Role and consequences of fish diversity in the functioning of African freshwater ecosystems: a review

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Abstract

The need for a better understanding of the role of biodiversity in the functioning of aquatic ecosystems has been raised recently by several authors. If the question is not entirely new, its formulation is. It is therefore the opportunity to re-examine the pool of data already available in order to discuss some results that may be relevant for that purpose, while some major ecological questions have been identified. The top-down view argues that the effects of fish predation cascade down the trophic chain and are responsible for controlling the state of the entire ecosystem. The influence of fish predation on prey assemblages (prey selection, ontogenic shift) has been fairly well documented by various studies of African fish. They are also challenging subjects for studies of resource partitioning, a well documented example being given by zooplanktivores in Lake Turkana. The principle of cascading trophic interactions has been documented in Lake Victoria, after the introduction of a top predator, *Lates niloticus*. Another striking example is that of Lake Nakuru where the introduction of a tilapiine resulted in a substantial increase of bird diversity, by the extension of the food chain to fish-eating birds. This introduced tilapiine may be considered as a keystone species, but this concept is questioned. A possible origin of fish biodiversity is adaptive radiation, that is to say the differentiation of species in morphology and resource use through competition. The cichlid flocks of the African Great Lakes where hundreds of rather similar species coexist, provide one of the best known examples of adaptive radiation. The question of niche overlap and functional redundancy has been raised and various studies have been conducted in the East African Lakes. The role of rare species has also been questioned. They may provide an insurance of ecosystem stability, which means that the more stable ecosystems in terms of key functions are those richest in species. In fact, in many large Nilo-Sudan river basins, there are apparently several groups of species which are able to replace the current assemblage when it experiences new ecological situations. Finally, the question has been raised as to what extent patterns of biodiversity are important for ecosystem productivity. The comparison of data for four African lakes shows no relationship between fish diversity and fishery production, and species richness does not appear to be a major determinant of basic production trends. At present we have only anecdotal, sometimes controversial, evidence of the role of fish diversity on the functioning of African freshwater ecosystems. We need to improve this knowledge on the importance of biodiversity in order to convince decision-makers that fish biodiversity needs protection.

Keywords: Fish, Africa, biodiversity, predation, resource partitioning, trophic cascade, keystone species, rare species, adaptive radiation, productivity.

Synthèse sur le rôle et les conséquences de la diversité piscicole dans le fonctionnement des écosystèmes aquatiques continentaux africains.

Résumé

La nécessité de mieux comprendre le rôle de la biodiversité dans le fonctionnement des écosystèmes aquatiques a été soulignée récemment par de nombreux auteurs. Ce n'est pas tellement la question mais plutôt la manière de la formuler qui est originale. Dans la mesure où de nouvelles problématiques ont été identifiés par les écologistes, il est bon de ré-examiner l'ensemble des données déjà disponibles afin de rechercher des informations qui pourraient contribuer à la réflexion. L'approche hiérarchique

descendante suppose que les effets de la prédation par les poissons se transmettent en cascade le long de la chaîne trophique et contrôlent ainsi l'état de l'écosystème dans son entier. L'influence de la prédation sur les communautés de proies (sélection des proies, changements de préférence alimentaire en cours de développement) est assez bien documentée par plusieurs études sur les poissons africains. Ces données peuvent également servir de support aux discussions concernant le partage des ressources, dont un exemple bien connu est celui des poissons zooplanctophages du lac Turkana. La théorie des cascades trophiques a été vérifiée dans le lac Victoria après l'introduction du grand prédateur *Lates niloticus*. Un autre exemple remarquable est celui du lac Nakuru où l'introduction d'un tilapia a permis une augmentation substantielle de la richesse en oiseaux, par l'extension de la chaîne trophique aux oiseaux ichtyophages. Ce tipalia introduit peut être considéré comme une espèce clé de voûte, mais ce concept est discuté. Une origine possible de la diversité piscicole est la radiation adaptative, c'est-à-dire la différentiation des espèces du point de vue morphologique résultant de la compétition pour l'utilisation des ressources. Les foules d'espèces de Cichlidés des grands lacs africains, où des centaines d'espèces assez proches coexistent, fournit un des exemples les plus remarquables de radiation adaptative. Le problème du recouvrement des niches écologiques et de la redondance fonctionnelle a été discuté à la lumière de nombreux travaux qui ont été réalisés dans les grands lacs d'Afrique orientale. La question du rôle des espèces rares a également été soulevée. Elles peuvent représenter une assurance de stabilité pour les écosystèmes, ce qui signifierait que les écosystèmes les plus stables en terme de fonctions essentielles, sont ceux qui ont la plus grande richesse spécifique. En réalité il semble exister plusieurs groupes d'espèces de poissons dans les bassins nilo-soudaniens, certains étant susceptibles de remplacer les peuplements actuels lorsque les conditions écologiques se modifient. Finalement la question est posée des liaisons éventuelles entre la biodiversité et la productivité des systèmes. La comparaison de données issues de quatre lacs africains peu profonds montre qu'il n'existe pas de relation évidente entre la diversité piscicole et la production de la pêche. La richesse spécifique ne semble donc pas être un facteur essentiel pour la productivité des systèmes. A l'heure actuelle nous avons seulement des informations anecdotiques, et parfois discutables, sur le rôle de la diversité piscicole dans le fonctionnement des écosystèmes d'eau douce africains. Nous devons améliorer ces connaissances sur l'importance de la biodiversité de manière à pouvoir convaincre les gestionnaires qu'elle doit être protégée.

INTRODUCTION

In studying the interactions between environmental factors and ecosystem functions, many ecologists, in the past, gave more emphasis to processes (storage and transfer of matter and energy at different temporal and spatial scales) rather than to the species involved. They used simplified approaches based on a system's underlying structure and function in order to explain its dynamics and left species diversity out of consideration (Le Cren and Lowe-McConnell, 1980). Therefore, the role and importance of species diversity has not been well investigated and this field of ecology is still largely open.

Diversity is a fundamental property of every biological system. Biological diversity (shortened to biodiversity) was defined as "the variety and variability of living organisms. This includes the genetic variability within species and their populations, the variety of species and their life forms, the diversity of the complexes of associated species and of their interactions, and of the ecological processes which they influence or perform" (Huntley, 1989). But it also includes the variety of life-history styles, and the number of interactions between organisms and the environment (Bruton, 1990).

The concept of biodiversity has been used in different ways. For a few people it is no more than an inventory of species, as is the case to certain extent when one considers that heralds of the biodiversity crisis originally paid most attention to the loss of species in deforested areas. Most ecologists now recognise that biodiversity defines a working system of interactions between species rather than just a list of species. In fact, the concept of biodiversity is very complex and embraces many different elements, often complementary but also very distinct. According to Noss (1990), biodiversity has three principal components:

– Composition: different genes, species, biological and physiological functions, habitats, communities and landscapes are the basic units of biodiversity;

– Structure: the patterns of organisation of biodiversity dictate how its components interact across the various boundaries separating cells, organisms, populations, and habitats;

– Function, e.g.: transfer of genes within species and speciation processes; behaviour of organisms and ecological interactions between and among different populations; role of biodiversity in the productivity and resilience of systems.

Currently, the functional relationships between species in ecosystems are still poorly understood, and one of the central questions dealing with biodiversity is: would it really matter if our living systems were

greatly simplified? The concept of biodiversity opens up a vast array of questions about the functional role of diversity in the ecological functioning of ecosystems, such as responses to perturbations or biological productivity. The massive loss of species, communities and ecosystems, as a consequence of landscape transformation and water management, makes it urgent to investigate the role of aquatic species in ecosystems. At present, there are few data with which to examine such questions, and even fewer for African freshwater systems. However, the re-examination of the pool of data already available is a unique opportunity to discuss some results that may be relevant for that purpose.

Of course, the function of biodiversity in ecosystems cannot be clarified by examination of only one group of animals, such as fish. The whole biota should theoretically be considered, and fish should be treated as part of the ecosystem, even while focusing on their particular ecological role. In the past, fishery biologists, particularly those working in tropical countries, traditionally have tended to consider fish in isolation, as a natural renewable resource, rather than as integral components of the aquatic ecosystem, interacting with other biotic and abiotic components of the whole system. This attitude led to major ecological disasters, such as he introduction of *Lates niloticus* in the Lake Victoria, and its dramatic consequences on the native rich endemic cichlid fauna. A better understanding of the role of fish diversity in the functioning of aquatic ecosystems should therefore be a prerequisite before further manipulation of African inland waters is undertaken (Lévêque, in press).

This paper does not provide new field data, but is an attempt to use the already published information in order to discuss some of the questions arising from the biodiversity concept. Given the assumed importance of biological diversity in ecosystem functioning, some major ecological questions have been identified:

— what is the linkage between species diversity and ecosystem function: is species composition responsible for particular ecological characteristics and processes of the system under study, when compared with other systems? Another related question could be: is the redundancy in function among species useful and necessary for ecosystems or is there an overriding influence of certain species in controlling both the structure and function of ecosystems (dominant species and keystone species) (di Castri and Younès, 1990a and b; Lawton and Brown, 1993; Paine, 1969);

— how is system stability and resistance affected by species diversity, and to what extent could the integrity and sustainability of ecosystems be maintained in spite of species deletions resulting from degradation of environmental conditions (Solbrig, 1991)? The ability to resist external episodic extreme perturbations could depend on system heterogeneity and species diversity;

— the relationship of species richness with such processes as biological productivity remains dubious and is an open question.

THE TOP-DOWN EFFECT

In the classical limnological approach, it was usual to envisage freshwater ecosystems as operating in a physical-chemical milieu which conditions the food chain from primary producers to top predators (Le Cren and Lowe McConnell, 1980). In this "bottom-up" control, competition between primary producers for limited nutrients determines the state of higher trophic levels. More recently, the role of fish in regulating the structure and functioning of freshwater ecosystems has become fashionable (Werner, 1986; Northcote, 1988).

The "top-down control" approach argues that the effects of fish predation cascade down the trophic chain and are responsible for controlling the state of the entire ecosystem. "The top-down view includes various ways in which fish affect the function and structure of an ecosystem in contrast with the bottom-up view which considers the ways in which food limitation and related physical-chemical factors affect fish" (Northcote, 1988). This author gave a review of some top-down effects of fish on inland waters and their consequences. Foraging activities of fish can directly affect water transparency and thereby primary and secondary production, either by stirring up bottom sediment or through intense phytophagous feeding. Fish also have direct effects on the abundance of phytoplankton, periphyton, and macrophytes, as well as on plankton and benthic communities. Size-selective predation by fish may not only play a major role in the population dynamics of prey species, but also result in shifts in the relative abundance of species. The influence of fish on nutrient cycling and transport, through nutrient release in faeces, and migration from one habitat to another, has certainly been underestimated in many studies. Diel vertical migration, for instance, may be an important means of transporting nutrients from deeper waters, perhaps below a thermocline, up into surface or pelagic waters. All the above effects are also time-related, and large seasonal changes may occur.

There is, of course, an important degree of complexity in the top-down processes involving fishes. Both top-down and bottom-up processes are involved, although in some systems, or at some times, one or the other may be paramount. Although most of the relevant studies have been conducted in temperate systems there are some results for African fish that could be re-interpreted from that perspective.

The influence of fish predation on prey assemblages

The effect of fish on the abundance and composition of their food had been widely documented (Lazzaro,

1987). It is not easy to evaluate the quantitative impact of fish on their prey in natural situation, and no confident study is available for African waters. However, many papers pointed out both the qualitative impact resulting from size selection, and the ontogenetic shift in the feeding niche during fish growth.

Prey selection

Passive size-selective predation by filter-feeders can dramatically lower the mean prey size and induce changes in the species composition of zooplankton communities. The retention efficiency depends on the structure and functioning of the branchial filtering apparatus, but many other factors are also involved, such as size and shape of the particles, mucus production, etc. (Lazzaro, 1987).

Various sympatric species may of course behave differently, and have specific impact on the prey communities. In Lake Chad for instance, the smallest prey captured by *Brachysynodontis batensoda*, a microzooplanktivore, are about 80 µm in length (Gras *et al.*, 1981). Nauplii and Rotifers are progressively selected as a function of their size up to 260 µm. The large microcrustaceans are mainly selected on the basis of their ability to avoid predation: the relatively big cladoceran *Moina micrura*, with low motility, is easily captured whereas the highly vagile Diaptomids are not. For *Alestes baremoze* which is another zooplanktivore in Lake Chad, large adults (230-250 mm SL) do not retain small sized nauplii and Rotifers, and the branchial filter retains particles from 400 µm in length. All filtered planktonic items above a size of 880 µm are collected (Lauzanne, 1970). The two species feeding on zooplankton therefore have different behaviour. *A. baremoze* feeds on bigger prey, and consumes more copepods than *B. batensoda*. The latter selects smaller prey such as rotifers and nauplii, more efficiently.

Planktivorous fish which select the largest available prey can rapidly reduce the density of large zooplankters, resulting in a shift of the prey community to small species, predominantly rotifers and small cladocerans. That could be demonstrated indirectly: where planktivorous fish are absent, large crustacean zooplankton predominate. For instance, in Lake Naivasha (Kenya), the presence and abundance of large cladocerans and copepods in the limnetic zone suggests a low predation pressure from fish (Mavuti, 1990). *Daphnia laevis* grows to between 2.0 and 2.5 mm, *Diaphanosoma excisum* occasionally attains 1.0 to 1.6 mm in length, whilst adults of *Tropodiaptomus neumanni* attain 2.6 mm (Mavuti, 1983). Actually, the present fish fauna of Lake Naivasha including juveniles is found almost exclusively in the littoral, rarely occurring in the limnetic zone. Predation pressure is therefore high on the littoral zooplankton, while it is low on the limnetic populations (Mavuti, 1983) and this is considered to be

a major trophic gap in the pelagic food chain (Mavuti, 1990).

In the absence of any experimental evidence on which to assess the impact of African fish on plankton assemblages, one can alternatively monitor the effect of the introduction of alien species on the planktonic communities of natural systems. For example, after the introduction of *Limnothrissa miodon* into Lake Kariba in 1967/1968, observations were made on the pelagic community (Begg, 1976). These was an obvious decline in the large zooplankters from 1968 to 1974, in particular *Ceriodaphnia, Diaphanosoma* and *Diaptomus*. This decline could be attributed to the introduced species. In 1973/1974 the diet of *L. miodon* included 80% *Bosmina longirostris* whereas *Mesocyclops leuckarti* numerically dominated the large zooplankton in the open lake. By 1976, *M. leuckarti* was the dominant food item of *L. miodon*, and *Bosmina* contributed only to 5% (Cochrane, 1978). Thus over a period of 10 years, the largest Cladocerans had declined markedly, and even the smallest ones such as *Bosmina* were disappearing. A small copepod later became the major food item, a situation approaching that in Lake Tanganyika (Turner, 1982).

In Lake Kivu where the clupeid fish *Limnothrissa* was introduced, the original open water zooplankton community, composed of large pigmented pond species of Cladocera and Copepoda, has also been modified with a drop in standing crop, a decrease in size of individuals and an increase in diversity (Dumont, 1986).

The influence of fish predation upon benthic communities has been observed in Lake Chad where malacophagous fish (*Synodontis clarias, S. schall, Hyperopisus bebe*) feed selectively upon young immature benthic molluscs, as demonstrated by the prey size frequencies in their gut contents (Lauzanne, 1975). This strong predation pressure results in a truncated size frequency in the benthic populations (*fig.* 1): despite sustained reproduction throughout the year, the size frequency distribution exhibits a domed shape, rather than that of a negative exponential. Predation on the young stages probably explains this unexpected demographic structure (Lévêque, 1972). Large molluscs are the main source of food for other malacophagous species such as *Tetraodon lineatus* (Lauzanne, 1977) and there is good evidence that the molluscivore fish populations controlled the benthic mollusc populations at the time when Lake Chad was not yet affected by the Sahelian drought. However, this domed shape structure has been observed in other living populations including molluscs and fish (Johnson, 1994). It has been dealt with in Johnson (1983, 1994) and is regarded as a general configuration of the dominant species in autonomous ecosystems.

Ontogenetic shift

Fish vary greatly in body size during their life, and often undergo drastic changes in ecology as they grow. Their dietary requirements and their feeding behaviour
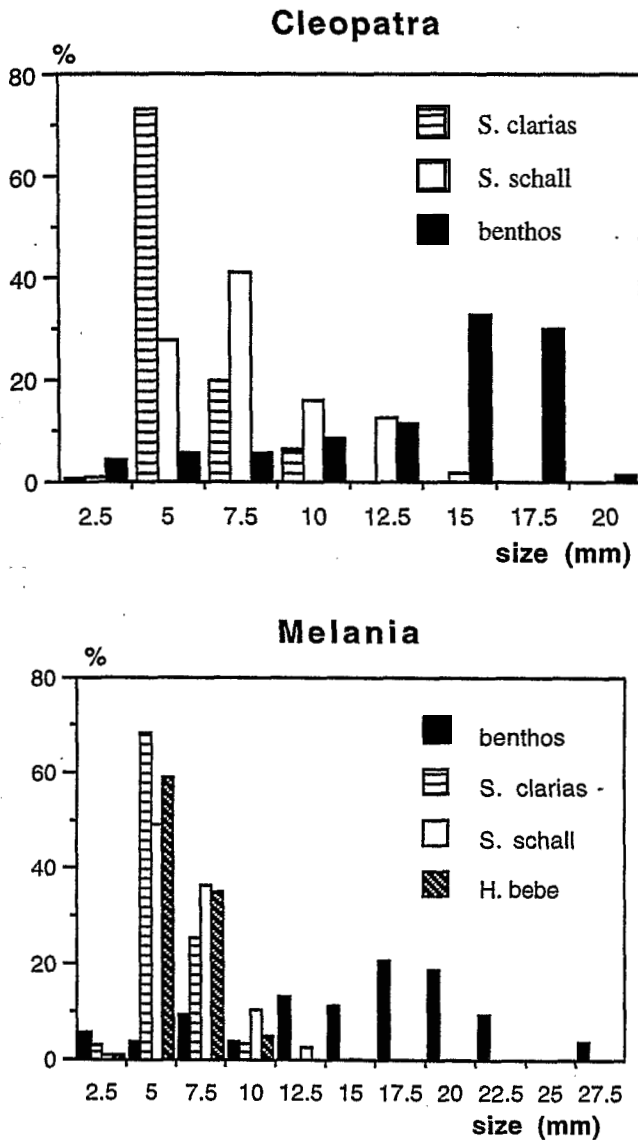
Cleopatra

Melania

Figure 1. – Comparison of size distribution of benthic molluscs in Lake Chad benthos and in the gut of malacophagous fish species (*Synodontis clarias, S. schall, Hyperopisus bebe*) (data from Lauzanne, 1975).

change also. Usually these changes are related to the ability of growing animals to handle particular food types. Most fish feed on plankton during at least part of their life. Many fish larvae of non-planktivorous species consume zooplankton or phytoplankton before switching to larger prey.

According to Werner (1986), when ontogenic shifts occur, they almost always involve shifts to larger prey, as corroborated by theoretical and empirical studies. This ontogenic niche shift involves trade-offs of current growth, mortality and birth rates and is closely related to the problem of optimal life histories. An implication of the existence of a relationship between body size and prey size is that juveniles

of large species have resource requirements similar to those of adults of smaller species. Such competition may result in a significant bottleneck to recruitment to the adult stages of larger species.

Size specific shifts in food or habitat type have been documented in many species. For *Hydrocynus forskalii* in the Chari River (Lauzanne, 1975), juveniles up to 300 mm are almost strictly zooplanktophages. Between 30 and 45 mm they eat both zooplankton and insects. Above 50 mm length, they become strictly piscivorous (*fig.* 2 A). In the Lake Chad eastern archipelago, a similar but less clear pattern has been observed, shrimps being another important food item in the diet of *H. forskalii* (*fig.* 2 B).

Diet also changes with individual growth in cichlids. A peculiar behavioural and morphological development has been reported for *Docimodus evelynae* a cichlid species from Lake Malawi (Ribbink, 1984, 1990), in which small juveniles (less than 50 mm SL) are facultative cleaners, removing fungi
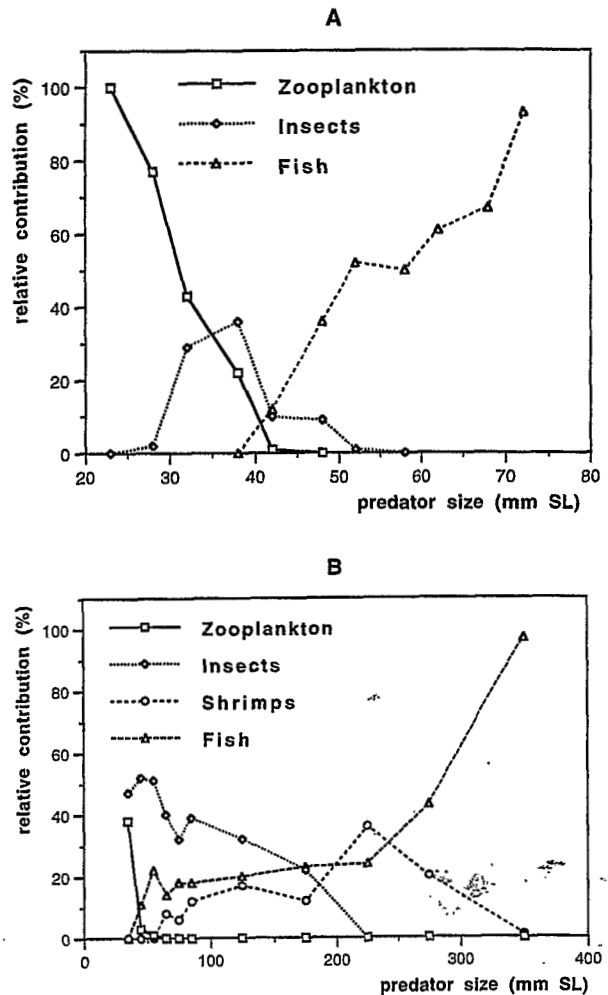
A

B

Figure 2. – Changes in the proportions of food items consumed by *Hydrocynus forskalii* in the Chari River (A) and the South-Eastern Archipelago of Lake Chad (B).

from other cichlids. From 50 to 70-80 mm SL, they are no longer cleaners, and feed upon plankton, insects and aufwuchs. Above 80 mm SL, their dentition changes (the juvenile tricuspid teeth are replaced by adult unicuspid teeth) and adult *D. evelynae* alter their diet to feed upon scales, fins and skin of their fish prey. Field data has also provided evidence that as *D. evelynae* grow, they move into deeper water. As a result of the depth restricted distributions observed for many species in Lake Malawi, the cichlids cleaned by juvenile *D. evelynae* in shallow water are not the same as those preyed upon by adults in deeper water. Similar changes in feeding behaviour are reported for many other species which are simply too small as juveniles to utilise the same foods as the adults.

Resource partitioning

The use of food resources by fish has a major influence on the dynamics of prey populations and on their availability, and it is possible that resource limitation and intra-specific density-dependence may occur in fish communities. Therefore, studies of species resource requirements. have been used in attempts to understand factors controlling the distribution and abundance of the prey (Ross, 1986). If resources shared by two species limit population sizes, it would be expected that an increase in the availability of resources may relax temporarily interspecific competition; species freed from this limitation may then become limited by some other factor such as predation, or an abiotic factor. Research on "resource partitioning", which means how species differ in their resource use, has as its primary goal description of the limits that interspecific competition places on the number of species that can stably co-exist (Roughgarden, 1976). Differences in resource use may be due to varying tolerance to environmental variables, local spatio-temporal resource availability, competition or predation risks.

Fish are challenging subjects for studies on resource partitioning because, unlike most vertebrates, they exhibit indeterminate growth, and many fish assemblages are temporarily structured (Ross, 1986). Analysis of 230 studies on the diets, spatial distribution, patterns of diel activity and use of other relevant dimensions by fish in an assemblage showed that temporal segregation was much less important than trophic or habitat separation. The greater importance of trophic rather than habitat partitioning in some aquatic habitats may result from the often pronounced morphological specialisation of fish trophic mechanisms for capturing prey, as well as low habitat specialisation by fish living in habitats of limited duration (Ross, 1986).

An example of trophic partitioning in an African lake is given by the study of tropho-dynamic relationships among 11 species of zooplanktivores investigated in Lake Turkana and daily changes in the pelagic fish assemblage (Hopson and Ferguson, 1982).

Resource partitioning was accomplished in several ways:

(i) spatial separation of competitive species achieved by differences in vertical and horizontal distribution and by diel migration;

(ii) interspecific differences in prey size selection;

(iii) interspecific differences in diel feeding patterns;

(iv) ontogenetic changes in diet.

During the day, *Alestes baremoze* fed principally on *Tropodiaptomus banforanus* in the surface layers while postlarval *Engraulicypris stellae* ingested copepod nauplii and diatoms. At intermediate depths two species of small *Alestes* coexisted: *A. minutus* preying chiefly on zooplankton, and *A. ferox* preying on small fish and prawns in addition to zooplankton. Adult *Engraulicypris stellae*, which fed entirely on zooplankton, were scattered over the lower part of the water column between the midwater and the bottom. In contrast, *Lates* spp. post larvae ranged throughout the entire column and thus overlapped with the preceding species, as well as with *Synodontis schall* which at times fed exclusively on zooplankton.

Considerable changes in the distribution of pelagic fish occurred towards night. *A. minutus* and *A. ferox*, which fed also at night, migrated upwards into the surface layers, and their food changed considerably. For *A. minutus*, Cladocera dominated in the food by day whereas *Tropodiaptomus banforanus* was eaten almost exclusively by night. For *A. ferox*, *T. banforanus* also became the predominant food at dawn. This shift from one prey to another may have an importance for survival in situations where particular prey species are likely to be periodically depleted. *Lates* sp. post larvae and *A. baremoze* do not feed at night whereas *S. schall* is principally a nocturnal feeder.

As usual, selectivity of prey varied both within and between species. Ontogenetic changes were important in *Engraulicypris stellae* where the smallest size groups fed entirely on diatoms, switching almost exclusively to adult copepods when they had grown above 20 mm length. *Lates* sp. post larvae longer than 6 mm fed exclusively on adult copepods.

Interspecific competition among the inshore zooplanktophages was also decreased by variations in the diel feeding cycle and habitat segregation. *Aplocheilichthys rudolfianus*, small *Raiamas senegalensis* of under 22 mm FL and *Lates* sp. of 22-37 mm TL fed exclusively on zooplankton. For *R. senegalensis* and *Lates* sp., feeding was limited to daytime. Other species with a mixed diet such as *Brycinus nurse*, large *Raiamas senegalensis* and inshore *E. stellae*, likewise fed on non-insect plankton during the day, but switched to planktonic insect food after dark. At times of food shortage, the minute characid *Micralestes acutidens* which usually fed on zooplankton with a large proportion of nauplii, may ingest the blue green algae *Microcystis* in large quantities.

Cascading trophic interactions

The concept of cascading trophic interactions reflects an elaboration of long-standing principles of fishery management based on logistic models. In simple words, a rise in piscivore biomass results in decreased fish zooplanktivore biomass, which in turn allows an increase in herbivore zooplankton biomass, and decreased phytoplankton biomass (*fig.* 3). Productivity at a given trophic level is maximised at intermediate intensities of predation at all trophic levels.
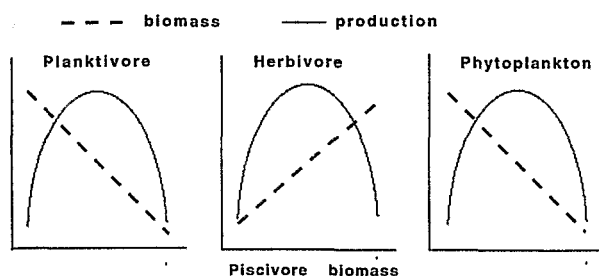

Figure 3. – Theoretical changes in biomass and production of vertebrate zooplanktivores, large herbivores, and phytoplankton in relation to piscivore biomass (from Carpenter *et al.*, 1985).

The concept of cascading trophic interactions links the principles of limnology to those of the fishery biologists. Potentially, variation of primary productivity is mechanistically linked to variation in piscivore populations. If piscivore populations can be controlled, it should therefore be possible to control the cascade of trophic interactions that regulate algal dynamics, through programmes of stocking and harvesting (Carpenter *et al.*, 1985). For these authors, "altering food webs by altering consumer populations may be a promising management tool".

In natural environments, sequences of cascading trophic interactions will be propagated from stochastic fluctuations in piscivore year-class strength and mortality. Fish stocks, reproduction rates and mortality rates exhibit enormous variance, and lags in ecosystem response occur because generation times differ among trophic levels. Examples of lags may be found in the development of the predator, when it acts first as a zooplanktivore (during its juvenile stage) and then as piscivore. As a planktivore, it drives the ecosystem toward small zooplankton and higher phytoplankton abundance which is the reverse of when the fish grows and becomes a predator of zooplanktivorous fish. If potentially a system may be managed by increasing or decreasing the intensity of piscivore predation, the system responses are non-equilibrium, transient phenomena that are difficult to detect using long-term averages. Nevertheless, in a few cases, following for instance the introduction of a new predator in an aquatic ecosystem, examples of trophic cascades have been documented.

A well-documented example of the effects of a predator on a tropical aquatic community was the accidental introduction of the cichlid piscivore, *Cichla ocellaris*, to Gatun lake, Panama, around 1967 (Zaret and Paine, 1973). In less than 5 years, the introduced species, which has voracious predatory habits, led to the elimination of six of the eight common fish and decimated a seventh. The removal of so many elements of the food chain, considerably simplified the system as a whole and changes were observed in the zooplankton and the phytoplankton.

In Africa, a striking example of a trophic cascade is known from Lake Victoria where the depletion of haplochromines by Nile perch shows how a predator can affect other trophic levels. The detritivore/phytoplanktivore group of haplochromines, as well as the zooplanktivores group, which constituted 40 and 16% respectively of the total demersal fish biomass, disappeared in the early 1980s simultaneously with the explosive increase of the introduced Nile perch. They seem to have been replaced by the native detritivorous atyid prawn *Caridina nilotica*, and the native zooplanktivore Cyprinid *Rastrineobola argentea* (Witte *et al.*, 1992; Goldschmidt *et al.*, 1993). The two latter species became major prey for the Nile perch after the decline of the haplochromines. The introduction of the Nile perch therefore severely disrupted the ecosystem, with a simplification of the food web through virtual eradication of haplochromines from many interactions, and the development of short food chains to the Nile perch. Whereas the haplochromines converted numerous protein sources (algae, zooplankton, insect larvae, molluscs, etc.) into fish protein for consumption by higher trophic levels, Nile perch now eats quite a lot of its own juveniles, which in some way feed on the same food items as the haplochromines did previously. Another consequence of the introduction of *Lates* into Lake Victoria, and the subsequent crash of the native cichlid populations feeding on invertebrates, was a population explosion of emergent insects, which at times resembled a cloud over the lake. This insect population in turn is now supporting a huge population of the sand martin *Riparia riparia* which winters in Africa, and has increased massively from small numbers to hundred of thousands (Sutherland, 1992). It should be noted, however, that there were always lake fly swarms over Lake Victoria (Beadle, 1981). other changes were also observed at the top of the food pyramid. The pied kingfisher (*Ceryle rudis*) shifted from a diet of mainly haplochromines to one that consists exclusively of *Rastrineobola* (Wanink and Goudswaard, 1994), but more fish need to be caught to meet daily energy demands (from 17 haplochromine in the former years to 55 nowadays) and hunting time is increased (Goudswaard and Wanink, 1993). A similar shift in diet was also found for the Great Cormorant *Phalacrocorax carbo* and the Long-tailed Cormorant *P. africanus* (Goudswaard and Wanink, 1993).

It may be of interest to compare the food web suggested by Witte *et al.* (1992) to the food-web proposed some 60 years ago by Worthington (*fig.* 4-5). One of the main differences is the disappearance of the crocodile from Lake Victoria which was a crocodile-infested lake according to Worthington (1933). "Crocodiles act as an important link between the larger water creatures and man, unless they take it into their heads to reverse the topmost link". The disappearance of crocodiles, some decades ago, certainly led to profound modifications in the lake fish assemblages, that unfortunately are not adequately documented. An interesting question would be to know if the introduced *Lates* would have been better controlled in Lake Victoria if the crocodiles were not extinct.
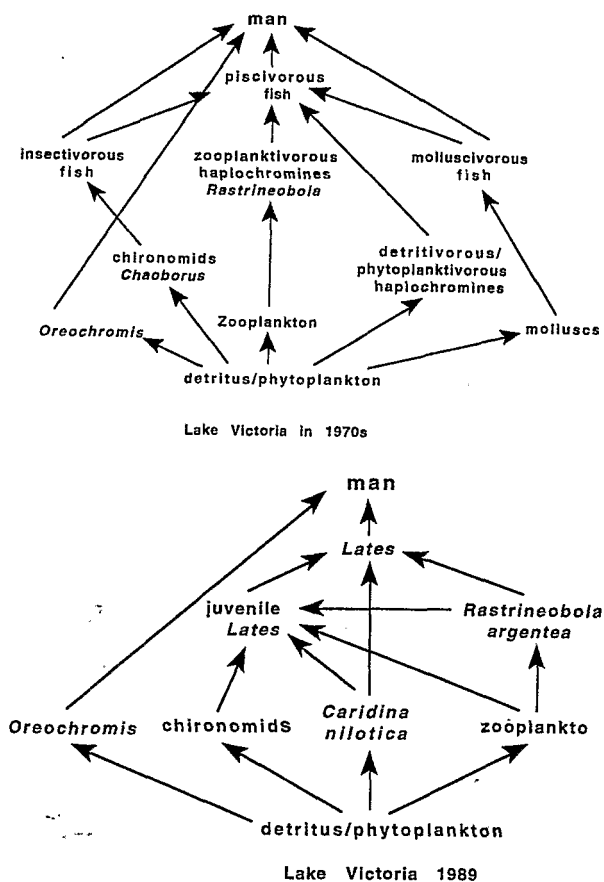

Lake Victoria in 1970s

Lake Victoria 1989

Figure 4. – Simplified diagrams of the food web in the sub-littoral area (6-20 m deep) of Lake Victoria in the 1970s and in 1989 (Modified from Ligtvoet and Witte, 1991).

Another example of a trophic cascade is provided by the introduction of *Oreochromis alcalicus grahami* to Lake Nakuru. In this saline lake, previously devoid of fish, the cichlid introduced in the 1950s developed quickly, feeding on the high standing crop of the cyanobacteria *Spirulina platensis*. All primary consumers in the lake – Lesser Flamingos, fish,
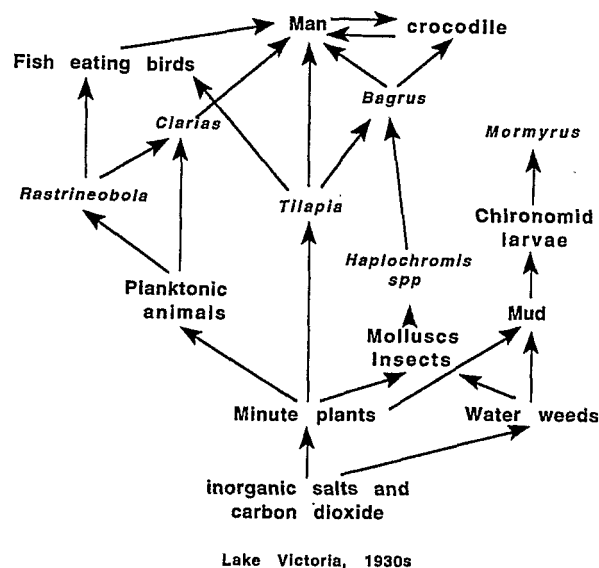

Lake Victoria, 1930s

Figure 5. – Simplified food chains of Lake Victoria during the 1930s (from Worthington, 1933).

copepods, rotifers, chironomid larvae and corixids – together consume about 1% of the algal biomass per day (Vareschi, 1978). It is therefore very unlikely that the grazing *Tilapia* compete with other grazers and/or significantly reduce the algal biomass whose turnover rate may even be accelerated by additional grazing. But the most striking effect of the introduction on the Lake Nakuru ecosystem has been a substantial increase in diversity by the extension of the food chain to fish eating birds, of which the Great White Pelican is dominant (85% of the biomass of fish eating birds) (Vareschi, 1979). The bird life of the lake was poor in the 1950s since there were few other water birds beside the huge number of flamingos: they later increased to more than 50 water bird species. Fish-eating birds started to invade Lake Nakuru around 1963, about two years after the fish were introduced. It was estimated that breeding pelicans harvested some 16-20 000 kg fresh weight of fish each day, removing some 72 kg of phosphorous and 486 kg nitrogen every day (Vareschi, 1979; Vareschi and Jacobs, 1984).

If we agree with the idea that it is possible to manage lake ecosystems through trophic manipulations and the introduction of species, one could understand that fish diversity may find a wide field of application. Selection of species according to their trophic behaviour needs a better knowledge of their life cycle and their ability to adapt to new ecological situations. A good knowledge of the ecological requirements of wild fish populations may be useful in the process of selecting candidates for biomanipulation. The above example of the introduction of *O. alcalicus grahami* to Lake Nakuru is an application of that knowledge, but less obvious and probably more sophisticated choices might be expected.

top predator

intermediate-level
predator

consumer
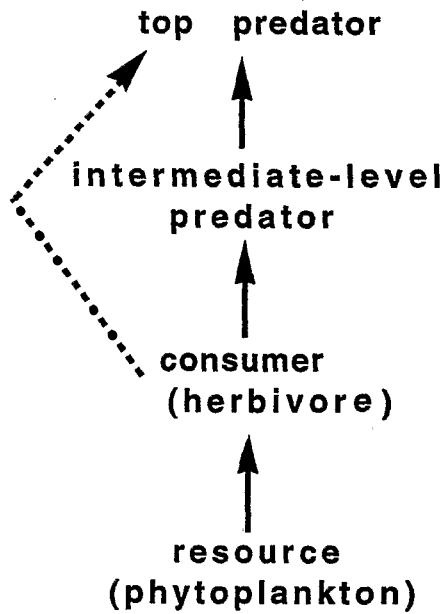(herbivore)

resource
(phytoplankton)

Figure 6. – The geometry of a cascading trophic interaction with and without intraguild predation. Trophic cascades are only possible if the IGP link is not strong compared to the link between the top and intermediate-level predators (from Polis and Holt, 1992).

Another level of complexity arises when species may be in a position to compete for prey at one stage of their ontogeny. Piscivorous species, for instance, usually begin their life by feeding on zooplankton or small invertebrates, in competition with species which will serve as an important fraction of their prey when they are large enough to become piscivorous.

Whereas many studies have analysed systems in which predators and competitors are considered as different species groups that interact, intraguild predation which is another class of interactions, combining predation and competition, has been less well integrated into the conceptual framework of ecology. Intraguild predation "is the killing and eating of species that use similar resources and are thus potential competitors" (Polis and Holt, 1992). Intraguild predation often occurs among species that eat the same food resource but differ in body size such that the smaller species is a potential prey for the larger. In particular, the young of many species are vulnerable to species with whom the adults may compete.

Intraguild predation interferes with trophic cascade scenarios that involve webs having between three and five links (e.g. plant-herbivore-intermediate level predator-top predator). A change in one trophic level could affect other levels. For instance, an increase in a top predator could result in a decrease of the intermediate level predator numbers, allowing herbivore abundance to increase, and ultimately increasing plant predation (*fig.* 6). This scenario could function in the absence of strong intraguild predation links (*i.e.* top predators that also eat herbivores). If
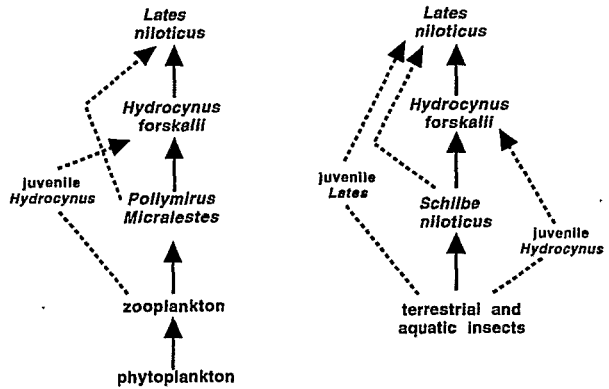
Figure 7. – Food webs with intraguild predation, illustrated with data from Lake Chad open water food chains (from Lauzanne, 1976). In the case of *Lates* and *Hydrocynus*, feeding on small pelagic zooplanktivores or on *Schilbe niloticus* (consumers), the top predator (*Lates*) also eats the other consumer. Both predator species when juveniles, also potentially compete with the consumer.

this link is strong, changes in the top predator will not cascade as predicted, or may even act in an opposite direction to that predicted above (Polis and Holt, 1992). The dynamic complexity of intraguild predation could possibly explain the difficulties (sometimes disasters) frequently encountered when exotic species are introduced into aquatic systems.

An example of intraguild predation may be suggested from food chain data obtained in the open waters of Lake Chad (Lauzanne, 1976) (*fig.* 7). The producers (phytoplankton) are consumed by zooplankton, itself serving as the main food source for small planktivore species (*Micralestes, Pollymirus*). The latter constitute the bulk of the food of the *Hydrocynus forskalii*, a piscivore when adult, but whose juveniles are at some stage zooplanktivores. *H. forskalii* is itself one of the few major prey species of the top consumer *Lates niloticus*, which also consume smaller planktivore fishes. Intraguild predation therefore occurs in this case at two different levels in the food chain. A similar pattern occurs with another food source. In the open waters of Lake Chad, Lauzanne (1976) stressed the importance of falling terrestrial insects in the food chain. They serve as the main food source of the pelagic *Schilbe niloticus* itself one of the major prey for *H. forskalii* and *Lates niloticus*. Juvenile *Lates* and *Hydrocynus* also consume terrestrial insects, and therefore theoretically compete for food with *S. niloticus* (*fig.* 7).

Keystone species

The question has been raised as to whether certain species are more important for global ecosystem functioning than others, and may have disproportionate influences on the characteristics of an ecosystem. The term keystone species was originally applied by Paine (1969) to a predator in the rocky intertidal zone. There are two hallmarks of keystone species: their presence

is crucial to maintaining the organisation and diversity of their ecological communities, and it is implicit that these species are exceptional, relative to the rest of the community, in their importance. For Chapin *et al.* (1992), keystone species is a functional group (see below) without redundancy, such that the addition or removal of that species causes massive changes in community structure and ecosystem process. The loss of such keystone species may transform or undermine the ecological process, even though they may appear numerically unimportant either in space and time (Mills *et al.*, 1993).

According to Solbrig (1991), three general classes of keystone species are recognised: (i) keystone predators, herbivores or pathogens that allow the maintenance of diversity among competing organisms by controlling the abundance of dominant species thus preventing competitive exclusion; (ii) keystone mutualists which link the fate of many partner species; (iii) species that provide keystone resources that are critical to the survival of dependent populations during bottlenecks of low resource availability. Keystone resource species are expected to be found in conditions where resource availability is low, whereas keystone predators should play a significant role in situations where competitive exclusion is not prevented by disturbances. This is a phenomenon similar to the intermediate disturbance hypothesis (Ward and Stanford, 1983), but in one case the species richness is maintained or increased by intermediate levels of disturbance involving abiotic factors, whereas in the other case, predation and competition, through control of dominant competitors, opens up room for maintenance of other species.

Long-term observations and/or experimentation are necessary in order to determine the existence of and to identity keystone species (Solbrig, 1991). For the moment, this concept of keystone species has not been investigated for African fish. But as discussed above (top-down effect), keystone predators have been convincingly demonstrated in aquatic communities. There is some empirical evidence that predators exert a control on prey populations, and examples are available for plankton, benthos and fish populations (see above). In Gebel Aulia Reservoir (Sudan), Hanna and Schiemer (1993) pointed out that *Alestes baremoze* and *Brycinus nurse*, exhibiting an opportunistic foraging behaviour, fill the niche of a zooplankton feeder in the absence of a specific zooplanktivorous fish, but can shift to insects and plant material in other circumstances. As a result of their high population density, it is likely that they can function as keystone species influencing zooplankton composition and in turn phytoplankton productivity and nutrient dynamics in Gebel Aulia Reservoir.

There are also experimental demonstrations of the existence of keystone predators using either fish removal experiments or species introductions. The most obvious demonstration of the existence of keystone predators is given by the introduced

Nile perch in Lake Victoria. The cascading effect, associated with other man-induced changes, has resulted in the disappearance of many haplochromines, and possibly in the increase of phytoplanktonic production (Goldschmidt *et al.*, 1993; Hecky, 1993; Mugidde, 1993). One can conclude therefore *a contrario* that the disappearance of *Lates* from any freshwater ecosystem where it presently occurs would also result in changes in the overall functioning of that system.

The introduced *Oreochromis alcalicus grahami* in Lake Nakuru (see above) might now be considered as a keystone resource species. Indeed, the disappearance of that species, supporting a huge population of piscivore birds, would dramatically affect the ecosystem as a whole. Such a disappearance could result from long-term climatic cycles, or for example temporary drying out of the lake, resulting in the elimination of the fish. This situation has certainly occurred in the past and explains the poor fish fauna currently present in various shallow lakes. In the case of Lake Nakuru, high water salinity also explained the absence of fish before the introduction of *O. alcalicus grahami*.

It should be stressed that piscivore fish are more vulnerable to fishing gear than benthivores or planktivores, and that explains why the proportion of fish predators, which is usually high in the catch when starting to fish a virgin stock, decreases rapidly when the fishing effort is maintained. The depletion of the predator stock following exploitation should have feedback consequences on the abundance of prey, which could initiate a host of indirect effects, including intense competition between species previously coexisting at lower densities. Unfortunately, documented data are not available for African inland waters.

The concept of keystone species has been questioned by Mills *et al.* (1993). If the term keystone species is very popular among both scientists and managers, it nevertheless lacks clear definition, and means different things to different people. Moreover, it is very difficult to define objectively which species are keystone, and it is likely that subjectively chosen groups of species will be so labelled, whereas other species of similar importance will be ignored (Bender *et al.*, 1984). Finally, the keystone role of a given species is particular to a specific set of environmental conditions and species assemblages, and that does not take into account the spatial and temporal variability of those associations (Gauthier-Hion and Michaloud, 1989).

Recognising that the concept has been useful in demonstrating that under certain conditions some species have particularly strong interactions, Mills *et al.* (1993) claimed however that emphasising strengths of interactions within communities, instead of a keystone/non-keystone dualism, is a better way to recognise the complexity as well as the temporal and spatial variability of interactions. In the long

run they expect that despite the danger of making communications between biologists and policy makers more difficult by the abandonment of a popular and evocative concept (keystone species), this attitude will favour the development of management guidelines which will explain more explicitly the complexity of interactions in natural systems.

Trophic interactions have been used by most authors to identify keystone species, but other kinds of interaction exist. Actually, we know nothing about the potential control of African freshwater fish populations by keystone pathogens although their role has been demonstrated in temperate waters.

FISH BIODIVERSITY AND RESPONSES OF ECOSYSTEMS TO PERTURBATION

"Perturbations" are changes that occur in environments. Some perturbations may cause no response. others could be described as "catastrophes", as, for example, when the habitat of some population is destroyed and the population becomes locally extinct. In between these extreme perturbations, any disturbance will usually cause some response by the populations under study. Detection of perturbations, and responses of communities, refers more or less implicitly to the concept of equilibrium. However, the definition of equilibrium in natural populations is not an easy task, given that organisms fluctuate widely in time and space, as well as do their food or their pathogens (Connell and Sousa, 1983).

A general definition of "disturbance" has been given by Pickett and White (1985) and modified by Resh et al. (1988): "any relatively discrete event in time that is characterised by a frequency, intensity, and severity outside a predictable range, and that disrupts ecosystems, community, or population structure, and changes resources or the physical environment". The word "stress" has also been used in a more or less similar way (Underwood, 1989).

When a population reacts to a perturbation, the capacity of the system to recover includes two components. The first important one, called stability, is the rate of recovery after the stress disappeared. There has been some confusion between stability and inertia, and the term "elasticity" (Orians, 1974) has also been proposed to mean rate of return to equilibrium. Stability must be measured in terms of a defined magnitude of stress. A population may recover at different rates with respect to stresses of different sizes. It should be noted that the word "resilience" has been used by some authors to mean the rate of recovery (see Begon et al., 1986).

The second component, which is the ability of a population to recover from different magnitudes of stress, has been called "resilience" (Holling, 1973). The magnitude of resilience could be measured by recording the amplitude of the largest response

to stress from which a population can reattain equilibrium.

There is no single answer to what determines resilience, but there are probably many factors operating. In the short term, the rate of recovery depends on the reproductive rate: the more young produced, the faster the population can recover its former level. It is likely that more resilient populations are to be found among species with high reproductive rates, which are usually small bodied species, with a short life span. But resilience in the long term also depends on the species interactions with other species in the community, and this could be explored through the length of food chain. Long food chains may be expected to reduce the resilience of the constituent species according to Pimm (1991). From this point of view, resilience may also depend on the availabity of food or the nutrients necessary for the species' growth, which is partially related to abiotic processes. At the ecosystem-level, the energy flow through the system and its availability for species could have consequences for the overall resilience of the system. There are therefore sets of factors at different hierarchical levels (population, community and ecosystem) which could be involved in resilience. Any one of these factors may predominate depending on the temporal or spatial scale under consideration.

Diversity and niche structure

According to ecological theory every species in an ecosystem occupies a specific niche which is a region in a factor space whose axes represent the critical resources or environmental variables to which species in the community respond differentially. The niche theory should, in principle, provide the theoretical framework to explain the number and types of species that exist in a community (Solbrig, 1991). According to Diamond (1988) the diversity of niches in a community could be determined by four sets of factors: quantity of resources, quality of resources, species interactions, community dynamics. However, application of niche theory to the prediction of the number of species in a community or to explaining why communities differ in number of species has proved very difficult in practice (Solbrig, 1991).

It could be more productive to view a niche as the identification of a specific array of environmental signals (a signal being a regular fluctuation in energy availability), constrained by the physiological capacity of the species and the encroachment of other species on the signals (competition) (Johnson, pers. comm.).

Adaptive radiation

If many species are present in tropical aquatic systems, is there a larger number of habitats or are there other different ways of exploiting the system than in temperate waterbodies? In some particular cases, fish speciation appears to be focused toward a better exploitation of the food resources available

in an ecosystem and, as well, in a large role of the fish community in the functioning of the aquatic ecosystem. Adaptive radiation is "a term used to describe diversification into different ecological niches by species derived from a common ancestor" (Futuyma, 1986). It is commonly viewed as the evolutionary diversification of a lineage across a variety of resources types. Among the suspected causes of the process is competition between species for resources: divergence of new species in morphology and resource use is hypothesised to be driven by competition between them for food, and facilitated by an absence of competition from species in other taxa.

The cichlid flocks of the African Great Lakes, where hundreds of species which are morphologically rather similar coexist, provide one of the best examples of adaptive radiation and speciation which have seemingly occurred rapidly and in the geologically recent past. That Cichlids show considerable adaptative radiation is demonstrated by the wide spectra of their trophic specialisations, correlated to anatomical and functional specialisations (Fryer and Iles, 1972; Greenwood, 1981, 1984) that have evolved in each of the lakes, where they occupy virtually every available habitat and niche. In Lake Victoria for instance, Witte and van Oijen (1990) distinguished 15 trophic categories (*fig.* 8). There are generalised detritivore bottom-feeders, phytoplanktivores, epilithic and epiphytic algal grazers, plant eaters, benthic invertebrates-feeders, zooplanktivores, molluscivores including oral shell-crushers and pharyngeal crushers, prawn-eaters, crab-eaters, piscivores including parasite-eaters removing leeches and crustacean parasites from other fish, scale eaters, and paedophages eating eggs and embryos from brooding female Cichlids. Parallel adaptations occurred in other lakes (Malawi, Tanganyika) where similar diversities of resources are used. Apparently, all the major potential food resources are utilised by Cichlids in each lake, which is not the case for the fish species belonging to other families.

Functional morphology has demonstrated that the trophic apparatus of African Great lakes Cichlids has undergone a spectacular functional diversification, unparalleled by any other family of fish (Liem, 1991 for review). It was noted (Greenwood, 1974; Coulter *et al.*, 1986) that only slight morphological and anatomical changes, e.g. in the feeding apparatus (mouth, teeth, guts), has resulted in profound changes in the feeding habits of species. This small diversity in body form has been pointed out by Greenwood (1984), and is an illustration that Cichlids have experienced a major ecological evolution independently of a morphological one.

Niche overlap and functional redundancy

One of the key questions is whether two species can have the same niche, and various authors raised the issue of "functional redundancy" (Solbrig, 1991;
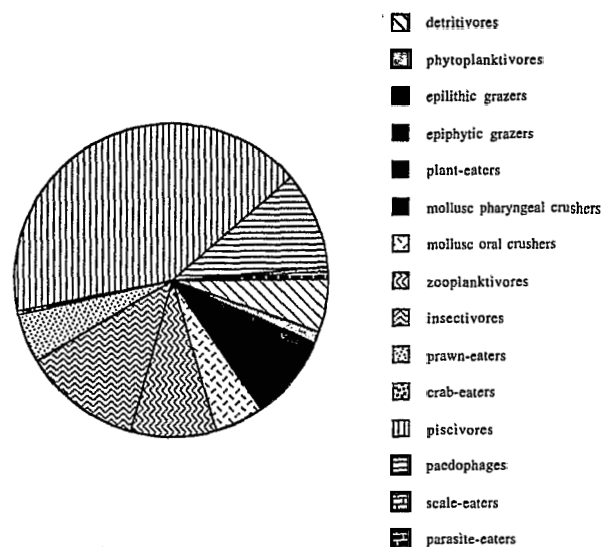

Legend:
- detritivores
- phytoplanktivores
- epilithic grazers
- epiphytic grazers
- plant-eaters
- mollusc pharyngeal crushers
- mollusc oral crushers
- zooplanktivores
- insectivores
- prawn-eaters
- crab-eaters
- piscivores
- paedophages
- scale-eaters
- parasite-eaters

Figure 8. – Trophic specialisations among Cichlids in Lake Victoria and relative number of species (data from Witte and van Oijen, 1990).

di Castri and Younès, 1990). According to this hypothesis, within some functional types there are multiple species that perform the same function and are ecologically equivalent. Is it necessary to maintain all these species to ensure the ecosystem functions or is it possible that some species can be lost from the community with little effect on ecosystem processes, as long as each functional group is represented. This question is central for ecosystem management and conservation purposes. It also has to be investigated in relation to the number of functional types in the ecosystem. An ecosystem in which species diversity is associated with many functional types so that only a few functionally analogous species belong to each type, is likely to respond differently to disturbances or environmental changes, from an ecosystem in which high species richness results from relatively few functional types, with many functional analogs within each types (Solbrig, 1991).

The corollary question to functional redundancy is, how similar can two coexisting species be in the same community? Present theory predicts that two species with similar niches cannot coexist but this seems to be verified only by few empirical studies (Roughgarden, 1989) and for tropical freshwater fish very few data are available.

One of the interesting ecological problems dealing with the cichlid communities of the African Great Lakes is how numerous allied species, sharing seemingly similar foods, manage to coexist. The niche theory predicts that the more the niches of different species overlap, the more likely it is that competition will occur. The question is to check for evidence of the presence of stably coexisting species which do not show any partitioning of resources in spite of their limited availability. This stimulated a number of studies on the patterns of resource use by species.

In Lake Victoria for example, the coexistence of many related species, often sharing the same resources, raises the question of the existence of factors which allow many sympatric species to avoid too intensive competition. There are 30 to 40% piscivorous haplochromine species and one of the explanations is that many species are localised to particular habitats and do not therefore coexist in the same locality (Mayr, 1988). Van Oijen (1982) demonstrated that piscivorous haplochromine cichlids are specialized predators: although able to feed on a range of organisms, the various species have a strong preference for certain food items. Besides specialisation on prey fish species, prey size partitioning plays an important role. The food specialisations are often correlated with habitat restrictions.

It has also been demonstrated by a few detailed ecological studies that niche segregation does exist in the zooplanktivores of Lake Victoria in spite of an apparent niche overlap (Witte, 1984). It has also been demonstrated (Van Oijen et al., 1981; Witte, 1984) that populations are spatially isolated in Lake Victoria, and intralacustrine allopatry of species is an important way to prevent direct competition between species feeding on the same resources.

From various detailed studies on the very specialised cichlid fish communities of the East African Lakes, it has become clear that species exhibiting broadly similar behaviour and requirements in fact have developed specific strategies so that they avoid niche overlap. Goldschmidt et al. (1990), studying a group of zooplanktivorous haplochromines from Lake Victoria which showed a large overlap in gross morphology, were able to observe distinct segregation patterns suggesting that these species were ecologically isolated to a great extent. Niche partitioning by habitat is the predominant way of avoiding competition between species. Clear horizontal segregation patterns were observed for the adults and the juveniles. Species which segregated little horizontally, did so vertically. Significant differences in diet could also be the consequence of a non-random distribution of food in space. Niche segregation may be reinforced by reproductive patterns. Among the Victoria zooplanktivores, the taxonomically most similar species differed most when breeding characteristics were taken into account (Goldschmidt and Witte, 1990). As a whole, space-sharing mechanisms include diurnal/nocturnal activity cycles, separate feeding areas both for developmental stages of one species and for related species, shelter sites, or spawning sites.

An important observation on cichlid fish from Lake Victoria, is that specialised trophic types are nevertheless facultative feeders, utilising a variety of different food resources. Paradoxically, species apparently specialised for certain food sources have the potential to exploit a wider range of food niches, while generalists cannot do the reverse and are unable to exploit exclusively specific trophic niches without

the necessary anatomical specialisations (Greenwood, 1984; Mayr, 1988). In Lake Victoria for instance, zooplanktivores, detritivores and insectivores all swtich to the diatoms Melosira sp. when there is a planktonic bloom (Witte, 1984).

Rare species

Species differ greatly in abundance, and some are extremely rare and highly localised. Using the word "rare" is a statement about the distribution and abundance of a particular species, but there are a large number of causes which may explain this rarity. Some of them relate to the geological and evolutionary history of the taxon in question, while others are the result of man's activities. Different causes of rarity also result from phenomena that are distinguished by different temporal and spatial scales (Fiedler and Ahouse, 1992).

Many fish species are rare species in one or more of the following senses: their distribution is clumped and individual abundance is low; their distribution is broad but they are found only at very low numerical abundance compared with others; the distribution is narrow yet populations are represented by many individuals where they are found. Rarity is undoubtedly a natural and common phenomenon, and causes include specialised habitat requirements, trophic position, limited dispersal abilities, and pattern of range expansion after speciation and of range contraction before extinction (Gaston and Lawton, 1990). For a long time, ecologists have considered that large-bodied animals occur at lower population densities than small-bodied animals, but recent studies show that the correlation between population density and body size is feeble and often non-existent (Lawton, 1989; Gaston and Lawton, 1990), and fish are no exception.

Do these rare species play a role in ecosystem function? For some authors they may be viewed as a record of the past: rare species are those that have, as yet, avoided extinction. Populations of a number of species have apparently persisted for thousands of years, even though many are small and very isolated as is the case, for example, for the remaining isolated fish populations in the northern Sahara (Lévêque, 1990). For other authors, they are alternative components of the ecosystem, or else as insurance policies so that roles will be fulfilled even though changes occur (Main, 1982). In fact, common organisms perform the bulk of essential ecosystem functions. However, biotic and abiotic environments change through time, leading to correlated changes in the relative abundance of species. One can assume that stable ecosystems are those in which essential functions are maintained in the face of disturbance. Thus rare species, which make up the bulk of the taxa in most ecosystems, provide an insurance of ecosystem stability, even though they might be considered as non-essential in terms of ecosystem function at the present moment

(Pate and Hopper, 1993). This hypothesis may lead to the conclusion that the most stable ecosystems in terms of key functions are those richest in species. However, there are not enough well documented studies of rare species substituting for declining common species in the maintenance of key ecosystems functions following disturbance.

A possible example is that of the changes in the fish assemblages of Lake Chad as a result of the Sahelian drought which was one of the major climatic events of the last two decades. The drought started in 1972 and resulted in drastic changes of the water level of the lake (Carmouze *et al.*, 1983). It started by an overall drying up from 1972 to 1974, with a severe change from a stable lacustrine appearance (called "Normal Chad") to an unstable marshy appearance. This first phase was followed by the drying of the north basin in 1975. The lake was therefore restricted to the south basin ("Lesser Chad") and moved towards a new equilibrium, mixing at the same time the lacustrine and marshy characteristics.

Modification of lacustrine hydrology caused serious disturbances to fish populations in the lake, but also in the associated lower reaches of the Chari and Logone rivers and their floodplains. Reduction of lake area had different consequences on the environment.

– Fish concentrate with the decrease of the water volume. The consequences were an increase in inter and intraspecific competition, and a higher vulnerability to fishing gear.

– The lacustrine landscape was completely modified with an extreme reduction of open waters without any vegetation, and conversely the development of marshy biota resulting from the decreasing depth.

– With decreasing depth, the wind disturbance allowed resuspension of sediment and consequently high water turbidity. In the same time, storms caused severe sediment disturbances resulting in mass mortalities of fish, as a result of deoxygenation of water.

– The drying of the shallows caused isolation of parts of the lake, preventing the supply of flood water and fish movements. An abundant marshy vegetation then developed and, when decaying, partly contributed to the deoxygenation of the water.

During the "Normal Chad" period the abundance of open waters species that are also migrating species may result from the abundance of food resources in the lake compared to the river, and from the existence of floodplains allowing spawning in the lower reaches of the Chari and Logone Rivers, and providing also food and shelter for juveniles. During the drying phase, the open water species moved to more suitable habitats, either from south to north basin, or to the lower reaches of the Chari river (Quensière, 1976). For some true lacustrine species, the disappearance was accelerated either by natural or mass mortalities, fishing, or absence of recruitment due, for instance, to the isolation or the drying of spawning areas.

Conversely, the changes in environmental factors selected the development of marshy or palustrine species physiologically adapted to new conditions prevailing in the lake. Such a selection is illustrated by changes in species composition of the experimental catches in the South-east Archipelago (*table* 1). In "Lesser Chad" period, the floodplains played again their role of nursery but the trophic capacities of the lake were less than during the previous period, and the risks of hypoxia increased dramatically as long as the lake was invaded by aquatic vegetation.

In fact, the fish species pool in many large Nilo-Sudan river basins includes apparently several groups of species which are able to replace the current assemblage, when it experiences new ecological situations. As discussed above, some species (*Polypterus senegalus, Brienomyrus niger, Schilbe mystus, Siluranodon auritus*, etc.) which were obviously rare in Lake Chad during the period of high water, became dominant after the drought because they were able to develop in more marshy environments, probably as a result of better physiological adaptation but also in a situation of relaxed predation constraints. In other cases, such as after the damming of a river, the coexistence of a pool of pelagic species alongside the pool of truly rheophilic species made possible the colonisation of newly created reservoirs. In current lotic situations, most pelagic and palustrine species may be considered as rare species, but they demonstrate high colonisation potential as soon as they are faced with suitable environments. This ability of Nilo-Sudan fish assemblages to adapt to changing environmental situations is certainly both a result of and a necessity of survival when considering the long-term climatic changes that have prevailed in this region for millions of years.

"At present a general theory of rarity does not exist although one is sorely needed, both as part of a broader understanding of the dynamics of populations, and as a basis for determining conservation priorities" (Gaston and Lawton, 1990). Much can be learnt from the classical "compare and contrast" approach using assemblages of species from a variety of taxa, including fish which have contributed little until now to the improvement of this theory whereas they may be a very valuable biological model.

However, from his experience in Arctic freshwater systems, Johnson (1990, 1994, and pers. comm.) developed a theory based on thermodynamic considerations. In autonomous or "closed systems", only energy and entropy are exchanged with the external world. Briefly speaking, the dominant fish population in undisturbed and highly autonomous arctic lakes are characterised as being in a state of "least specific dissipation": the greatest biomass attainable for a given energy input. Such dominant populations exhibit a uniform type of structure characterised by individuals of large, uniform size, and low incidence of juveniles, and this pattern is widespread. Johnson concluded that ecosystems are formed at the point of intersection

Table 1. – Changes in fish species composition in the Lake Chad Eastern Archipelago during a period of drought (from Benech and Quensière, 1989). M: large-scale migratory fishes; R: aerial respiration; J-J: period January to July; A-D: period August to 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 deliciosus	*	*	*	*	*						
	Hippopotamyrus sp.	*	*	*	*	*	*					
	Bagrus bayad	*	*	*	*	*	*					
	Chrysichthys auratus	*	*	*	*	*						
	Labeo coubie	*	*	*		*						
	Brycinus macrolepidotus	*	*	*		*						
M	Hydrocynus brevis	*	*	*	*	*						
	Hydrocynus forskalii	*	*	*	*	*	*	*				
M	Citharinus citharus	*	*	*	*	*						
M	Hemisynodontis membranaceus	*	*	*	*	*	*					
	Lates niloticus	*	*	*	*	*		*				
M	Hyperopisus bebe	*	*	*	*	*	*	*				
M	Marcusenius cyprinoides	*	*	*	*	*	*	*				
M	Petrocephalus bane	*	*	*	*	*	*	*				
M	Pollimyrus isodori	*	*	*	*	*	*	*				
M	Labeo senegalensis	*	*	*	*	*	*	*				
M	Schilbe niloticus	*	*	*	*	*	*	*				
	Synodontis clarias	*	*	*	*	*	*	*				
MR	Polypterus bichir	*	*	*	*	*	*	*				
R	Polypterus endlicheri	*	*	*	*	*	*		*	*		
	Auchenoglanis sp.	*	*	*	*		*	*		*		
M	Schilbe uranoscopus	*	*	*	*	*	*	*		*	*	
M	Brachysynodontis batensoda	*	*	*	*	*	*	*	*	*	*	
	Synodontis frontosus	*	*	*	*	*	*	*		*	*	
M	Synodontis schall	*	*	*	*	*	*	*		*	*	*
M	Alestes dentex	*	*	*	*	*	*	*		*	*	*
M	Alestes baremoze	*	*	*	*	*	*	*		*	*	*
	Brycinus nurse	*	*	*	*	*	*	*	*	*	*	*
M	Distichodus rostratus	*	*	*	*	*	*	*	*	*	*	*
R	Gymnarchus niloticus	*	*	*	*	*	*	*	*	*	*	*
R	Clarias sp.	*		*	*		*	*	*	*	*	*
	Tilapia zillii	*	*	*	*	*	*	*		*	*	*
	Sarotherodon galilaeus	*	*	*	*	*	*	*		*	*	*
	Oreochromis niloticus	*	*	*	*	*	*	*	*	*	*	*
	Oreochromis aureus		*	*		*	*	*		*	*	*
R	Polypterus senegalus			*	*	*	*	*	*	*	*	*
	Schilbe mystus			*		*	*	*		*	*	*
R	Heterotis niloticus	*				*	*	*		*	*	*
R	Brienomyrus niger	*				*	*	*	*	*	*	*
	Siluranodon auritus					*	*	*		*	*	*

of two established physical principles: the "principle of most action" (the population proceeds toward the maximum accumulation of energy-biomass which is retained for the longest time possible) and the "principle of least action" which stipulates that energy tends to pass through a system as rapidly as possible. For a system to survive over ecological time, the principle of most action must override the principle of least action. Over the long-term both principles induce change and evolution is the resultant of these two countervailing forces. An increased in diversity results either in increased energy uptake or more rapid energy flow (such as increased grazing or predation). Given that increased diversity is self-augmenting, the trend to least action through increased diversity dominates system behaviour over evolutionary time.

However, different species within an ecosystem have different capacities to acquire and conserve energy. Thus, a hierarchy is formed in which each hierarchical level exhibits an increasing capacity to conserve and concentrate energy. The highest level is that of the dominant species which impose "top-down" regulation on the system, whereas "bottom-up" regulation is effected by the cycle of primary production. A hierarchy of increasing complexity promotes energy flow as more internal work becomes essential to support that increased complexity.

These basic hypotheses are very exciting and may provide the framework of a more general ecological theory taking into account both the diversity observed in different freshwater systems at different latitudes,

and the co-existence of dominant and rare species within a system.

Biodiversity and stability

The relationships between community complexity and stability have received some attention. For a long time, the so-called "conventional wisdom" in ecology (Begon *et al.*, 1986), was that increased complexity within a community leads to increased stability. Complexity is used here to mean more species, more interactions between them, and more pathways. Some authors like Elton (1958) supported the view that more complex communities are more stable, and MacArthur (1955) suggested that the greater the complexity, the greater is the ability of the community to respond to a perturbation. The basic assumption is that if the number of pathways increases, any blockage at one point of the network would be compensated for by the opening of another pathway. However, until now this conventional wisdom has not received any support from field or experimental work, and mathematical simulation models have led to different conclusions.

May (1973) constructed a model of randomly assembled food webs, including a number of interacting species. He defined as "connectance" of the web, the fraction of all possible pairs of species which interacted directly. The overall result was that increase in number of species, increase in connectance and increase in interaction strength tended to increase instability. Other models (May, 1981) also suggested that complexity leads to instability, which is in opposition to the ideas of Elton and MacArthur. However, some criticisms arose concerning the characteristics of the model communities used, as long as models often refer to randomly constructed communities, whereas in natural communities, interactions are probably not random but are in part the result of coevolution which will have selected the more stable associations. The behaviour of randomly assembled, computer communities may therefore be irrelevant for real ones.

Another important field in which complexity and instability could be associated is the range and predictability of environmental conditions which can vary from place to place. In a stable and predictable environment, one expects to find an assemblage of species which is stable only within a narrow range of environmental constraints (a so-called dynamically fragile community). That should be particularly true if the relatively stable conditions have lasted for a long time as, for instance, in the Great African Lakes .were fish species have become highly specialised. On the other hand, in a variable and/or unpredictable environment, a dynamically robust community (which is stable over a wide range of conditions and characteristics) will be able to persist. Such is the case for fish communities of Nilo-Sudan rivers characterised by the more or less predictable alternation of flood and severe low-waters, with

superimposed and unpredictable long-term climate changes. It seems likely that communities from stable and predictable environments are much more susceptible to man-made disturbances than the more robust communities from variable environments 'which are already used to adapting to changing situations (Begon *et al.*, 1986).

What is of major importance, of course, is the amplitude of stress. For fish inhabiting inland aquatic systems, the most extreme stress is the drying up of the aquatic biota and the extinction of the fish populations. In such a case, and apart for a few species biologically adapted to temporary habitat desiccation (*Polypterus*, small cyprinodonts), there are no possibilities for recolonisation given that most river basins are, like islands, isolated from each other by terrestrial barriers impassable for fish. In most cases, however, fish move to refuge areas where they will be able to survive during the drought period. That has been observed for example in Lake Chad and Lake Chilwa. When environmental conditions improve, fish are then able to recolonise the lakes from the refuge zones which serve as sources of inoculum.

It should also be pointed out that properties of communities, and their ability to respond to disturbances, also depend on the biological characteristics of their component populations. Life history strategies differ according to environmental conditions (see above). In stable environments, the selection of K strategies would be expected, and populations will have high inertia, but once perturbed will have low stability or resilience. By contrast, the reverse (or selection, low inertia, high stability or resilience) is expected in variable environments.

To conclude, while most ecologists feel that an ecosystem is resilient if the number of its biological constituents return after perturbation to their original equilibrium values, the present evidence suggests that diversity does not contribute significantly to this kind of resilience.

BIODIVERSITY AND PRODUCTIVITY

The question has been raised as to what extent are patterns of biodiversity important in determining the behaviour of ecological systems (Solbrig, 1991; Lubchenko *et al.*, 1991). Surprisingly, there are very few theories or empirical studies that might help to answer that fundamental question (Lawton and Brown, 1993). One can state that all species contribute to the integrity of the ecosystem and some ecologists considered that the greatest species richness appears to occur in highly productive habitats. Different investigations suggested that mechanisms were involved by which increased energy availability tends to result in proliferation of different species rather than increased population of existing species (Wright, 1983). It has been suggested that more productive environments support more but smaller

Table 2. – Fish diversity, feeding groups, and fish production estimated by fishery catches (Lakes Chad, Chilwa, George) or by estimation of fish consumption by birds (Lake Nakuru).

Lakes	Nakuru	Chilwa	George	Chad
nb species	1 *Oreochromis*	3 *Clarias-Barbus* *Oreochromis*	30 including 21 cichlids	100 various species and families
feeding	phytoplanktivore	detritivores zooplanktivores	biomass: 64% phytoplanktivores 20% piscivores	every type
fishery production kg/ha/year	625-2 436	80-160	100-200	100-150

populations of specialised species which are therefore more susceptible to extinction and unable to persist in unproductive environments (Schulze and Mooney, 1993). However, empirical observations also provide evidence of a decrease in species richness in aquatic environments when overall productivity of the system increases.

An alternative hypothesis is that species richness is irrelevant. What is important is the biomass, and the ecological processes in general may function perfectly well with very few species. Available information suggests that major patterns of energy flow may be broadly insensitive to the number of species involved (see below).

There is no simple relationship between biodiversity and ecological processes such as productivity. Simple systems, both natural and artificial, appear to be more productive than diverse ones. Moreover, a similar level of production can be observed in species rich ecosystems and in ecosystems with a low level of diversity.

Species diversity and fish production

One way to investigate the role of fish species diversity in ecosystem production is to compare the productivity of different assemblages (expressed for instance by an index such as the mean annual catch per hectare of commercial fisheries) in aquatic ecosystems as close as possible in their ecological characteristics. Such an attempt was made for three shallow tropical African lakes: Lakes Chad, George and Chilwa (Lévêque and Quensière, 1988). Fisheries data available (*table* 2) must, of course, be used with caution but it appeared that the annual catch per hectare was more or less in the same order of magnitude, *i.e.* 100-200 kg, in the three lakes under comparison, whereas the fish diversity and trophic chains were rather different: in Lake Chad, there are about one hundred species, belonging to different trophic levels from detritivores to top consumers, which are actively fished; in Lake George 21 of the 30 species recorded are cichlids, and four of them which are phytoplanktivores and exploit the Cyanobacteria, make up 60% of the fish biomass (Gwahaba, 1975); in Lake Chilwa, the fish community

is still more reduced, the bulk of the catch being made up of three species (*Barbus Clarias, Oreochromis*) which are more or less opportunists. It should be noted that zooplanktivores are poorly represented in Lake George in spite of a large biomass of zooplankton similar to the biomass observed in Lake Chad.

The fishery production of the above lakes may be compared to the fish production of Lake Nakuru, a shallow hypereutrophic equatorial soda lake in East Africa whose area covers up to 50 km^2. The only fish species is *Oreochromis alcalicus grahami*, introduced from Lake Magadi around 1960 (Vareschi, 1979; Vareschi and Jacobs, 1984). This fish feeds almost exclusively on the blue-green algae, *Spirulina platensis*. There is no commercial fishery, but these fish support a huge population of fish eating birds (90% *Pelecanus onocrotalus*). The total fish yield taken by the birds was estimated to be between 2 700-9 500 metric tons per year or 625 to 2 436 kg ha^{-1} yr^{-1} which is one of the highest fish yield evaluations for natural lakes, and this high production results from a single species. The short food chain may be one of the reasons, as well as the very high phytoplankton productivity, and the short life cycle of the cichlid. On present evidence, species richness is not a major determinant of basic production trends.

More or less similar conclusions were made in the Great Lakes of North America. For over a century they have been subjected to pollution and intensive fishing resulting in the loss of several native species. In addition, a number of other fish species have been introduced. Despite dramatic changes in the contribution of each species to the total catch, and the observation that the lakes no longer function in the same way as they did in the past, the secondary productivity of these ecosystems has changed remarkably little during that period (Pimm, 1993).

CONCLUSION

Some scientists contend that all species are useful, while other have argued that not all species can, or will, be saved and that choices have to be made. Nevertheless, at present we have only anecdotal,

sometimes controversial, examples to use as evidence for either argument because, until recently, this type of question was not popular among ecologists. This is undoubtedly due, at least in part, to the complexity of the problems, and the difficulties of designing an experimental approach. However, information on the role of species diversity in the functioning of ecosystems could have implications for environmental management policy. If it is demonstrated that diversity *per se* plays a major role in ecological functioning, then ecological research should contribute to decisions on what to preserve. Indeed, better information on the importance of biodiversity to ecosystem functioning could potentially alter the perceptions of decision-makers about the seriousness of threats to biodiversity. At the moment, policy makers only want to know how many species can we afford to lose and how far can the species composition be altered before the functional properties of the ecosystem are significantly altered. The argument that biodiversity should be maintained in order to preserve the integrity and functioning of ecosystems might be more convincing to a wider range of people than some of the reasons currently advanced for the conservation of biodiversity. Moreover, information on the functional importance of biodiversity would demonstrate the linkage between the effects of climate change on both biodiversity and effects on ecosystem-climate interactions.

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