Role of fish in ecosystem functioning

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The functional relationships between the species in an ecosystem are still poorly understood, but represent one of the main concerns of modern ecology. The role of biological diversity in the functioning of ecological systems is of particular interest. Are all the species found in an ecosystem truly needed to ensure its proper functioning? Do some species have redundant functions, and are there species with more important roles than others (keystone species)? Scientists also wonder about the role of biological diversity in the stability of ecosystems and their capacity to resist or adapt to disturbances, and study the relationships between specific richness and biological productivity.

The answers to these questions are important for the management of aquatic environments and the preservation of biodiversity. But their complexity makes it difficult to propose satisfactory hypotheses. It is nevertheless possible to analyse available data and attempt to find partial answers to the questions raised (Lévêque, 1995b and 1997).

Impact of fish predation on aquatic communities

Limnologists have long thought that the organization of ecological systems was essentially controlled by the nature and dynamics of the physico-chemical system in which the organisms live. In the standard view of bottom-up control, we look for example at the manner in which environmental factors or the availability of trophic resources influence fish biology and ecology, and the consequences in turn on the organization of fish communities. This deterministic approach regarding communities on the basis of abiotic characteristics remains relevant but needs to be refined. Indeed, several investigations have shown that fishes themselves can have a deciding influence on the ecological functioning of aquatic systems. The hypothesis of top-down control (Northcote, 1988) posits that the effects of predation by fishes cascade down the whole trophic chain and can control the state of the entire ecosystem. A number of studies on African fishes helps illustrate this hypothesis (Lévêque, 1995b).

Prey selection

Zooplanktivorous fishes visually select preys or use their gills for passive filtration of zooplankton (Lazzaro, 1987). In both cases, this leads to a decrease in the average size of organisms composing the zooplankton. In other words, large species disappear, to the advantage of smaller species, which modifies the specific composition of planktonic populations.

Thus, following the introduction of the planktivorous Clupeidae species *Limnothrissa miodon* in Lake Kariba in 1967-68, there was a marked reduction in the abundance of large planktonic crustaceans such as *Ceriodaphnia*, *Diaphanosoma*, and *Diaptomus* (Begg, 1974). Similarly, there was a disappearance of Cladocera and large Copepods from Lake Kivu after the introduction of *Limnothrissa* (Dumont, 1986).

Sympatric species can have a very specific impact on planktonic communities. In Lake Chad, for example, *Alestes baremoze* filters zooplankton through its gills, which starts retaining particles sized at least 400 µm. All particles larger than 880 µm are collected; in other words, large planktonic crustaceans are consumed whereas rotifers and nauplii are not (Lauzanne, 1970). Meanwhile, a micro-zooplanktivorous fish such as *Synodontis batensoda* captures prey with a length of at least 80 µm (Gras *et al.*, 1981) (figure 17.1). Nauplii and rotifers are progressively retained depending on their size by the gill filter, and all particles larger than 260 µm are captured. The two species thus have a different impact on the zooplankton.

If fish predation leads to the reduction, if not the outright elimination, of large zooplankton, we can imagine that in the absence of predation, these large forms would develop. If so, the abundance of large zooplanktonic species in the open waters of Lake Naivasha would be due to the fact that the zooplanktivorous fish species, all introduced, remain in the coastal area and do not colonize the pelagic environment (Mavuti, 1990).

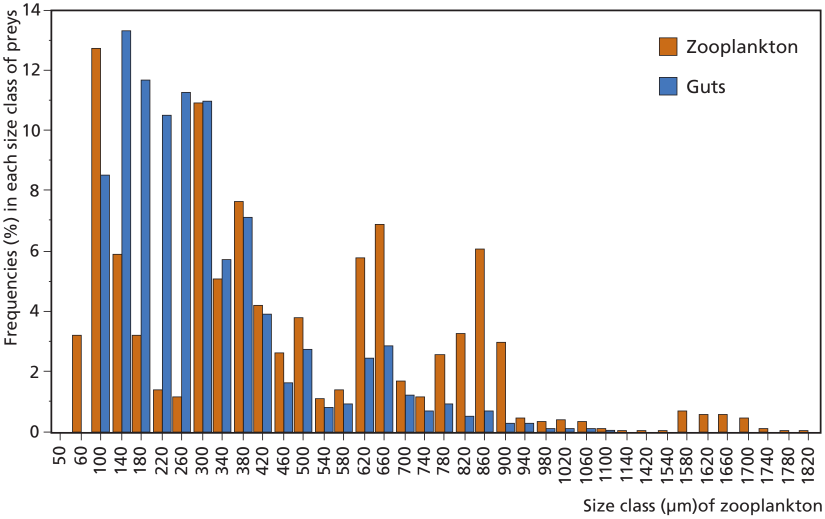

FIGURE 17.1.
Relative frequencies in each size class of preys (rotifers, nauplii, *Macrothrix, Moina, Diaphanosoma,* diaptomids and cyclopoids) in zooplankton and in stomachs of *Synodontis batensoda* in Lake Chad (from Gras *et al.*, 1981).

Similar observations have been made on benthic fauna. When fish predation selectively affects certain prey sizes, it can have a strong influence on the demography of a species. For example, molluscivorous fishes in Lake Chad such as *Synodontis clarias, S. schall* and *Hyperopisus bebe* mainly consume young individuals of benthic molluscs (*Cleopatra, Bellamya, Melania*) (figure 17.2). This strong selective predation explains why, despite nearly continuous reproduction throughout the year, benthic mollusc populations have a truncated size distribution, with a small proportion of juveniles and a large proportion of adults (Lauzanne, 1975 ; Lévêque, 1972).

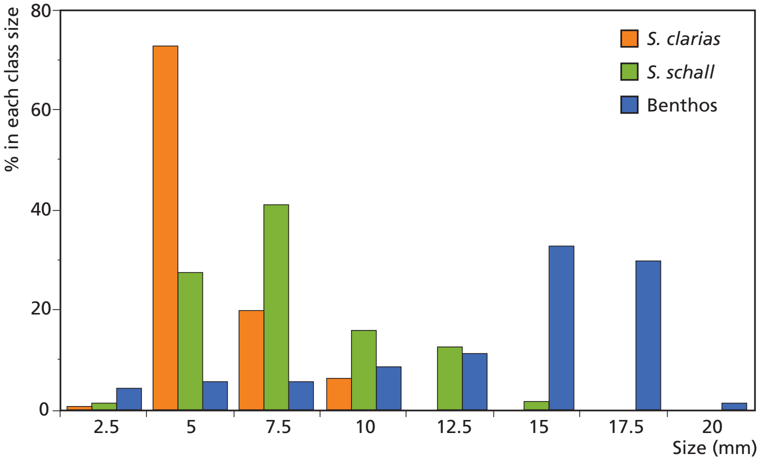

FIGURE 17.2.
Comparison of size distribution of benthic molluscs *Cleopatra bulimoides* in Lake Chad and in the gut of two malacophagous fish species *Synodontis schall* and *S. clarias* (from Lauzanne, 1975).

Changes in feeding habits during ontogeny

Fish size changes considerably during development and this has significant consequences on their ecology and feeding behaviour. Many fishes feed on plankton during their larval stage, then consume larger preys as they grow.

For *Hydrocynus forskalii*, in the Chari, juveniles up to 30 mm long are strict zooplanktivores (Lauzanne, 1975). Between 30 and 45 mm they eat both zooplankton and insects, and beyond 50 mm they are strictly piscivorous.

In Lake Victoria, *Bagrus docmak* juveniles of up to 15-20 cm long consume mainly invertebrates (insect larvae, shrimp). From 20 cm, they show a preference for fishes, and are strictly piscivorous beyond a size of 50 cm (Okach & Dadzie, 1988).

Cascading trophic interactions

The concept of the trophic cascade stems from a principle known to managers of lake fisheries. In a system with, for instance, four trophic levels (piscivorous fish – zooplanktivorous fish – herbivorous zooplankton – phytoplankton), an increase in the biomass of piscivores will have repercussions on all the lower levels of the trophic chain (Carpenter *et al.*, 1985). Increased predation by piscivores leads to a decrease in the biomass of zooplanktivorous fishes, which in turn allows an increase in the biomass of zooplankton that are subjected to less predation pressure. Meanwhile, this larger biomass of herbivorous zooplankton will lead to a direct increase in predation, and subsequent decrease in phytoplankton biomass.

It is difficult to identify trophic cascades in natural systems, but the introduction of new fish species in aquatic systems serve as large-scale experiments that allow for a number of observations. A spectacular example can be seen in the introduction of *Lates* in Lake Victoria. In the 1980s, predation by this piscivore led to the near-disappearance in some areas of the lake of Haplochromines (endemic Cichlidae) from the detritivorous/phytoplanktivorous group, as well as from the zooplanktivorous group, which represented 40% and 16% respectively of the biomass of demersal fishes. They were replaced by the indigenous detritivorous shrimp *Caridina nilotica* and the zooplanktivorous Cyprinidae species *Rastrineobola argentea* (Witte *et al.*, 1992a, b). These last two species are now the main food sources of *Lates* after the disappearance of the Haplochromines. Introduction of *Lates* thus led to a simplification of trophic chains, given that this predator also eats its own juveniles which, in a way, played the same zooplanktivorous role of the Haplochromines of the past (figure 17.3). Another consequence was the reduction in insectivorous Cichlidae and a significant increase in the larvae of aquatic insects whose adults form enormous swarms above the lake at certain periods.[1] This insect population in turn feeds the sand martin *Riparia riparia* which winters in Africa, and whose population massively increased (Sutherland, 1992). Meanwhile, the diet of the pied kingfisher *Ceryle rudis* has changed. It used to feed on Haplochromines but now feeds mainly on the pelagic Cyprinidae *Rastrineobola* (Wanink & Goudswaard, 1994). It seems that a similar change occurred in the diet of the great cormorant *Phalacrocorax carbo*.

NOTE 1
At certain times, insect densities are so high that local people collect them and use them for food purposes.

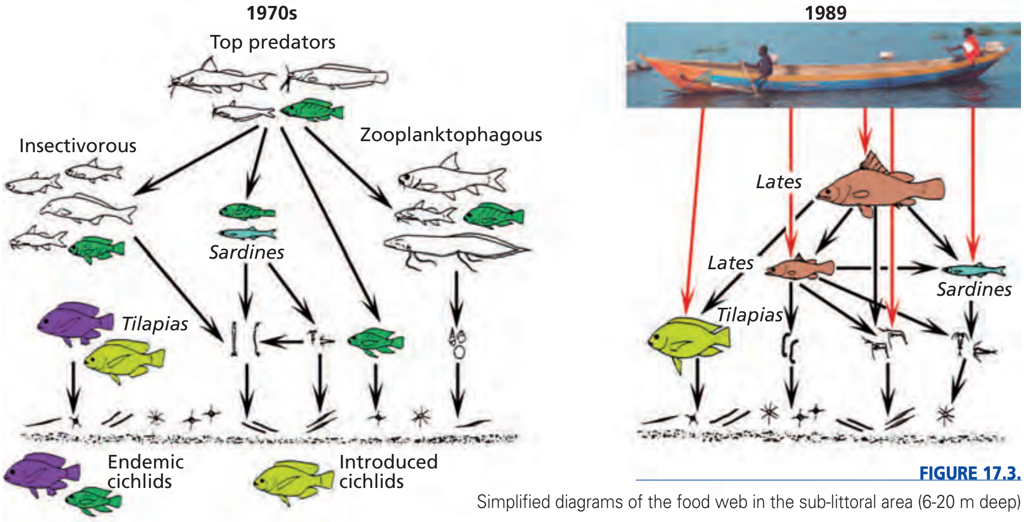

FIGURE 17.3.
Simplified diagrams of the food web in the sub-littoral area (6-20 m deep) of Lake Victoria in the 1970s and 1989, *i.e.*, before and after Nile perch introduction. Only organisms that are an important part of the diet of the main fish species have been mentioned. In the 1970s, *Haplochromis* were dominant in numbers and biomass in all trophic groups except the piscivorous. (modified from Ligvoet & Witte, 1991 and Witte *et al.*, 1992a).

We can compare the abovementioned trophic chains to the one suggested over 60 years ago by Worthington & Worthington (1933). An essential difference lies in the disappearance of crocodiles which used to be plentiful in Lake Victoria; their disappearance undoubtedly led to profound changes in the ecosystem's function, changes which were unfortunately not observed. It is worth asking if the introduction of *Lates* would have had the same consequences had the crocodiles not disappeared.

Some authors have suggested that the disappearance of Haplochromines from Lake Victoria could partly explain the increase in phytoplanktonic production, in line with the theory of trophic cascades. But this hypothesis has not been really confirmed, given the simultaneous eutrophication of the lake from urban and agricultural causes.

Another example of a trophic cascade concerns the introduction into Lake Nakuru (Kenya) of *Alcolapia grahami*, a species endemic to Lake Magadi (Kenya), to fight mosquito larvae. In this fish-free saltwater lake, the Cichlidae introduced in the late 1950s rapidly developed, feeding on the abundant populations of the cyanobacterium *Spirulina platensis* (Vareschi, 1978). The most marked effect was the development of a very large population of ichthyophagous birds including the white pelican which, by the late 1970s represented about 85% of ichthyophagous birds (Vareschi, 1979). Ichthyophagous birds began invading Lake Nakuru in 1963, only a few years after the introduction, and it has been estimated that pelicans consume 16 to 20 tonnes of fresh fish daily (Vareschi, 1979; Vareschi & Jacobs, 1984). Avifauna, which was essentially composed of pink flamingos prior to the introduction of Cichlidae, thus markedly diversified, and now counts over 50 aquatic bird species.

The concept of the trophic cascade was behind the idea of biologically manipulating aquatic systems. Indeed, if it is possible to modify trophic chains by controlling the biomass of consumers, one could then modify algal dynamics by selective fishing or stocking programmes. While the idea makes sense for combatting the eutrophication of aquatic systems, for instance, the interactions between trophic levels are much more complex in practice.

Role of species in ecosystem functioning

While the number of species makes it possible to characterize a fish community, each of the species within that community often plays a different role. Ecosystem functioning can thus vary depending on its specific composition. Ecologists have been investigating the functions of species in ecosystems, mainly by attempting to identify those that play a dominant role in trophic chains. But we have also realized that fishes can play an indirect role via the recycling of nutritional elements.

Keystone species

The concept of a keystone species applies to forms whose presence is crucial in maintaining the organization and diversity of ecological communities. Their disappearance can profoundly modify the ecological processes and specific composition of communities. Several broad sets can be distinguished:

- **key predators** are species whose presence strongly limits the presence of other groups. Thus, certain planktivorous fishes limit the abundance or even the presence of large zooplankton in the lakes (see above). Piscivorous predator fishes that play a role in the structuring of ecological systems through trophic cascades are thus often considered key species. Reduction in the biomass of piscivorous predators as an effect of fishing is probably a fairly frequent occurrence if we know that they are not only more vulnerable to gillnets (Bénech & Quensière, 1989), but are also in highest demand for consumption. Fishing thus probably has indirect consequences on the functioning of aquatic ecosystems, but there is generally a lack of precise information for African continental waters. What we know of the consequences of the introduction of *Lates* in Lake Victoria on trophic chains suggests, on the contrary, that the disappearance or reduction of members of this species can also have consequences on the ecology of aquatic environments. Hanna & Schiemer (1993a and b) also believe that the species *Alestes baremoze* and *Brycinus nurse*, which occupy the niche of zooplanktivorous fishes in the Jebel Aulia reservoir (Sudan) are keystone species that, owing to their abundance, exert a strong influence on zooplankton and hence on phythoplankton production in the lake;
- **key preys** represent resources that are critical for the survival of other populations, and are also considered keystone species. This can be illustrated by Lake Nakuru, where large ichthyophagous bird populations currently depend on the existence of *Alcolapia grahami*. The disappearance of this fish (epidemics, change in environmental conditions) would quite simply result in the disappearance of ichthyophagous birds.

Rare species

In systems that have undergone little disruption, ecologists are also interested in the role of rare species. As used in this context, "rare" is a qualifier that involves the abundance and distribution of a species. There are several possible interpretations. A species can have limited distribution but abundant populations; limited distribution with few individuals; or wide distribution with very few members. The diverse causes of rarity include the need to find highly specialized habitats, poor dispersion capacity, trophic position, etc. (Gaston & Lawton, 1990). The species could also have a special behaviour that makes it elusive to sampling techniques, but we could also consider it a relic of the past, one that is dying out.

What role do these rare species play in the functioning of ecological systems, given that in general, common forms fulfil the bulk of functions? It is clear that species could have differentiated according to highly particular local conditions. Their strong endemicity is, in that case, often associated with the occupation of a specific ecological niche. This holds true for many lacustrine species, especially those that are part of so-called species flocks. In this scenario, there was a co-evolution between biological species and ecological function.

How about groups with a wide distribution but few individuals? To some ecologists, these rare species – though they do not currently perform any major ecological functions – could represent a sort of insurance or guarantee of the stability of ecosystems, in the sense that they could replace currently abundant species should there be a significant change in ecological conditions. We know that aquatic ecosystems can change fairly rapidly depending on climatic conditions (see chapter *Variability of climate and hydrological systems*). To illustrate this hypothesis, we can look at how the composition of fish communities in Lake Chad evolved during a drying-out period (Bénech & Quensière, 1989). Species that were rare during the period of high waters (*Polypterus senegalus, Brevimyrus niger, Schilbe intermedius, Siluranodon auritus*, etc.) became dominant during the dry period, when lacustrine conditions shifted to a marshier system (see chapter *Fish communities in shallow lakes*). We thus saw the disappearance of lacustrine species to the advantage of palustrine ones, and this was only possible because the latter were already present, albeit in low quantities. More generally speaking, Nilo-Sudanian fauna inhabiting aquatic systems with high temporal and spatial variability would include numerous species that can replace ones that are currently more abundant should there be a change in the conditions of the habitat.

Recycling of nutrients

Limnologists long worked on the nutrient cycle by taking into account only the dissolved phase and the sediment storage phase. Scientists later realized that living organisms, particularly fish, were likely to play an important role in the storage, transport, and recycling of nutrients (Vanni, 1996). Most studies were conducted in temperate environments. This particular role of fish has hardly been investigated in African aquatic systems. Nonetheless, in Africa as elsewhere, there are fish species that may disturb the sediment layer in their search for food, allowing nutrients to re-enter a solution (bioturbation). Moreover, fishes can transport nutrients from one location to another, for instance when they feed in a littoral environment and excrete phosphorous in a pelagic one, which helps maintain primary production. Finally, detritivorous fishes contribute to recycling nutrients stored in organic debris.

The role of fishes in biogeochemical cycles in general remains a little-explored area of research in Africa. Yet results obtained in temperate systems show that this role can be very important, and should no longer be ignored by limnologists.

Fish biodiversity and responses of ecosystems to perturbations

A fundamental question for ecologists is whether or not all the species present in an environment are truly necessary for the smooth functioning of that same environment. Earlier, we saw that the concept of keystone species implicitly recognizes that some species play a more important role than others. Other hypotheses have been put forth in an attempt to justify the need for maintaining the greatest species diversity possible in ecosystems.

Nonetheless, ecologists are still debating whether the most complex systems – in terms of species composition and networks of interaction – are also the most stable in terms of adapting to perturbations from the outside. In reality, the degree of perturbation is an important aspect for aquatic systems, because extreme situations, such as drying out, lead to the elimination of species. In these conditions, the notion of refuge zones, where populations subsist that are capable of recolonizing the system once conditions are again favourable, is particularly important. This has been observed in Lake Chilwa and Lake Chad where fish populations can find refuge in tributaries when the lake dries up.

Experience from the introduction of *Lates* in Lake Victoria (see chapters *Diet and food webs* and *Species introductions*) tends to show that species diversity and the wide range of trophic specializations that existed in the lake were unable to support the resiliency of the ecological system which, on the whole, was significantly transformed and simplified.

A system's response to perturbations thus presumes, in the case of fishes, the simultaneous execution of multiple strategies: presence of refuge zones, development of biological strategies in order to address different types of stress (droughts, floods, etc.).

Specific richness and fisheries production

Ecological theories exist on the relationships between biological productivity and biodiversity, and there is considerable divergence in the different viewpoints. We might think that fisheries production in lakes with short trophic chains is greater than in systems with long trophic chains, where there is a concomitant significant loss of energy for each change in trophic level. In other words, given equivalent energy input, a lake composed mainly of phytophagous species should be more productive than one containing many ichthyophagous ones. This hypothesis supports an inverse relationship between specific richness and fisheries production, which can be empirically verified in areas with fisheries.

There is little data to help verify the above hypothesis. Nonetheless, it was possible to compare quantitative data on fish production estimated by fishery catches or estimated fish consumption by birds, in four shallow African intertropical lakes with very different fish communities (table 17.I). These data should be used very cautiously given the numerous sources of uncertainty in assessing catches. That said, we can note that fish production in Lake Nakuru, a saltwater lake with a single, introduced cichlid species, is higher than the other lakes. This species, whose production was estimated by the consumption of ichthyophagous birds (Vareschi & Jacobs, 1984), feeds on the cyanobacterium *Spirulina platensis* which has very high production in this type of environment. The short trophic chain can explain such high production in part. Meanwhile, in the other three lakes (Lake Chad, George, and Chilwa), fish production as estimated by fish catches appears to be equivalent despite their very different fish communities and the existence of short (Lake George) or complex (Lake Chad) trophic chains.

It is thus difficult to draw conclusions from these observations, as they do not seem to confirm the hypotheses made earlier but suggest no alternatives. It is possible that the great diversity of fishes observed in Lake Chad allows use of a wider range of resources, contrary to what occurs in Lake George phytoplanktophagous species are strongly dominant whereas the large zooplanktonic biomass. In these conditions, equivalent fish production (as measured) would in fact correspond to different use of trophic resources, only part of which are used by the fishes in Lake George. More precise data is needed to pursue these attempts to interpret information.

Lakes	**Nakuru**	**Chilwa**	**George**	**Chad**
Specific richness	1: *Oreochromis*	3: *Clarias*, *Barbus*, *Oreochromis*	30: including 21 Cichlidae	100: numerous families
Feeding	phytoplanktophagous	detritivorous, zooplanktophagous	biomass: 64% phytoplanctophagous, 20 % piscivores	every type
Fishery production (kg/ha/yr)	625-2436	80-160	100-200	100-150

TABLE 17.I

Fish diversity, feeding groups and fish production estimated by fishery catches (Lakes Chad, Chilwa and George) or by estimation of fish consumption by birds (Lake Nakuru) (from Lévêque, 1995b).

Fish predators

There is sometimes a tendency to act as though man is the only major predator of fish. In reality, in many water bodies, other vertebrates consume large quantities of fish. This is the case for various species of water birds with piscivorous diets, and whose presence in an aquatic environment depends on the availability of food. Their impact on fish communities, long underestimated, is sometimes considerable and can rival fishing, at least in appearance. In fact, piscivorous birds consume many diseased fishes that are incapable of escaping predators, and some scientists believe that they thus contribute to limiting the spread of certain epizootic diseases.

The white pelican (*Pelecanus onocrotalus*) has been found to consume 1.2 kg daily (Din & Eltringham, 1974). Other estimates range from 1.33 kg to 0.77 kg daily for breeding adults and immature birds respectively (Brown & Urban, 1969). These values correspond to fish consumption of approximately 10% of body weight. In areas with high concentrations of pelicans, such as Lake Nakuru (Vareschi & Jacobs, 1984), annual consumption can reach high values of between 650 and 2,400 kg (fresh weight) ha^{-1} yr^{-1}.

Hustler (1991) studied the consumption of the cormorant *Phalacrocorax africanus* and the darter *Anhinga melanogaster,* the most important piscivorous species on Lake Kariba. Daily, they respectively consume 20% and 11 % of their weight, the equivalent of 12% to 16% of artisanal coastal fishing. Their diet is mainly composed of small-sized fishes. The crocodile *Crocodylus niloticus* population, meanwhile, consumes 225 tonnes of fish a year, that is, 10% of the yield of artisanal coastal fishing (Games, 1990).

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