter in Mozambique, but also at the north-eastern shores of the deeper parts of the lake. The rocky habitat of large islands are special in two respects; they harbour a higher species diversity of *mbuna* than comparable areas on the mainland and also a higher level of intra-lacustrine endemism (Hanssens & Snoeks, 2004).

There may be over 30 *mbuna* species living at a particular rocky site in combination with various *non-mbuna* species (Genner & Turner, 2005). While there is a large variety of micro-habitats in the rocky zone, as a result of the size of the rocks, the exposure to surge waves, the depth and slope, the amount of algae, etc., that create opportunities for fine-scaled differences in trophic niche of the numerous *mbuna* species at a given site, a substantial overlap in diet and space use has been found between coexisting morphologically similar *mbuna* species but also between coexisting species that differ widely in morphology. Ecological niche differentiation was found to occur on a fine scale among the *mbuna* (Genner *et al.*, 1999). According to niche theory, this differentiation is likely to promote coexistence if resources are limited. However, species were also found to co-occur without any evidence of niche differentiation (Genner *et al.*, 1999). After a full year of observations of two coexisting species couples in the lake, Martin & Genner (2009) concluded that, in contrast to predictions of ecological specialization during resource scarcity, substantial trophic overlap persisted in all seasons and no direct evidence of competition-driven divergent ecological selection was found.

Not much is known about the endemism of *non-mbuna* in the rocky habitat. Since there has not been a lake-wide survey for this group, the information is just not sufficient to draw conclusions. What is known is that some species have a lake-wide distribution, while others do not. Some species are only known from one or a few localities, reflecting the poor sampling effort (Snoeks & Hanssens, 2004b).

Lake Malawi harbours a special assemblage of small to medium-sized planktivorous cichlids that predominantly occur near rocky outcrops and reefs, feeding on plankton in the currents created by these "virundu". *Utaka* are characterized by numerous gill-rakers and long, protractile premaxillary pedicels which are part of a highly protrusible mouth that can form a sort of short sucking tube when feeding (Eccles & Trewavas, 1989). The group includes members of the genera *Copadichromis* and *Mchenga*. These fish form the basis of important fisheries with so-called "chirimila" nets (open-water seines). While indeed they frequent the water column, they are linked to the rocky habitat and are therefore more a component of the littoral community than of the pelagic, except for one species (see above). One species, *Copadichromis chrysonotus*, is a mid-water spawner (Eccles & Lewis, 1981).

The soft bottom littoral occupies the major part of the shoreline of Lake Malawi but represents clearly less diversity in micro-habitats than the rocky shore. A division can be made between the sandy habitat and the sediment-rich areas

with aquatic plants associated with sheltered bays and river estuaries. Both these zones are mainly occupied by *non-mbuna*. While stenotopy is clearly less developed in these communities, genetic and morphological differences have been observed that either could be linked to a geographical pattern or not (e.g. Duponchelle *et al.*, 2000; various chapters in Snoeks, 2004a; Anseeuw *et al.*, 2008). One of the most important roles of the sandy zone is to provide space for reproduction, often in large leks. Many species also breed in the intermediate rock-sand habitat. Most studies did not distinguish between the littoral and the deep-water sand communities. Hence for further information, we refer to the part on the benthic communities.

The deeper benthic communities

Lake Malawi is special in harbouring a deep-water community, which appears to be more separated from the littoral and sub-littoral communities than in Lake Tanganyika. Duponchelle *et al.* (2003) reported a change in species composition between 50 and 75 m. The deep-water community is characterized by the presence of deep-water *Placidochromis*, many species of *Diplotaxodon* and deep-water *Lethrinops*, and endemic *Bathyclarias*. In fact, with 47 species reported, the deep-water *Placidochromis*, represents one of the most species-rich assemblages in the lake (Hanssens, 2004). While there are no obvious barriers known in these deep benthic areas, the species seem to have limited distributions. However, since the assemblage is very poorly studied, it remains to be seen how much intra-lacustrine endemism this group displays.

While the littoral and sublittoral communities are clearly different from the deeper benthic communities in species composition, this does not result in sharp differences in species richness or fish biomass. A two year lake-wide biodiversity sampling programme with bottom trawling and gillnetting at various depths during five sandy and demersal cruises resulted in the following observations (Snoeks & Hanssens, 2004b). There is a slight decrease in catch weight with increasing depth for both the experimental trawl and the gillnet catches. Even so, the largest catch (exceptionally large) was taken at a mean depth of 128.5 m. This is probably due to the trawl having targeted one or more large leks with breeding cichlids. There is also a steady decrease in species richness with increasing depth for the trawl catches, though species numbers remain relatively high in the deeper regions (going from an average of ca. 40 in the littoral zone to ca. 25 at 150 m for a trawl of about 20 minutes). With regard to soft-bottom substrates, the highest species numbers were observed over fine sand habitats while the lowest numbers were found over sticky mud. Furthermore, for these habitats, species richness is not evenly distributed over the lake. Taking into account the influence of catch weight, relatively low species numbers were found in the trawls at Wissman Bay (north), Lukoma (north east) and the southern areas, while a relatively high species diversity was recorded at Nkhotakota, Chiwanga, and Senga Bay, all situated in the central or south-central part of the lake. Chilola and the central part of the southeast arm may also represent areas of a higher-than-average diversity, but this could not be confirmed for all depths (Snoeks & Hanssens, 2004b).

Darwall *et al.*, (2010) found evidence for a strong benthic–pelagic coupling; their model clearly demonstrated that the productive demersal fishery appeared to be over 80% reliant on production from the pelagic. Part of this link is also reflected in the presence of the same part of the fish community of both habitats, such as various *Diplotaxodon* species (see above).

Experimental trawls over one year at various depths clearly showed a change in communities with depth. This change was supposed to be linked to a change in granulometry of the bottom substrate (Duponchelle *et al.*, 2003). Cichlids dominated the captures at all depths with a biomass between 75 and 92%; the remaining part was mainly taken up by various catfish families (Bagridae, Mochokidae and Clariidae). This study also demonstrated that even if more than 150 species were found during the whole sampling programme, some ten species including three catfish made up 70 to 80% of the catches at a given depth. This suggests that the majority of the species, at least in the southern area, are relatively rare.

The communities of Lake Victoria

Lake Victoria is the largest tropical lake and second-largest lake in the world. In many aspects it is different from lakes Tanganyika and Malawi. It is saucer-shaped with a surface area of about 68,800 km², and relatively shallow (maximum depth 84 m and average depth ca. 30 m) (Kolding *et al.*, 2008), which means it harbours no real deep-water community. In addition, the major part of the littoral zones consists of sandy areas, with rocks being relatively rare. Its origin is relatively recent, ca. 400 000 BP (Fuggle, 2004), and the lake went through a desiccation phase ca. 15 000 years ago. Whether or not it dried out completely is a matter of debate (e.g. Johnson *et al.*, 1996; Fryer, 1997 and 2004; Snoeks, 2000; Verheyen *et al.*, 2003; Stager & Johnson, 2008; Elmer *et al.*, 2009). The lake supports one of the most productive inland fisheries of the world (Ogutu-Ohwayo & Balirwa, 2006).

A discussion on the fish communities should start with highlighting that, much more than any other large lake in the region, the ecology of Lake Victoria has changed dramatically in the last three decades. These changes have been so profound that a comparison can be made in the terrestrial environment with a shift from a biodiversity-rich equatorial rain forest to an almost desert. While these changes can be attributed to a large part to the introduction of Nile perch in 1954 (Goudswaard *et al.*, 2008) into a complex system that was mainly supported by the interactions of some 600 or more haplochromine cichlids, the situation is much more complex, with many other factors having influenced and still influencing the lake's fish communities. Among these are deforestation, pollution and eutrophication, introduction of water hyacinth, and overfishing, most of which are directly linked to the quickly growing riparian human population. As a result, occasional hypoxia in the deepest waters turned into a permanent anoxia below 50 m, with levels of low oxygen concentrations extending into the sublittoral waters (Njiru *et al.*, 2011).

The lake's native fish fauna is dominated by some 500-600 closely related haplochromine cichlids. Because of anthropogenic changes, some 200 are supposed to have become extinct, which has been referred to as the greatest vertebrate mass extinction in the modern era (Baskin 1992). While reports mention the return of some species in recent years, it is clear that many have disappeared forever. In addition, the lake harbours some 46 other fish species (Witte *et al.*, 2007a).

Greenwood studied Lake Victoria haplochromines extensively during several decades, based on fieldwork in the fifties and sixties (e.g. Greenwood, 1981). During the late seventies the Dutch Haplochromis Ecology Survey Team (HEST) started surveying the Mwanza Gulf, collecting data in collaboration with the Tanzania Fisheries Research Institute (TAFIRI) over several decades, thus providing much needed collections and baseline information on the ecological changes in the lake. These studies were triggered by the development of a more intensive trawl fishery on the poorly known haplochromines.

Many different trophic groups exist among the haplochromines of the lake: detritivores, phytoplanktivores, zooplanktivores, insectivores, molluscivores, crabeaters, prawn eaters, parasite-eaters, scale-eaters, higher plant eaters and algae-eaters and piscivores amongst which paedophages. Many of them display characteristic morphological features (Witte & van Oijen, 1990).

Lake Victoria cichlids do not present the level of intra-lacustrine endemism found in lakes Tanganyika and Malawi, except maybe for the specialized rock dwellers. However, since haplochromine taxonomy is very difficult and lake-wide surveys resulting in detailed distribution data of the taxa have never been done, this assumption is difficult to verify. Wider distributional range, however, does not mean the haplochromines have a random distribution; horizontal and vertical ecological segregation patterns have been observed in certain groups such as the piscivorous and zooplanktivorous species (van Oijen, 1981; Goldschmidt *et al.*, 1990).

After the Nile perch boom, the haplochromine catches in the sublittoral and deeper zone decreased to virtually zero, but haplochromines in the littoral zones remained less affected, because of the lower densities of Nile perch in shallower areas (Witte *et al.*, 1992a). Concomitant with the decrease of the Nile perch came a resurgence of haplochromines. However, the recovery is limited to certain trophic guilds, but is noticed all over the lake.

Trophic group composition differs between habitats. Rocky habitats are relatively scarce in Lake Victoria, compared to lakes Tanganyika and Malawi. However, they also harbour a characteristic stenotopic cichlid community, named Mbipi (Seehausen *et al.*, 1998). More than 100 of these lithophylics have been discovered in the nineties. Before that time, this diverse community was virtually unknown to scientists. In these rocky habitats, many trophic guilds are represented but most characteristic are the algae scrapers.

An analyses of the catches within the Mwanza gulf before the introduction of the Nile perch revealed that on soft bottom substrate, species diversity was higher in the littoral sandy zone compared to littoral and sublittoral muddy zones (table 19.I) and the number of species within each trophic

group differed considerably according to the zone (Witte *et al.*, 1992b). Insectivores dominated shallow soft bottom habitats. Oral shelling molluscivores and insectivores were mainly associated with the sandy habitat, while detritivores/phytoplanktivores and zooplanktivores were dominant on sub-littoral mud bottoms (table 19.II). Piscivores, representing about 40% of the species in the lake (van Oijen *et al.*, 1981), were clearly the species richest group in the lake but were only caught in small numbers (<1%).

TABLE 19.I.

Species number by trophic group, caught during experimental bottom trawls in different stations in the Mwanza Gulf (following Witte *et al.*, 1992b).

Depth	2-6 m	2-6 m	7-8 m	10-11 m	13-14 m
Trophic group	Sand	Littoral mud	Sublittoral zone		
Detritivores/phytoplanktivores	7	6	9	9	10
Grazers	4	0	0	0	0
Mollusc eaters	12	6	10	3	3
Zooplanktivores	8	10	9	9	10
Insectivores	8	6	7	3	4
Prawn eaters	0	0	1	2	1
Piscivores <i>sensu stricto</i>	14	11	7	9	9
Paedophages	4	2	2	4	4
Scale eaters	1	1	1	1	1
Parasites eaters	0	0	0	0	1
Unknown	7	1	1	0	1
Total	65	43	47	40	44

TABLE 19.II.

Proportion (% number of individuals) of haplochromines by trophic group, caught by bottom trawling between 1979 and 1982, in a sublittoral station over a muddy bottom (depth 7-8 m) in the Mwanza Gulf (following Witte *et al.*, 1992b).

Trophic groups	1979/1980 (% number of individuals)	1981/1982 (% number of individuals)
Detritivores/phytoplanktivores	77	75
Zooplanktivores	18	23
Insectivores	2	<1
Mollusc eaters	<1	<1
Piscivores	1	<1
Others	1	1

The pelagic community is dominated by the cyprinid *Rastrineobola argentea*. It sustains the second most important fishery (Wanink, 1999). In contrast to some pelagic zooplanktivorous haplochromines, *R. argentea* continued to thrive after the upsurge of the Nile perch.

The other lakes in the region

Lake Kivu

Lake Kivu is a high altitude, natural deep dam lake of relatively recent origin. The proto Lake Kivu, for a long time, was connected with Lake Edward until the connection got blocked by the Virunga volcanoes. For part of its subsequent history, the basin was endorheic, until it found its outlet via the Ruzizi, some 9500-9200 years ago (Snoeks *et al.*, 2012). At present 29 species are recorded from the basin, including five introduced species.

The majority of the fishes belongs to the large group of haplochromines; all fifteen species are endemic to the lake (Snoeks, 1994). Lake Kivu is regarded as the cradle of the haplochromines in the region, known as the Lake Victoria region super flock haplochromines (Verheyen *et al.*, 2003; Elmer *et al.*, 2009). While the lake is currently part of the Congo basin, zoogeographically it is part of the East Coast ichthyofaunal province (Snoeks *et al.*, 1997).

In addition to the endemic haplochromines, there is one autochthonous tilapia, *O. niloticus*, five cyprinids and two *Clarias* species. In the fast flowing parts of the affluents, *Amphilius cf. uranoscopus* occurs.

Of the five introduced species, the most successful in economic terms is *Limnothrissa miodon*. This freshwater sardine, endemic to Lake Tanganyika, was introduced in 1959, accidentally mixed with *Stolothrissa tanganyicae* that was targeted to feed on the supposedly unexploited pelagic resources. Currently, a pelagic fishery is thriving, targeting these sardines. Recently, another Lake Tanganyika endemic species popped up in this fishery, *Lamprichthys tanganyicanus*. Either it was introduced with the sardines and was only discovered fifty years later, or it was introduced more recently, maybe by an aquarist (Muderhwa & Matabaro 2010; Snoeks *et al.*, 2012).

Most of the coastline is rocky shore, dominated by haplochromine cichlids. Some species are also found in vegetated areas over sand (*Haplochromis astatodon*) or in the more pelagic regions (*H. kamiranzovu*). No intra-lacustrine endemism has been found in Lake Kivu. Typical for Lake Kivu haplochromines is the large amount of polychromatism relative to the other lakes in the region. Polychromatism is the presence of two colour morphs within one species, in this case the presence of piebald or bicolour black-blotched specimens alongside the normal coloured morph. Four out of the fifteen species are polymorph. Almost all piebald specimens are females; in some species about half of the females are of the piebald type. It has been postulated that the success of polychromatism is linked with being less visible for predators. Indeed, in the very clear waters of Lake Kivu, this disrupted colour pattern may provide some evolutionary advantage (Snoeks, 1995).

Lake Edward/George

Lake Edward forms with the smaller Lake George one large system that is connected through the Kazinga channel. An estimated 60 haplochromines occur in the system, and some 21 non-cichlids (Snoeks, 2000). The basin is part of the Nile system, but lacks some typical Nilotic elements such as *Lates*,

Hydrocynus and Polyteridae. Fisheries rely mostly on six species: *Oreochromis niloticus*, *O. leucostictus*, *Bagrus docmak*, *Protopterus aethiopicus*, *Clarias gariepinus* and *Labeobarbus altianalis*, but the numerous endemic haplochromines are increasingly becoming a target as well. Human impact has disrupted the ecosystem of the lake. This includes overfishing but also a reduction of the nutrient input though the severe reduction of the hippo population (Languy & de Merode, 2006) that were responsible for the transfer of plenty of nutrients from the terrestrial to the aquatic environment.

Lake Edward has a northern outflow, the Semliki towards Lake Albert. The falls and rapids on this effluent apparently block the migration of fish from Lake Albert into Lake Edward (Greenwood, 1976).

Lake Albert

Lakes Albert and Turkana are special as they are the only large rift valley lakes within the Nile system not having a large number of endemic haplochromines (Snoeks, 2001).

Forty-eight species are recorded from Lake Albert, amongst which some 37 non-cichlid species and only 11 cichlids, seven of which are haplochromines. Greenwood (1979) noted the haplochromine fauna to be Nilotic-Congolese, rather than Victorian, and included most species in his genus *Thoracochromis*. However, a quick review of some collections revealed that there are many new species that have not yet been described. Notably there seems to be a small group of rock-dwelling species that bear much resemblance to the Lake Victoria Mpibi (Snoeks, pers. obs.).

Lake Turkana

Lake Turkana is part of the eastern branch of the East African rift system. During its history in the early Holocene the lake regularly overflowed into the Nile but currently, it is part of an endorheic system (Johnson & Malala, 2009). Its fish fauna reflects the former connection with the Nile system and includes 36 non-cichlids and 8 cichlids (Snoeks, 2000).

Lake Rukwa

Lake Rukwa is situated in the western branch, to the east of the southern part of Lake Tanganyika. It is relatively shallow with a maximum depth between 10–15 m (Seegers, 1996). The total drainage area of this endorheic system includes 64 species, about half of which are found in the lake itself. The ichthyofaunal composition appears to be a mix from various neighbouring systems, but includes some endemic cichlids and non-cichlids, including six haplochromines (Seegers, 1996). Fisheries are mainly targeting tilapias and *Clarias*.

Lake Mweru

Some may debate whether or not Lake Mweru should be regarded as a rift valley lake, but in view of its geological setting, it is. It is situated south-west of the southern part of Lake Tanganyika. The lake has a maximum depth of about 27 m (Bos *et al.*, 2006) and is part of the Luapula-Mweru sub-region within the Upper Congo system; it contains some 135 fish species (Van Steenberge *et al.*, 2014). As in many other lakes in the region, overfishing is a serious problem.

Conclusion

The region of the East African lakes represents the world's richest region in terms of freshwater fishes. Each of the three large lakes, Tanganyika, Malawi and Victoria, harbour more species than any other lake in the world. In these lakes exceptional numbers of cichlid species, estimated respectively at 250, 800-1000, and 500-600, occur. In addition, more than 95% of these species are endemic to one particular lake. Given the extraordinary species richness and the high level of endemism, these lakes are the largest centres of vertebrate diversity and unique natural laboratories to study adaptive radiation and explosive speciation.

The region of the East African lakes is experiencing a significant and ever-increasing demographic pressure, which translates to a more intense human impact on the aquatic environment and a higher demand for fish as the main source of animal protein in the region. Most lakes are shared between two or three countries, rendering decision-making on a lake-wide scale rather complex. In addition, multispecies fisheries are difficult to manage since the interactions between species are poorly understood. In many areas, cichlids are targeted, but several hundred still remain to be described from the region (Snoeks, 2001). Therefore, basic information on many taxa and their life history, including those of non-cichlids, is lacking.

In Lake Tanganyika, fisheries are merely concentrated on the pelagic sardines and its main predator *Lates stappersi*. However, the pressure on the littoral communities is dramatically increasing (e.g. Sturmbauer, 2008; Mushagalusa *et al.*, 2014).

In Lake Malawi, fisheries are concentrated on the cichlids, though various non-cichlids are targeted as well. Overfishing has been ongoing for several decades in the southern part of the lake and several large cichlid species have virtually disappeared from the catches (Weyl *et al.*, 2010). Lake Malawi's high valued *chambo* (endemic tilapias) fisheries are overexploited or have collapsed in certain areas. In addition, the migratory cyprinid species, such as the endemic *Labeo mesops*, *Opsaridium microlepis* (local name *mpasa*) and *O. microcephalus* (*sanjika*) have been decimated through habitat degradation and intensive fishing efforts along their migrating route (Weyl *et al.*, 2010).

Lake Victoria is the setting for the largest vertebrate extinction in human history. A conservative estimate by Witte *et al.* (1992b) places the number of haplochromine species that disappeared at 200, due to a combination of anthropogenic factors. While the upsurge of *Lates niloticus* can be considered both an ecological disaster and an economic blessing, the economic benefits may well decrease dramatically in the future now that catches of Nile perch are dwindling.

Not only the big three, but also the other, smaller lakes in the region experience such impacts on various scales. Clearly the major challenge is a difficult one: reconciling the need to conserve these unique natural laboratories and their exceptional ichthyofaunas and the need for access to a much-needed natural food resource for the riparian human populations. Clearly both ambitions benefit from sustainable management of the ecosystems involved.

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The Inland Water Fishes of Africa

Diversity, Ecology and Human Use



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