Environmental Biology of Fishes 27: 161–175, 1990.
© 1990 *Kluwer Academic Publishers. Printed in the Netherlands.*

The conservation of the fishes of Lake Victoria, Africa: an ecological perspective*

Michael N. Bruton
J.L.B. Smith Institute of Ichthyology, Private Bag 1015, Grahamstown 6140, South Africa

Received 1.6.1988 Accepted 13.6.1989

Key words: Tropical fish, African Great Lakes, Introduced species, Extinction, Captive propagation, Co-evolution, Community ecology, Phenotypic plasticity, Fisheries management

Synopsis

The African Great Lakes are considered to be dynamically fragile ecosystems that are relatively resistant to minor changes with which they have co-evolved but vulnerable to major perturbations such as overfishing, the introduction of alien species and pollution. These lakes are inhabited by large species flocks of cichlid fishes which are characterised by a complex structure of interaction both between and within species, as is typical of mature ecosystems. Major perturbations, such as the disruption of trophic interactions through the introduction of alien fishes, may reverse the domination of relatively precocial, specialised forms and result in the creation of conditions that are conducive to the survival of more altricial, generalised forms with strong colonising abilities. The introduction of Nile perch and Nile tilapia, as well as other alien fishes, into Lake Victoria, combined with overfishing for the indigenous cichlid species, has resulted in marked changes to the fish communities and the fisheries that depend on them. The most important impacts of the Nile perch appear to be predation and aggressive effects whereas those of the tilapias include hybridization, overcrowding, competition for food and possibly the introduction of parasites and diseases. While the three proposed methods of conserving the indigenous flocks of cichlid fishes (captive propagation, reducing Nile perch stocks and closure of the haplochromine trawl fishery) all have merit, the changes that are occurring in Lake Victoria are basically irreversible. The highest priority should be to assist the governments of the riparian countries (Tanzania, Uganda and Kenya) with monitoring and research programmes and to support their policies of non-introduction of further alien fishes into any of the African Great Lakes so as prevent the same cycle of events from occurring, for example, in Lakes Tanganyika and Malawi. The diverse animal and plant communities of the African Great Lakes are a heritage of all mankind and it is the duty of every country to play a role in their conservation. It is therefore proposed that an internationally funded research programme should be mounted on the African Great Lakes on the scale of the tropical forest biome project of the IUCN.

Introduction

The African Great Lakes, with their great variety of natural resources, provide food, income and employment for many people in lakeside communities. Furthermore, they have furnished scientists with unequalled opportunities to study the patterns and processes of evolution. In the past four decades, advances in technology and increased human population pressures have threatened the survival

* Editorial

of some animal communities in these lakes, especially the species flocks of cichlid fishes (Fig. 1). Specific threats are posed by overfishing, habitat alterations, the introduction of alien fish predators and the possibility of oil pollution from commercial drilling operations (Fryer 1960, 1972, 1973, 1984, Ogutu-Ohwayo 1984, 1985, 1988, 1990, Okaronon et al. 1984, Barel et al. 1985, Balon & Bruton 1986, Barel & Witte 1986, Coulter et al. 1986, Ribbink 1987). Reductions in the abundance of indigenous cichlid species as a result of overfishing, predation by introduced Nile perch, *Lates niloticus*, and competition with the introduced Nile tilapia, *Oreochromis niloticus*, appear to be particularly severe in Lake Victoria (e.g. CIFA 1985a, Okemwa 1984, Goudswaard & Witte 1985, Ogari 1985, Ogutu-Ohwayo 1984, 1985, 1988, 1990, Barel et al. 1985, Barel & Witte 1986, HEST 1986a, b, Hughes 1986, Goudswaard & Ligtvoet 1987, Acere 1988).

The Nile perch is alien to Lake Victoria and the cichlid fishes there have not co-evolved with it, which may explain their vulnerability to *L. niloticus* predation. This is not to say that cichlid fishes cannot co-evolve and co-exist with large centropomid predators – *Lates mariae, L. microlepis, L. angustifrons* and *L. stappersii* are all endemic to Lake Tanganyika and co-exist with a cichlid species flock there which numbers over 300 species (Coulter 1970, 1976, 1981, Coulter & Jackson 1981, Coulter et al. 1986). The Nile perch *L. niloticus* itself is indigenous to Africa and is widespread in many major river systems including the Niger, Nile and Chad basins (Hopson 1972, Skelton 1988), where it co-exists with cichlids.

Lake Victoria is the largest freshwater body in the tropics with a surface area of 68680 km^2, a mean depth of 40 m and a maximum depth of 80 m. The lake straddles the equator and lies mainly in Tanzania (51%) and Uganda (43%) but also borders Kenya (6%) (Acere 1988). The stocks of Nile perch in Lake Victoria (and Lake Kyoga) were introduced from lakes Turkana and Albert (Arunga 1981) in the 1950s and early 1960s (see Acere 1985, 1988, Barel et al. 1985, Ogutu-Ohwayo 1985, 1989) despite repeated objections from scientists (e.g. Fryer 1960, Jackson 1960, Anderson 1961). As pointed out by Ribbink (1987), African Great Lake cichlids are particularly vulnerable to predation due to the insular nature of their habitats as well as their narrow stenotopy and philopatry. The African Great Lakes can as a whole be regarded as inverted islands and their faunas may therefore have the same vulnerability to extinction as normal island faunas (Norton 1986).

The Nile perch is an opportunistic predator (Ogari 1985, Ogutu-Ohwayo 1985, Ssentongo & Welcomme 1985, Ogari & Dadzie 1988) and has now become well established in Lake Victoria where it preys heavily on haplochromine cichlids (Gee 1969, Okedi 1971, Oguto-Ohwayo 1985, 1990, HEST & TAFIRI 1987) and supports a major fishery (Goudswaard & Ligtvoet 1987, Ligtvoet et al. 1987, Acere 1988, Ligtvoet 1989, Ogutu-Ohwayo 1990). The Nile perch presently constitutes over 90% by weight of the trawl catch in the Tanzanian waters of Lake Victoria and standing stock estimates of up to 90 kg ha^{-1} have been given (Wanink et al. 1988). The success of the Nile perch fishery has stimulated the development of subsidiary filleting, canning and marketing industries in the three riparian countries but a further problem has now emerged – the local processing techniques (frying and smoking) consume a large amount of wood, an essential but increasingly scarce source of energy in the riparian countries (Ligtvoet 1989). The increased catches of Nile perch have, however, provided a readily available source of protein at a time of critical food shortages in parts of East Africa (see, for example, Stoneman & Rogers 1970, Acere 1988). Thus, although the introduction of Nile perch and Nile tilapia into Lake Victoria is considered by some to be an ecological and conservational disaster (see Balon & Bruton 1986, Coulter et al. 1986, Ribbink 1987, Ligtvoet 1989, Ogutu-Ohwayo 1990), it is regarded as a partial economic success in the riparian countries (HEST 1986a, Ligtvoet et al. 1987, Acere 1988, Ligtvoet 1989) due to the increased catches of the introduced species (Ogutu-Ohwayo 1990). Whether or not the increased catches will be sustained is unknown, but what is clear is that the introductions are irreversible and the management of the lake will in future have to take the populations of Nile perch and Nile tilapia into account.

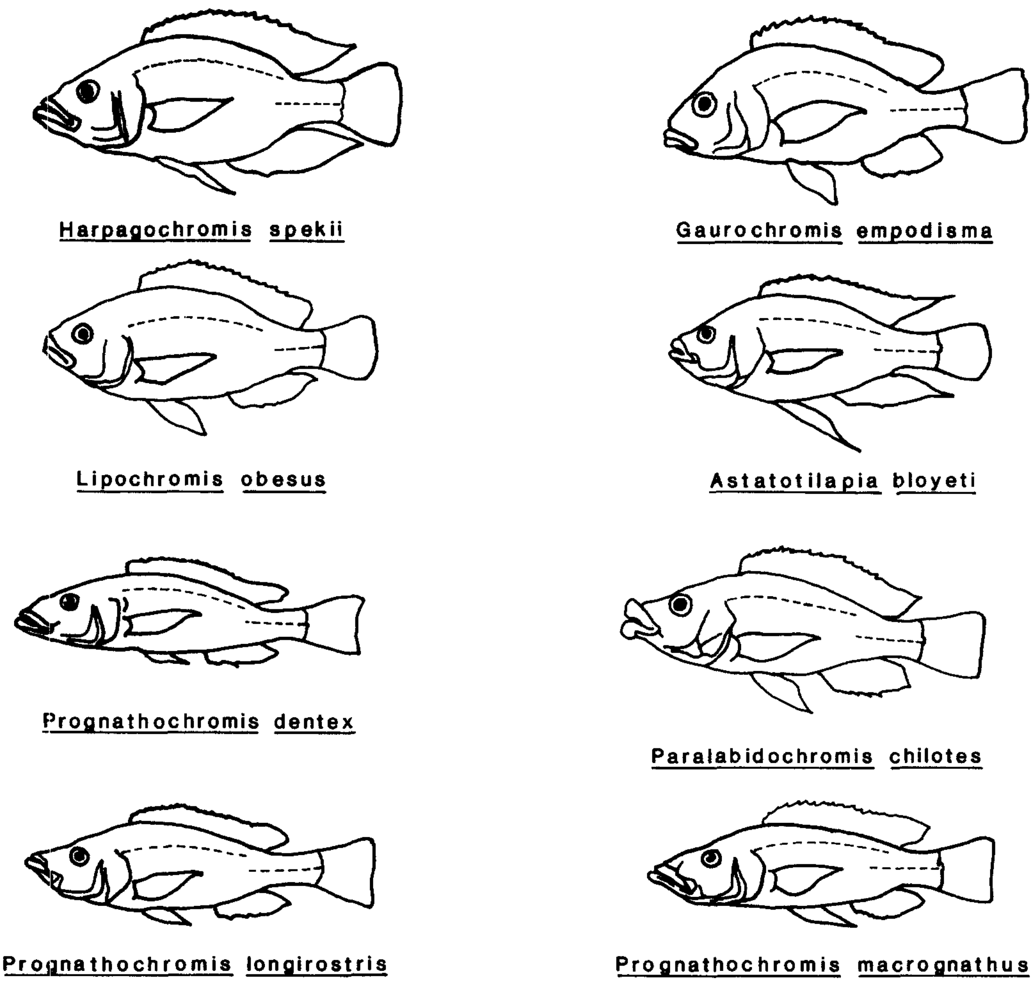

Fig. 1. Outline drawings (not to scale) of various Lake Victoria haplochromine species to show the range of body form in this species flock [After P.H. Greenwood. 1974. Cichlid fishes of Lake Victoria, East Africa: the biology and evolution of a species flock. British Museum (Natural History), London. 134 pp.]

Recent expeditions from the National Museums of Kenya and the British Museum (Natural History) to the Kenyan shores of the lake have found that the areas of Lake Victoria where haplochromines are scarce are those in which there is an intense fishing effort (Anon. 1988, 1989). In other areas where fishing is not allowed (as in parts of the Winam Gulf, previously the Kavirondo Gulf, Kenya) or where there is little fishing effort, as in certain remote regions of the southern Tanzanian shoreline, large numbers of haplochromines are caught (P.H. Greenwood personal communication). From these collections, and particularly those made in Winam Gulf, it would seem that overfishing, as well as the increased predation pressure exerted by the Nile perch, are affecting the haplochromine populations (Ogari & Dadzie 1988, Ogutu-Ohwayo 1988, 1990, Anon. 1989). A parallel situation is known from the Laurentian Great Lakes in North America where overfishing followed by sea lamprey predation caused a major decline in the native fish communities (e.g. Smith 1968, Christie 1974). There is a strong likelihood that some cichlid species will be lost from Lake Victoria although perhaps not as many as suggested by HEST (1986a, b, see Greenwood 1987). The more critical scenario is that the structure and function of the fish communities, and in particular the cichlid fish communities, will be irreversibly altered, as discussed below.

Alien organisms rarely affect indigenous species in isolation but are usually part of an overall environmental change that causes stress to local animal communities. In addition to trophic alterations (predation and competition for food), alien fishes are known to have several other harmful effects, including habitat alterations, introduction of parasites and diseases, hybridization with endemic species and spatial alterations (aggressive effects and overcrowding) (Taylor et al. 1984, Bruton & Merron 1985, Bruton & van As 1986). Of these, predation and aggressive effects are likely to be the most important impacts of the Nile perch, whereas hybridization, overcrowding, competition for food and possibly the introduction of parasites and diseases are those of the Nile tilapia and other introduced cichlids. The introduction of alien fishes into Lake Victoria is therefore likely to have had an impact on three critical aspects of the lake ecosystem: the maintenance of essential ecological processes and life-support systems, the preservation of genetic diversity and the sustainable utilisation of species and ecosystems (cf. IUCN 1979).

Various suggestions have been made as to how to conserve the cichlid species flocks of Lake Victoria, including closure of the haplochromine trawl fishery (Witte & Goudswaard 1985, Ribbink 1987), increased fishing pressure on the Nile perch (Bwathondi 1985, CIFA 1985b, Mainga 1985, Ogutu-Ohwayo 1985, 1990, HEST 1986b, Ribbink 1987) and the captive propagation of cichlid fishes (see the Resolution of the Cichlid Workshop at the Fifth Congress of European Ichthyologists held in Stockholm in August 1985, this journal 16: 225–226, Barel 1986, Ribbink 1986, 1987, Ribbink & Twentyman-Jones 1989, IARCEC, this journal 22: 313). The latter scheme proposes that fishes threatened with extinction in Lake Victoria should be kept and bred in aquaria in Africa or Europe and then restocked into the lake if conditions there have 'improved'. These proposals are assessed here in the light of some ecological insights, and especially from the point of view that Lake Victoria and the other African Great Lakes are more than a collection of species: they are highly evolved ecosystems with a rich diversity of interspecific interactions and energy pathways which, once altered, can never be re-created by man. Researchers should rather use the opportunity provided by Lake Victoria to study in detail the processes of ecological and taxa evolution which will follow the major perturbations in this biological system, and attempt to derive some understanding of the processes that will facilitate more effective management of this and other lakes in future.

In order to assess the magnitude and nature of the impact of introduced fish species on the fish communities of Lake Victoria and the other African Great Lakes, it is necessary to review first the characteristics of these ichthyofaunae and then of the ecosystems in which they live.

Characteristics of the cichlid fishes of the African Great Lakes – an ecological perspective

The fish communities of the African Great Lakes are dominated by representatives of the family Cichlidae, a group of labroid fishes with a wide range of trophic specializations but a narrow range of reproductive guilds (sensu Balon 1975, 1981). Most African Great Lakes cichlids are mouthbrooders (Fryer & Iles 1972, Ribbink et al. 1983). These fishes have a life style characterised by a high parental investment in relatively few young and a long period of intensive brood care.

African cichlids have repeatedly been shown to be phenotypically plastic (Meyer 1987) and recent epigenetic and ecological research (Balon 1985, 1989, Bruton 1986) has indicated that they are able to alter the duration and timing of ontogenetic events so as to shift from an altricial to a precocial alternative homeorhetic state (Fig. 2). The altricial state is characterised by the production of a relatively large number of small eggs, a smaller size and less developed state at first exogenous feeding, and a shorter life span (Balon 1975, 1981, 1983, 1985, 1989, Noakes & Balon 1982, Bruton 1989, Flegler-Balon 1989). The precocial state is characterised by the production of relatively few large eggs with a large amount of yolk, the reduction or elimination of the larval period in the life cycle, a larger size and more advanced state of development at first exogenous feeding and a longer life span. Altricial fishes are best able to survive in relatively unstable, capricious environments (such as floodplain rivers) and precocial fishes in relatively stable, predictable environments (such as the African Great Lakes, Bruton 1989). In an abiotically harsh but biotically unsaturated environment, the best reproductive style would be to direct maximal amounts of energy and matter into reproduction and to produce many progeny as soon as possible. In contrast, in a saturated environment, where density effects are pronounced and competition is keen, the best reproductive response may be to put more energy into developing the competitive abilities of the young, and to produce larger but fewer, more expensive progeny (Balon 1985, 1989).

The evolutionary success of cichlid fishes has been attributed to a number of key features possessed by them, e.g. advanced parental care (Dobzhansky 1951), assortative mating and sexual selection (Kosswig 1947, Mayr 1982, Dominey 1984) and their flexible morphology (Liem 1973, 1978, Liem & Osse 1975, Meyer 1987, Stiassny & Jensen 1987). Liem (1973) suggested that the possession of a well-developed pharyngeal jaw apparatus in cichlid fishes represents a new innovation which frees the oral apparatus and thus allows it to become specialised for particular feeding tasks. Such a key innovation would be of utmost importance for ecological specialisation and niche diversification. There is some evidence that the trophic specialisations of Ethiopian and Neotropical cichlid fishes may be ecophenotypically modified by the nature of the environment or the availability of particular foods (Greenwood 1965, Sage & Selander 1975, Kornfield et al. 1982, Witte 1984, Meyer 1987, Hoogerhoud 1986). Cichlid fishes may therefore show considerable flexibility both with respect to their epigenetic development as well as their feeding modes. Although the reproductive guild of a particular species is genotypically fixed (at least within the time frame that we are discussing here), the homeorhetic state adopted within that guild may differ in response to the biotic and abiotic environment in accordance with the altricial/precocial dichotomy.

One of the remarkable features of cichlid fishes is therefore their flexibility. Their behaviour, and to some extent their form, is determined by the biotic and abiotic pressures exerted on them at a given time. We can therefore expect that, if the selection pressures are changed, the fishes will also change. A 'species' of cichlid, as an ecological unit, therefore only exists in its entirety in the context of the environment with which it has co-evolved.

Characteristics of the African Great Lakes environment

The African Great Lakes can be considered to be relatively stable relative to an African river, floodplain or shallow lake. The concept of environmental stability refers to the tendency for a natural system to remain near an equilibrium point or return to it after a disturbance (Orians 1975). The dual aspects of resistance and resilience describe most forms of environmental stability (see reviews in van Dobben & Lowe-McConnell 1975). Resistance, or constancy, is characterised by a narrow amplitude of change in a system whereas resilience refers to the ability of a system to recoil to more or less the same state after perturbation. Resistance leads to a static persistence in a system whereas resilience leads to a dynamic persistence. Natural systems that have a high resilience sometimes also have a wide amplitude of natural fluctuations. Precocial species would be expected to thrive in an environment that is relatively resistant to change whereas a more resilient environment would favour altricial species (Bruton 1989). In general, species which co-evolved with a resistant environment can be expected to perceive as major those changes that are perceived as relatively minor by species which co-evolved with more resilient environments.

In terms of the theories of 'non-equilibrium ecology' developed by Holling (1976) and others, an ecosystem such as a riverine floodplain may be regarded as a 'healthy' and resilient system although it is far from a static equilibrium state. Jantsch (1985) has argued that it is precisely the local instability of an ecosystem that furthers its global stability. The closer a system approximates

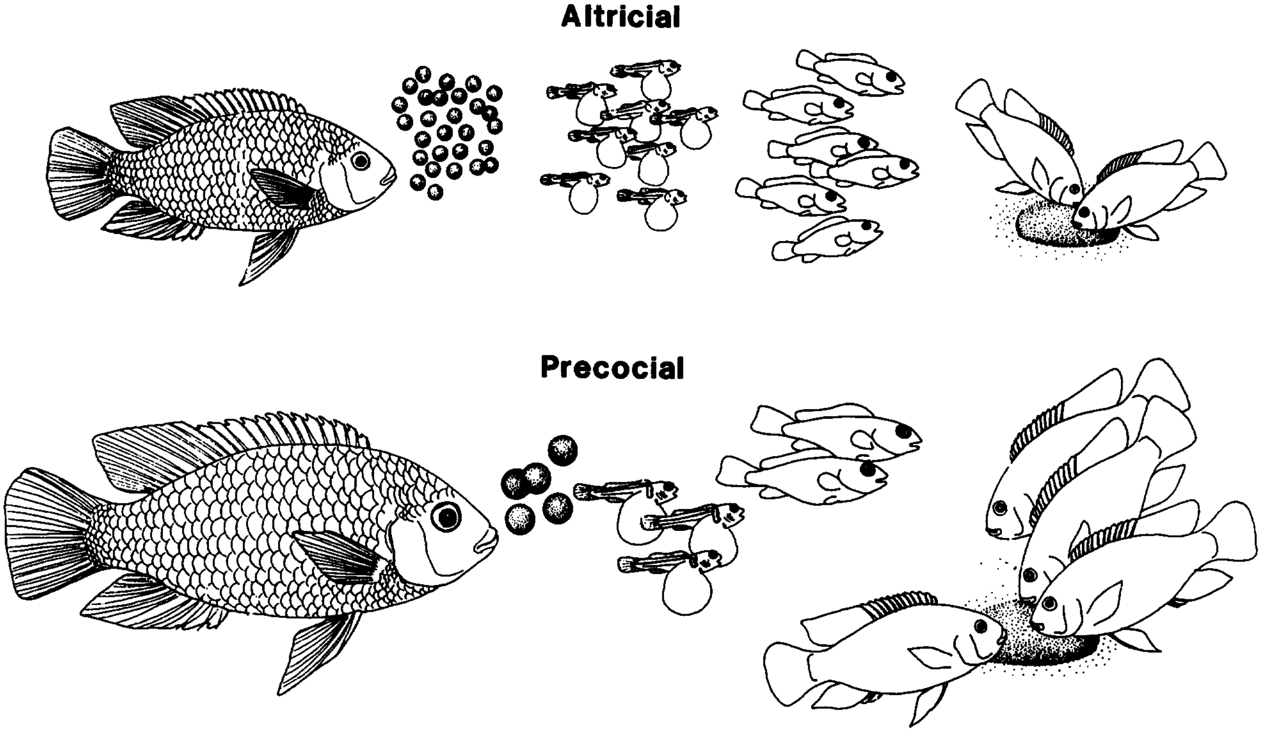

Fig. 2. Diagrammatic representation of altricial and precocial alternative homeorhetic states.

to equilibrium, as is the trend for increasingly mature ecosystems, the less resilient it becomes. The higher the resistance to major changes, the more devastating the effects of the changes that do break through are likely to be (Jantsch 1985). A system near equilibrium would thus be vulnerable to a marked change in physico-chemical conditions (e.g. as a result of pollution), to major changes in species interactions (e.g. due to the introduction of alien species, Bruton 1986), or to changes in community composition (as could be caused by intensive fishing, Coulter et al. 1986).

Complex ecosystems, with their many species and rich interaction structure, are now considered to be, in general, dynamically fragile (May 1975). Although the communities in these ecosystems are able to thrive in the predictable (= resistant) environments, they are likely to be more vulnerable to perturbations imposed by man than are communities in relatively simple but more robust systems. It is therefore parsimonious to predict that the fish (and possibly other animal communities) of the Great Lakes of Africa have a relatively good capacity to resist low amplitude natural changes (i.e. they have a relatively high inertia) because of their high species richness and the multiplicity of energy pathways which have been established in them. Furthermore, it is possible that they may have a low elasticity (ability to recoil to the original state) and low amplitude (the area over which they are potentially stable) compared, for instance, with African floodplain rivers, because of the low dispersal rates of their fauna, as well as niche and habitat specializations, and other factors, in the African Great Lakes. These are important ecological considerations which need to be investigated further in the African Great Lakes.

During the evolution of a species or a community in a relatively resistant system, there would be a higher probability of passing from an altricial to a precocial state than the reverse (Bruton 1989). In this ecological succession, a stabilising factor for the ecosystem will be the increasing importance of species that establish interspecific connections that are increasingly extended over time and space e.g. feeding relationships, commensalism, symbiosis, cooperative broodcare, etc. (common among cichlids in the African Great Lakes, cf. Fryer & Iles 1972, Ribbink et al. 1983, Ribbink & Eccles 1988). This trend results in precocial species becoming increasingly dominant in the system and developing an increasingly complex structure of interaction between and within species. This tendency to develop relationships that are more complex and predictable is typical of a maturing ecosystem (Jantsch 1985). Margalef (1968) has described this evolution of an ecosystem as a process of information accumulation. He points out that the information gained is applied to the acquisition of increasing autonomy, and fluctuations arriving from outside become more and more dampened. Thus, in place of a rhythm dictated by reactions to external environmental events, the endogenous rhythm of the system unfolds to a greater extent, with biotic interactions taking on more and more importance.

It seems reasonable to assume that the complex and sensitive relationships of a mature ecosystem, once dislocated by disturbance, will be reconstituted less easily than the simpler relationships of less stable communities. Man's constant intervention in the environment will usually break down more complex, stable situations into simpler, less stable ones, thus causing specialised species which are more closely in tune with their environment to become rare or extinct. Put in another way, man affects ecosystems by 'resetting the clock of succession', usually to an earlier, less mature state, thus selecting for more altricial species and creating conditions that are less suitable for precocial species. Therefore the form of stability possessed by diversified ecosystems is one based on their uniquely co-evolved interactions, but it will be stable only in relation to the amplitude of disturbances encountered during its evolution. This is an obvious point, but one that has often been ignored.

This discussion further strengthens the prediction that the cichlid species flocks of the African Great Lakes are particularly susceptible to the effects of major perturbations caused by man, such as overfishing and the introduction of alien fish predators (see also Coulter et al. 1986). This vulnerability extends not only to the possibility of species becoming rare or absent, but also to the probability of interference with and eventual loss of the rich pattern of interaction between species, which itself is a major contributing factor to the biotic diversity of these lakes. I further predict that the introduction of an alien fish predator would have even more devastating impacts on the cichlid communities of lakes Malawi and Tanganyika than has been the case in Lake Victoria. The former lakes have more diverse species flocks than Lake Victoria and have shown a more marked trend towards specialization in their cichlid fishes (Fryer & Iles 1972).

I would also predict that relatively altricial, generalised species with strong colonising abilities would thrive in African Great Lakes which have been disturbed, either through the introduction of alien species or through other interferences with biotic interrelationships, or through pollution. It is interesting, therefore, that the one endemic fish species in Lake Victoria which seems to have benefitted from the changed conditions is the relatively altricial, non-guarding, open-substrate spawning cyprinid *Rastrineobola argentea,* locally known as 'dagaa'. According to Wanink et al. (1988) and Ogutu-Ohwayo (1990), *R. argentea* now features prominently in commercial catches in Lake Victoria and is the only fish other than the Nile perch which is abundant in Lake Kyoga. Furthermore, the mean length of *R. argentea* has decreased by 17.5% (Wanink et al. 1988), a response that is also predictable under conditions of disturbance (Bruton 1989). It is also perspicacious to follow the series of events that occurred in another African Rift Valley lake, Lake Kivu, that was subject to the introduction of alien fish species. Lake Kivu has a rich planktonic fauna but lacks a pelagic fish that can consume it. Between early 1958 and late 1960 several large but unquantified shipments of 'sardines' from Lake Tanganyika were released into Lake Kivu (Dumont 1986). The objective of the introduction was to introduce a planktivore which would channel zooplankton protein through fish to humans. The original idea was to introduce *Stolothrissa tanganicae* but the more euryphagic clupeid *Limnothrissa miodon* was successful instead. *L. miodon* have now depleted the zooplankton of Lake Kivu and are also feeding on their own young and possibly also those of endemic cichlids.

Thus in both lakes Victoria and Kivu a relatively altricial species has become abundant and is likely to start exerting its own biotic pressures on the ecosystem (in addition to those exerted by the Nile perch, itself an altricial species relative to the haplochromines, in Lake Victoria). It is already a well-established trend in both terrestrial and aquatic ecosystems that the loss or reduction of species from highly interrelated ecosystems is likely to have cascading effects, one of which is the increased importance of altricial pestiferous species (Norton 1986, Vermeij 1986, Bruton 1989). Furthermore, the precocial species which are threatened with extinction by altricial species are often those which are most useful to man. When the biotically competent species is extirpated from an ecosystem, its niche is not usually filled by another specialist species (Hsu 1982) as their respective specialisations are too great to allow interchangeability. Instead, the specialised species are replaced by generalised, weedy species which are successful colonisers and thrive under disturbed conditions (Bruton 1986). There is therefore a danger of system simplification and reversal to a dominance by altricial species.

Comments on the proposed conservation measures

Against the background of the above ecological perspectives, we can now comment on the three conservation measures proposed – the captive propagation of endangered cichlid species, the reduction of Nile perch densities and the closure of the trawl fishery for haplochromine species.

Captive propagation

The establishment of self-sustaining captive populations of rare and endangered animals, or animals from highly disturbed habitats, is a widely supported conservation measure (Martin 1975, Myers 1979, Frankel & Soule 1981) that has been endorsed by the International Union for the Conservation of Nature and Natural Resources (IUCN 1987). These programmes are most effective when they are conducted in parallel with field studies and conservation efforts aimed at the species in its natural environment (IUCN 1987). Captive propagation has proved to be successful in the case of several bird and mammal species. For example, ex situ stocks of American bison, *Bison bison,* have provided critical support for wild populations of this species, and the Arabian oryx, *Oryx leucoryx,* was saved from extinction by the re-introduction of captive stocks into the wild (IUCN 1987). Captive propagation techniques have also been used for fishes, most often for stocking angling or aquaculture species, but also more recently for conservation purposes (e.g. Ribbink & Twentyman-Jones 1989). Cichlid fishes are probably the most suitable candidates for captive propagation because they readily breed in aquaria (Ribbink 1986).

The re-introduction of species into their natural environment as an ameliorative measure is not always a simple or even a desirable measure. With respect to species which have become extinct in the wild, the IUCN (1987) recommendation is that re-introductions should take place only into localities in which the original causes of extinction have been removed and where the habitat requirements of the species are satisfied. There should be no re-introduction if a species became locally extinct because of a habitat change that is unremedied, or where significant habitat deterioration has occurred since the extinction (IUCN 1987). The IUCN further recommends that sufficient funds should be made available before beginning a re-introduction project to ensure that the project can be completed. Ribbink & Twentyman-Jones (1989) have pointed out that the advantage of captive propagation is that it maintains the option of re-introducing rescued taxa 'should the seemingly impossible occur, and the degraded environment revert to a habitable state for the species'.

The likely scenario in Lake Victoria is that cichlid fishes would be restocked into areas where some members of the species are still surviving. In these circumstances the IUCN (1987) recommends that restocking should only occur when the causes of reduction have been largely removed and natural increases of the threatened population can be excluded. Before deciding whether restocking is necessary, the carrying capacity of the area proposed to be restocked should be investigated to determine whether the desired population level is sustainable. If it is, then further investigations should be undertaken to discover the reasons for the low population levels. Action should then be taken to help the resident population expand to the desired level. Only if this fails should restocking be done, as it is likely to be an expensive, high-risk exercise that will require skilled manpower. Re-introduction or restocking should therefore be a last resort, if it is carried out at all, and not the primary initiative for resurrecting a threatened species.

Furthermore, the subtle dangers of artificial selection and 'relaxed selection' (Frankenham et al. 1986) in captivity should not be overlooked. They could lead to the production of stocks which might be genetically unsuited to respond to conditions obtained in the lake at the time of their re-introduction. The problems of hybridization (particularly in cichlids, Crapon de Caprona & Fritzsch 1984), loss of vigour and of genetic diversity, genetic drift and genetic 'bottlenecks' would also have to be overcome, as discussed by Foose et al. (1986), Ribbink (1986, 1987) and Ribbink & Twentyman-Jones (1989). Genetically impoverished stocks should not be used to re-stock threatened species as their ability to survive may be inhibited by their genetic homogeneity. The possibility also needs to be considered that species bred and raised in the relatively homogeneous environment of an aquarium may reduce the fitness of hardy and resistant individuals in the natural lake with which they may interbreed after introduction.

While the protocols of captive propagation are well established for birds and mammals (Martin 1975, Soule & Wilcox 1980, Schonewald-Cox 1983, Foose et al. 1986), they are less well-established for fish (Meffe 1987). As the success of a captive breeding programme is dependent on the rapid growth of numbers from a founder stock in such a way that genetic variability is enhanced (Ribbink 1987, Ribbink & Twentyman-Jones 1989), the prevention of hybridisation and the reduction of genetic and phenotypic changes would be of overriding importance.

Reducing Nile perch stocks

It has been proposed that the Nile perch should be fished intensively in an attempt to restore the lake to near its original condition. Even if it were possible to exert an adequate fishing effort in this massive lake, the fact that *L. niloticus* has now colonised the feeder rivers of Lake Victoria (Crapon de Caprona & Fritzsch 1989) makes this eradication exercise even less practical. It would surely be impossible, through intensive fishing for Nile perch, to so reduce this species that the rich interactions between species which were previously an integral part of the Lake Victoria ecosystem are re-established. All that can be done is to allow the system to settle into a new steady state based on the species which remain and on the interactions which they presently have and will develop in the future. Reductions in the abundance of Nile perch through targetted fishing may help to reset the balance more quickly, but even this is questionable. The non-guarding, open substrate spawning habits of *Lates niloticus,* which involve the production of large numbers of small eggs and young (Ogutu-Ohwayo 1988), are likely to produce a population whose numbers fluctuate widely in accordance with the availability of food and other resources. The Nile perch may therefore itself create constantly changing biotic conditions in the lake. The point is that we do not as yet know what effect it will have and the ongoing studies by Kenyan, Tanzanian and Ugandan as well as foreign scientists will provide vital information in this regard.

Closure of the trawl fishery

Information from HEST research (1986a, b), supported by recent collections made for the British Museum (Natural History) in Kenyan waters (P.H. Greenwood personal communication), strongly suggests that overfishing – not only by trawling – has played an important role in the decline and even the eradication of haplochromine cichlids in various parts of Lake Victoria. The effect of trawling on Nile perch numbers and biology is currently being studied (see HEST & TAFIRI 1987, Ogutu-

Ohwayo 1988, 1990) but is largely unknown. It is possible that a drastic reduction in trawling activity could have beneficial results for the haplochromine species occupying the habitats that have regularly been trawled. Any decision to halt trawling would, however, have to take into account a variety of socio-economic factors. Nevertheless, on the information available at present, the decision is one that should be considered seriously.

An additional conservation measure that should be considered is the establishment of nature reserves along some of the more remote or lightly fished shores of Lake Victoria. Although these reserves would not exclude Nile perch or Nile tilapia, they would act as refugia from fishing mortality as well as inocula for adjacent depleted areas. However, because of the philopatry and stenotopy of many (but not all) cichlids in the lake, these reserves will only conserve local components of the ichthyofauna. Reserves established by the Kenyan government in Winam Gulf have apparently been a success (Anon. 1988, 1989) and could play an important role in the conservation of endangered cichlid species.

Discussion

There is already a considerable body of evidence (e.g. Ogutu-Ohwayo 1985, 1990, Coulter et al. 1986, HEST 1986a, b, HEST & TAFIRI 1987, Ribbink 1987, Acere 1988, Wanink et al. 1988, Anon. 1988, 1989) that biotic interactions in Lake Victoria have been severely disrupted not only by the introduced fish species but also by overfishing. The disruption of the ecosystem has largely taken the form of a simplification of the food web through the virtual eradication of haplochromines from many interactions and the development of short food chains to the Nile perch (Wesseling 1986, Wanink et al. 1988, Ligtvoet 1989). Whereas the haplochromines converted numerous protein sources (algae, zooplankton, insect larvae, shrimps, molluscs, diatoms, bacteria, etc.) into fish protein for consumption by higher trophic levels (including man), the Nile perch eats mainly juvenile Nile perch and shrimps and the juveniles feed mainly on zooplankton (Hughes 1986, Barel & Witte 1986, Wesseling 1986, Ligtvoet 1989). This tragic simplification of the fish (and presumably other) communities of Africa's largest lake has not only involved a reduction in the population sizes and diversity of unique endemic assemblages but also in the concomitant reduction of the diversity of life cycles and biotic interactions. The result is a much depauperated lake with an unpredictable ability to support artisanal and commercial fisheries on which many people are dependent. Thus the conservational and ecological consequences of the man-made changes to the fish communities of Lake Victoria must be regarded as negative and the economic consequences to be, at best, positive in the short term but of unknown value in future. The most regrettable outcome of all is that the options for the management of the Lake Victoria fishery have now been sharply reduced and policies in future will have to ensure that a worst case scenario, e.g. gradual eutrophication, deoxygenation and palustrinisation (Crapon de Caprona & Fritzsch 1989), does not occur.

In conclusion, therefore, the fourth recommendation made by the Fifth Congress of European Ichthyologists (increased research effort) should be strongly supported. However, only a small body of resource managers and scientists in Africa and elsewhere has the necessary expertise to assist the governments concerned with effective research on and management of the African Great Lakes. It is important therefore that all present and future resources of time and money should be spent in the most effective way. In place of a rescue-return operation involving captive propagation, an internationally funded research programme (on the scale of the tropical forest biome project of the Worldwide Fund for Nature) should be initiated to intensify field and laboratory research on the indigenous and alien fishes of Lake Victoria and other threatened African Great Lakes.

Concurrently with that research, scientists also have an opportunity to study natural processes in action on a scale and at a rate never before available to students of evolution. In the past, most evolutionary and ecological studies on the fishes of Lake Victoria, and on other animals elsewhere, have been concerned with reconstructing patterns and processes on the basis of past and present-day evidence. Now we have a chance to study both as they actually occur and develop. Lake Victoria also offers opportunities on a unique scale for the study of ecological events associated with the resetting of the ecological succession and its progression towards a new equilibrium. The way in which the fishes create alternative life-history styles and phenotypic traits in response to the new range of conditions should be particularly enlightening, and of great value to the understanding of an important biological phenomenon.

Although it may seem a rather pessimistic view, I feel that nothing can be done to stave off the irreversible changes in Lake Victoria. We should rather use the limited time, funds and manpower available to study the processes of change that are occurring in this lake so that we can obtain a better understanding of the sometimes devastating effects of man's intervention in Nature. At the same time we should retain an accurate record of the diversity of species remaining in Lake Victoria through the deposition of properly documented specimens in recognized museums (the fifth recommendation of the Fifth Congress of European Ichthyologists), as is currently being done by the Kenyan National Museums, British Museum (Natural History) and Leiden University (HEST 1986b). Stock assessments of the commonly caught haplochromines, tilapiines and centropomids should also be continued in order to provide a baseline for future comparisons.

A limited captive propagation programme of certain Lake Victoria cichlids, which is already underway at the Horniman Museum (London) and the New England Aquarium (Boston), could increase our understanding of the behaviour, breeding and feeding biology, and genetics of these species, which is an essential requirement for their management. These studies should be made in parallel with field studies based on experimental and commercial catch returns and field observations. Intensified field studies on the Nile perch, expanding those that have already been initiated by the fisheries departments of Kenya, Uganda and Tanzania, are also of great importance. It would, however, require a large scale international scientific effort to adequately monitor the many changes that are occurring in the different habitats that constitute Lake Victoria, changes which involve not only all the species of fishes, but all the other elements of the flora and fauna as well as the lakes' physical and chemical parameters.

The problems caused by invasive aquatic animals are well appreciated in Africa (Welcomme 1984, CIFA 1985b, Bruton & van As 1986, MacDonald et al. 1986, de Moor & Bruton 1988, Moureau et al. 1988). International support should therefore be given to the policies of the governments of Malawi, Tanzania and Zambia that have decided that Nile perch and other non-indigenous species should not be introduced into Lakes Malawi and Tanganyika, so as to avoid the same cycle of events from occurring there. The deleterious consequences of the introduction of an alien fish predator, or any other alien organisms, are likely to far outweigh the short-term beneficial effects (if any) in these dynamic but fragile systems. A simple protocol for evaluating the desirability of introducing alien aquatic animals needs to be used based on that developed by Kohler & Stanley (1984) for the United States of America and suggested by CIFA (1985b) and Bruton & van As (1986) for Africa. A computerised version of this protocol is currently being developed in the J.L.B. Smith Institute of Ichthyology in Grahamstown.

The comments made here are intended to provide additional insights that may contribute to the debate on the Nile perch controversy in particular and to the problem of invasive aquatic animals in general. It is not my intention to underestimate the potential threat posed by *Lates niloticus* to the endemic fish fauna of Lake Victoria. What I wish to emphasize is the lack of fundamental data, both qualitative and quantitative, relating to the biological effects of the Nile perch, Nile tilapia and other introductions, and to encourage international participation in their study. The problem is a large and biologically complex one and it is the responsibility of all mankind to find a solution that retains at least some part of the integrity and utilisation potential of this magnificent lake. The communities of plants and animals in Lake Victoria can never be restored to their previous condition, but there is still the opportunity to manage them effectively in the future for the benefit of the lakeside communities and to the satisfaction of all people who are concerned with the conservation of biotic diversity.

Acknowledgements

I am most grateful to E.K. Balon, P.H. Greenwood, P.B.N. Jackson, A.J. Ribbink, G.W. Coulter and A. Meyer for their critical comments on a draft of this paper.

References cited

Anon. 1988. Monster fish may be innocent of ecological crimes. New Scientist (1622): 34.

Anon. 1989. Perch not to blame. Oryx 23: 40.

Acere, T.O. 1985. Observations on the biology, age, growth, maturity and sexuality of Nile perch, *Lates niloticus* (Linne), and the growth of its fishery in the northern waters of Lake Victoria. pp. 42–61. *In:* CIFA Report of the Third Session of the Sub-Committee for the Development and Management of the Fisheries of Lake Victoria, Jinja, Uganda, 4–5 October 1984. FAO Fish. Rep. no. 335, FAO, Rome.

Acere, T.O. 1988. The controversy over Nile perch, *Lates niloticus,* in Lake Victoria, East Africa. Naga (ICLARM Newsletter) 11: 3–5.

Anderson, A.M. 1961. Further observations concerning the proposed introduction of Nile perch into Lake Victoria. E. Afr. agric. J. 26: 195–201.

Arunga, J. 1981. A case study of the Lake Victoria Nile perch *Lates niloticus* fishery. pp. 165–183. *In:* Proceedings of the Workshop on Aquatic Resources of Kenya, July 1981. Kenya Marine and Fisheries Research Institute, Mombasa.

Balon, E.K. 1975. Reproductive guilds of fishes: a proposal and definition. J. Fish. Res. Board Can. 32: 821–864.

Balon, E.K. 1981. Additions and amendments to the classification of reproductive styles in fishes. Env. Biol. Fish. 6: 377–389.

Balon, E.K. 1983. Epigenetic mechanisms: reflections on evolutionary processes. Can. J. Fish. Aquat. Sci. 40: 2045–2058.

Balon, E.K. 1985. The theory of saltatory ontogeny and life history models revisited. pp. 13–28. *In:* E.K. Balon (ed.) Early Life Histories of Fishes. New Developmental, Ecological and Evolutionary Perspectives, Dr W. Junk Publishers, Dordrecht.

Balon, E.K. 1989. The epigenetic mechanisms of bifurcation and alternative life-history styles. pp. 467–501. *In:* M.N. Bruton (ed.) Alternative Life-History Styles of Animals, Perspectives in Vertebrate Science 6, Kluwer Academic Publishers, Dordrecht.

Balon, E.K. & M.N. Bruton. 1986. Introduction of alien species or why scientific advice is not heeded. Env. Biol. Fish. 16: 225–230.

Barel, C.D.N. 1986. The decline of Lake Victoria's cichlid species flock. Zoologisch Laboratorium, University of Leiden. 96 pp.

Barel, C.D.N. & F. Witte. 1986. Cichlid species flock of Lake Victoria on the verge of extinction. Ann. Mus. Roy. Centr., Sc. Zool. 251: 171–173.

Barel, C.D.N., R. Dorit, P.H. Greenwood, G. Fryer, N. Hughes, P.B.N. Jackson, H. Kawanabe, R.H. Lowe-McConnell, M. Nagoshi, A.J. Ribbink, E. Trewavas, F. Witte & K. Yamaoka. 1985. Destruction of fisheries in Africa's lakes. Nature 315: 19–20.

Bruton, M.N. 1986. Life history styles of invasive fishes in southern Africa. pp. 201–208. *In:* I.A.W. MacDonald, F.J. Kruger & A.A. Ferrar (ed.) The Ecology and Management of Biological Invasions in Southern Africa, Oxford University Press, Cape Town.

Bruton, M.N. 1989. The ecological significance of alternative life-history styles. pp. 503–553. *In:* M.N. Bruton (ed.) Alternative Life-History Styles of Animals, Perspectives in Vertebrate Science 6, Kluwer Academic Publishers, Dordrecht.

Bruton, M.N. & S.V. Merron. 1985. Alien and translocated aquatic animals in southern Africa: a general introduction, checklist and bibliography. S. Afr. Nat. Sci. Progr. Rept (113): 1–71.

Bruton, M.N. & J.G. van As. 1986. Faunal invasions of aquatic ecosystems in southern Africa, with suggestions for their management. pp. 47–61. *In:* I.A.W. MacDonald, F.J. Kruger & A.A. Ferrar (ed.) The Ecology and Management of Biological Invasions in Southern Africa, Oxford University Press, Cape Town.

Bwathondi, P.O.J. 1985. The future of the fisheries of the Tanzanian part of Lake Victoria, in view of the predominance of Nile perch *Lates niloticus.* pp. 143–145. *In:* CIFA Report of the Third Session of the Sub-Committee for the Development and Management of the Fisheries of Lake Victoria, Jinja, Uganda, 4–5 October 1984. FAO Fish. Rep. no. 335, FAO, Rome.

Christie, W.J. 1974. Changes in the fish species composition of the Great Lakes. J. Fish. Res. Board Can. 31: 827–854.

CIFA. 1985a. Committee for Inland Fisheries of Africa. Report of the Third Session of the Sub-Committee for the Development and Management of the Fisheries of Lake Victoria. Jinja, Uganda, 4–5 October 1984. FAO Fish. Rep. no. 335, FAO, Rome.

CIFA. 1985b. Introduction of species and conservation of genetic resources. Report of the Committee for Inland Fisheries of Africa, Report 85/13: 1–18.

Coulter, G.W. 1970. Population changes within a group of fish species in Lake Tanganyika following their exploitation. J. Fish Biol. 2: 329–353.

Coulter, G.W. 1976. The biology of *Lates* species (Nile perch) in

Lake Tanganyika, and the status of the pelagic fishery for *Lates* species and *Luciolates stappersii* (Blgr.). J. Fish Biol. 9: 235–259.

Coulter, G.W. 1981. Biomass, production and potential yield of the Lake Tanganyika pelagic fish community. Trans. Amer. Fish. Soc. 110: 325–335.

Coulter, G.W. & P.B.N. Jackson. 1981. Deep lakes. pp. 114–124. *In:* J.J. Symoens, M. Burgis & J.J. Gaudet (ed.) The Ecology and Utilization of African Inland Waters, UNEP Reports and Proceedings, Series 1, Nairobi.

Coulter, G.W., B.R. Allanson, M.N. Bruton, P.H. Greenwood, R.C. Hart, P.B.N. Jackson & A.J. Ribbink. 1986. Unique qualities and special problems of the African Great Lakes. Env. Biol. Fish. 17: 161–184.

Crapon de Caprona, M.-D. & B. Fritzsch. 1984. Interspecific fertile hybrids of haplochromine Cichlidae (Teleostei) and their possible importance for speciation. Neth. J. Zool. 34: 503–538.

Crapon de Caprona, M.-D. & B. Fritzsch (ed.) 1989. Proceedings of the workshop on biology, ecology and conservation of cichlids. Bielefeld, West Germany. Ann. Mus. Roy. Afr. Centre., Sc. Zool. 257: 145–150.

de Moor, I.J. & M.N. Bruton. 1988. Atlas of alien and translocated indigenous aquatic animals in southern Africa. South African National Scientific Programmes Report No. 144: 1–310. CSIR, Pretoria.

Dobzhansky, T. 1951. Genetics and the origin of species. Columbia University Press, New York. 364 pp.

Dominey, W.J. 1984. Effects of sexual selection and life history on speciation: species flocks in African cichlids and Hawaiian *Drosophila*. pp. 231–249. *In:* A.A. Echelle & I. Kornfield (ed.) Evolution of Fish Species Flocks, University of Maine Press, Orono.

Dumont, H.J. 1986. The Tanganyika sardine in Lake Kivu: another ecodisaster for Africa? Env. Conserv. 13: 143–148.

Flegler-Balon, C. 1989. Direct and indirect development in fishes – examples of alternative life-history styles. pp. 71–100. *In:* M.N. Bruton (ed.) Alternative Life-History Styles of Animals, Perspectives in Vertebrate Science 6, Kluwer Academic Publishers, Dordrecht.

Foose, T.J., R. Lande, N.R. Flesness, G. Robb & B. Read. 1986. Propagation plans. Zoo. Biol. 5: 139–146.

Frankel, O.H. & M.H. Soule. 1981. Conservation and evolution. Cambridge University Press, Cambridge. 327 pp.

Frankenham, R., H. Hemmer, O.A. Ryder, E.G. Cothran, M.E. Soule, N.D. Urray & M. Snyder. 1986. Selection in captive populations. Zoo. Biol. 5: 127–138.

Fryer, G. 1960. Concerning the proposed introduction of Nile perch into Lake Victoria. E. Afr. agric. J. 25: 267–270.

Fryer, G. 1972. Conservation of the Great Lakes of East Africa: a lesson and a warning. Biol. Conserv. 4: 256–262.

Fryer, G. 1973. The Lake Victoria fisheries: some facts and fallacies. Biol. Conserv. 5: 305–308.

Fryer, G. 1984. The conservation and rational exploitation of the biota of Africa's great lakes. pp. 135–154. *In:* A.V. Hall (ed.) Conservation of Threatened Natural Habitats, South African National Scientific Programmes Rep. (92), CSIR, Pretoria.

Fryer, G. & T.D. Iles. 1972. The cichlid fishes of the Great Lakes of Africa: their biology and evolution. Oliver & Boyd, London. 641 pp.

Gee, J.M. 1969. A comparison of certain aspects of the biology of *Lates niloticus* (Linne) in some east African lakes. Rev. Zool. Bot. afr. 80: 244–262.

Goudswaard, P.C. & W. Ligtvoet. 1987. Recent developments in the fishery for haplochromines (Pisces: Cichlidae) and Nile perch *Lates niloticus* (L.) (Pisces: Centropomidae) in Lake Victoria. *In:* Reports from the Haplochromis Ecology Survey Team (HEST) operating in Lake Victoria no. 35, Mwanza, Tanzania/Leiden, the Netherlands. 14 pp.

Goudswaard, P.C. & F. Witte. 1985. Observations on Nile perch, *Lates niloticus* (L.), 1758, in the Tanzanian waters of Lake Victoria. *In:* CIFA Report of the Third Session of the Sub-Committee for the Development and Management of the Fisheries of Lake Victoria, Jinja, Uganda, 4–5 October 1984. FAO Fish. Rep. no. 335: 62–67. FAO, Rome.

Greenwood, P.H. 1965. Environmental effects on the pharyngeal mill of a cichlid fish. *Astatoreochromis alluaudi,* and their taxonomic implications. Proc. Linn. Soc. Lond. 176: 1–10.

Greenwood, P.H. 1987. The cichlid fishes of Lake Victoria – was their obituary premature? pp. 31–32. *In:* A.P. Harvey (ed.) Report on the British Museum (Natural History) 1984–86, Trustees of the British Museum (Natural History), London.

HEST. 1986a. Report of the meetings on: 'The Nile perch effect on Lake Victoria fisheries'. *In:* Reports from the Haplochromis Ecology Survey Team (HEST) operating in the Mwanza Area of Lake Victoria no. 34, Mwanza, Tanzania/Leiden, the Netherlands. 11 pp.

HEST. 1986b. Reports of the meetings on 'Cichlid species flock of Lake Victoria on the verge of extinction'. *In:* Reports of the Research-group Ecological Morphology of Fishes (continuing Reports of the Haplochromis Ecology Survey Team, HEST) no. 46, Mwanza, Tanzania/Leiden, the Netherlands. 96 pp.

HEST & TAFIRI. 1987. The increase of the Nile perch in Lake Victoria. pp. 59–75. *In:* Reports from the Haplochromis Ecology Survey Team operating in Lake Victoria no. 37, Mwanza, Tanzania/Leiden, the Netherlands.

Holling, C.S. 1976. Resilience and stability of ecosystems. pp. 73–92. *In:* E. Jantsch & K.D. Waddington (ed.) Evolution and Consciousness, Addison-Wesley, Reading.

Hoogerhoud, R.J.C. 1986. Taxonomic and ecological aspects of morphological plasticity in molluscivorous haplochromines (Pisces, Cichlidae). Ann. Mus. Roy. Afr. Centr., Sc. Zool. 251: 131–134.

Hopson, A.J. 1972. A study of the Nile perch [*Lates niloticus* (L), Pisces: Centropomidae] in Lake Chad. pp. 1–93. *In:* Overseas Research Publication no. 19, Overseas Development Administration, London.

Hsu, K.J. 1982. Mass mortality and its environmental and evolutionary consequences. Science 216: 249–250.

Hughes, N.F. 1986. Changes in the feeding biology of the Nile perch, *Lates niloticus* (L.) (Pisces: Centropomidae), in Lake Victoria, East Africa, since its introduction in 1960, and its impact on the native fish community of the Nyanza Gulf. J. Fish Biol. 29: 541–548.

IARCEC. 1988. The conservation of endangered species of cichlid fishes. Env. Biol. Fish. 22: 313–315.

IUCN. 1979. World Conservation Strategy. International Union for the Conservation of Nature and Natural Resources, Morges. 70 pp.

IUCN. 1987. The IUCN policy statement on captive breeding. Survival Service Commission, Captive Breeding Specialist Group, Gland, Switzerland. 4 September 1987. 4 pp.

Jackson, P.B.N. 1960. On the desirability or otherwise of introducing fishes to waters that are foreign to them. CSA Symposium Hydrobiol. Inl. Fish. CSA/CCTA Publ. 63: 157–164.

Jantsch, E. 1985. The self-organizing universe. Scientific and human implications of the merging paradigm of evolution. Pergamon, Oxford. 343 pp.

Kohler, C.C. & J.G. Stanley. 1984. A suggested protocol for evaluating proposed exotic fish introductions in the United States. pp. 387–406. *In:* W.R. Courtenay & J.R. Stauffer (ed.) Distribution, Biology and Management of Exotic Fishes, Johns Hopkins University Press, Baltimore.

Kornfield, I.L., D.C. Smith, P.S. Gagnon & J.N. Taylor. 1982. The cichlid fish of Cuatro Cienegas, Mexico: direct evidence of conspecificity among distinct trophic morphs. Evolution 36: 658–664.

Kosswig, C. 1947. Selective mating as a factor for speciation in cichlid fishes of East African lakes. Nature 159: 604–605.

Liem, K.F. 1973. Evolutionary strategies and morphological innovations: cichlid pharyngeal jaws. Syst. Zool. 22: 425–441.

Liem, K.F. 1978. Modulatory multiplicity in the functional repertoires of the feeding mechanisms of cichlid fishes. I. Piscivores. J. Morphol. 158: 323–360.

Liem, K.F. & J.W. Osse. 1975. Biological versatility, evolution, and food resource exploitation in African cichlid fishes. Amer. Zool. 15: 427–454.

Ligtvoet, W. 1989. The Nile perch in Lake Victoria: a blessing or a disaster? Ann. Mus. Roy. Afr. Centr., Sc. Zool. 257: 151–156.

Ligtvoet, W., A.I. Chande & O.I.I.W. Mosille. 1987. A preliminary description of the artisanal Nile perch (*Lates niloticus*) fishery in southern Lake Victoria. pp. 43–56. *In:* Reports from the Haplochromis Ecology Survey Team (HEST) and the Tanzanian Fisheries Research Institute (TAFIRI) operating in Lake Victoria no. 38, Mwanza, Tanzania/Leiden, the Netherlands.

Macdonald, I.A.W., F.J. Kruger & A.A. Ferrar. (ed.) 1986. The ecology and management of biological invasions in southern Africa. Oxford University Press, Cape Town. 324 pp.

Mainga, O.M. 1985. Preliminary results of an evaluation of fishing trends in the Kenya waters of Lake Victoria from 1981 to 1982. pp. 110–116. *In:* CIFA Report of the Third Session of the Sub-Committee for the Development and Management of the Fisheries of Lake Victoria, Jinja, Uganda, 4–5 October 1984. FAO Fish. Rep. no. 335, FAO, Rome.

Margalef, R. 1968. Perspectives in ecological theory. University of Chicago Press, Chicago. 111 pp.

Martin, R.D. 1975. Introduction. pp. xv–xxv. *In:* R.D. Martin (ed.) Breeding Endangered Species in Captivity, Academic Press, London.

May, R.M. 1975. Stability in ecosystems: some comments. pp. 161–168. *In:* W.H. van Dobben & R.H. Lowe-McConnell (ed.) Unifying Concepts in Ecology, Dr W. Junk Publishers, The Hague.

Mayr, E. 1982. Speciation and macroevolution. Evolution 36: 1119–1132.

Meffe, G.K. 1987. Conserving fish genomes: philosophies and practices. Env. Biol. Fish. 18: 3–9.

Meyer, A. 1987. Phenotypic plasticity and heterochrony in *Cichlasoma managuense* (Pisces, Cichlidae) and their implications for speciation in cichlid fishes. Evolution 4(6): 1357–1369.

Moureau, J., J. Arrignon & R.A. Jubb. 1988. Les introductions d'espèces étrangères dans les eaux continentales africaines. Intérêts et limites. pp. 395–425. *In:* C. Lévêque, M.N. Bruton & G.W. Ssentongo (ed.) Biologie et Ecologie des Poissons d'eau douce Africains/Biology and Ecology of African Freshwater Fishes, ORSTOM, Paris.

Myers, N. 1979. The sinking ark. Pergamon Press, Oxford. 307 pp.

Noakes, D.L.G. & E.K. Balon. 1982. Life histories of tilapias: an evolutionary perspective. pp. 61–82. *In:* R.S.V. Pullin & R.H. Lowe-McConnell (ed.) Biology and Culture of Tilapias, ICLARM, Manila.

Norton, B.G. 1986. On the inherent danger of undervaluing species. pp. 110–137. *In:* B.G. Norton (ed.) The Preservation of Species. The Value of Biological Diversity, Princeton University Press, Princeton.

Ogari, J. 1985. Distribution, food and feeding habits of *Lates niloticus* in Nyanza Gulf of Lake Victoria (Kenya). pp. 68–80. *In:* CIFA Report of the Third Session of the Sub-Committee for the Development and Management of the Fisheries of Lake Victoria, Jinja, Uganda, 4–5 October 1984, FAO Fish. Rep. no. 335, FAO, Rome.

Ogari, J. & S. Dadzie. 1988. The food of Nile perch, *Lates niloticus* (L.) after the disappearance of the haplochromine cichlids in the Nyanza Gulf of Lake Victoria (Kenya). J. Fish Biol. 32: 571–577.

Ogutu-Ohwayo, R. 1984. Predation by the Nile perch, *Lates niloticus* introduced into Lake Kyoga (Uganda) and its effects on the populations of fish in the lake. MSc thesis, University of Dar es Salaam, Tanzania. 147 pp.

Ogutu-Ohwayo, R. 1985. The effects of predation by Nile perch, *Lates niloticus* (Linne) introduced into Lake Kyoga (Uganda) in relation to the fisheries of Lake Kyoga and Lake Victoria. pp. 18–41. *In:* CIFA Report of the Third Session of the Sub-Committee for the Development and Management of the Fisheries of Lake Victoria, Jinja, Uganda, 4–5 October 1984, FAO Fish. Rep. no. 335, FAO, Rome.

Ogutu-Ohwayo, R. 1988. Reproductive potential of the Nile perch, *Lates niloticus* L. and the establishment of the species in Lakes Kyoga and Victoria (East Africa). Hydrobiologia 162: 193–200.

Ogutu-Ohwayo, R. 1990. The decline of the native fishes of lakes Victoria and Kyoga (East Africa) and the impact of introduced species, especially the Nile perch, *Lates niloticus*, and the Nile tilapia, *Oreochromis niloticus*. Env. Biol. Fish. 27: 81–96.

Okaronon, J.D., T.D. Acere & D.L. Ocenodongo. 1985. The current state of the fisheries in the northern portion of Lake Victoria (Uganda). *In:* CIFA Report of the Third Session of the Sub-Committee for the Development and Management of the Fisheries of Lake Victoria, Jinja, Uganda, 4–5 October 1984. FAO Fish. Rep. no. 335: 89–98. FAO, Rome.

Okedi, J. 1971. Further observations on the ecology of the Nile perch (*Lates niloticus* Linne) in Lake Victoria and Lake Kyoga. Ann. Rep. E. Afr. Freshwat. Fish. Res. Org. (1970): 42–55.

Okemwa, E. 1984. Potential fishery of Nile perch *Lates niloticus* Linn. (Pisces, Centropomidae) in Nyanza Gulf of Lake Victoria, East Africa. Hydrobiologia 108: 121–126.

Orians, G.H. 1975. Diversity, stability and maturity in natural ecosystems. pp. 139–150. *In:* W.H. van Dobben & R.H. Lowe-McConnell (ed.) Unifying Concepts in Ecology, Dr W. Junk Publishers, The Hague.

Ribbink, A.J. 1986. Perspectives in species conservation. Ann. Mus. Roy. Afr. Centr., Sc. Zool. 251: 163–170.

Ribbink, A.J. 1987. African lakes and their fishes: conservation scenarios and suggestions. Env. Biol. Fish. 19: 3–26.

Ribbink, A.J. & D.H. Eccles. 1988. Fish communities in the East African Great Lakes. pp. 277–301. *In:* C. Lévêque, M.N. Bruton & G.W. Ssentongo (ed.) Biologie et Ecologie des Poissons d'Eau Douce Africains/Biology and Ecology of African Freshwater Fishes, ORSTOM, Paris.

Ribbink, A.J., B.A. Marsh, A.C. Marsh, A.C. Ribbink & B.J. Sharp. 1983. A preliminary survey of the cichlid fishes of rocky habitats in Lake Malawi. S. Afr. J. Zool. 18: 149–310.

Ribbink, A.J. & V. Twentyman-Jones. 1989. Captive propagation as a conservation tool. Ann. Mus. Roy. Afr. Centr., Sc. Zool. 257: 145–150.

Sage, R.D. & R.K. Selander. 1975. Trophic radiation through polymorphism in cichlid fishes. Proc. Nat. Acad. Sci. U.S.A. 72: 4669–4673.

Schonewald-Cox, C.M., S.M. Chambers, B. MacBryde & L. Thomas (ed.). 1983. Genetics and conservation: a reference for managing wild animals and plant populations. Benjamin/Cummings Publ., Menlo Park. 618 pp.

Skelton, P.H. 1988. The distribution of African freshwater fishes. pp. 65–91. *In:* C. Lévêque, M.N. Bruton & G.W. Ssentongo (ed.) Biologie et Ecologie des Poissons d'Eau Douce Africains/Biology and Ecology of African Freshwater Fishes, ORSTOM, Paris.

Smith, S.H. 1968. Species succession and fishery exploitation in the Great Lakes. J. Fish. Res. Board Can. 25: 667–693.

Soule, M.E. & B.A. Wilcox (ed.). 1980. Conservation biology: an evolutionary-ecological perspective. Sinauer Associates, Sunderland. 395 pp.

Ssentongo, G.W. & R.L. Welcomme. 1985. Past history and current trends in the fisheries of Lake Victoria. pp. 123–138. *In:* Report of the Third Session of the CIFA Sub-Committee for the Development and Management of the Fisheries of Lake Victoria, Jinja, Uganda, 4–5 October 1984, FAO Fish. Rep. no. 335, FAO, Rome.

Stiassny, M.L.J. & J.S. Jensen. 1987. Labroid interrelationships revisited: morphological complexity, key innovations, and the study of comparative diversity. Bull. Mus. Comp. Zool. 5: 269–319.

Stoneman, J. & J.F. Rogers. 1970. Increase in fish production achieved by stocking exotic species (Lake Kyoga, Uganda). Uganda Fisheries Department, Occasional Paper (3): 16–19.

Taylor, J.N., W.R. Courtenay & J.A. McCann. 1984. Known impacts of exotic fishes in the continental United States. pp. 322–373. *In:* W.R. Courtenay & J.R. Stauffer (ed.) Distribution, Biology and Management of Exotic Fishes, Johns Hopkins University Press, Baltimore.

van Dobben, W.H. & R.H. Lowe-McConnell (ed.). 1975. Unifying concepts in ecology. Dr W. Junk Publishers, The Hague. 302 pp.

Vermeij, G.J. 1986. The biology of human-caused extinction. pp. 28–49. *In:* B.G. Norton (ed.) The Preservation of Species. The Value of Biological Diversity, Princeton University Press, Princeton.

Wanink, J.H., W. Ligtvoet. A.I. Chande, P.C. Goudswaard, J. Kashindye, E.F.B. Katunzi, O.I.I.W. Mkumbo, B. Msuku & F. Witte. 1988. HEST/TAFIRI research in Lake Victoria: some preliminary results and their relevance for fishery management. pp. 1–9. *In:* Reports from the Haplochromis Ecology Survey Team (HEST) and the Tanzanian Fisheries Research Institute (TAFIRI) operating in Lake Victoria no. 44, Mwanza, Tanzania/Leiden, the Netherlands.

Welcomme, R.L. 1984. International transfers of inland fish species. pp. 22–40. *In:* W.R. Courtenay, Jr. & J.R. Stauffer, Jr. (ed.) Distribution, Biology, and Management of Exotic Fishes, Johns Hopkins University Press, Baltimore.

Wesseling, M. 1986. Nile perch in the china shop. Natuur en Milieu 7–8: 4–7 (in Dutch).

Witte, F. 1984. Ecological differentiation in Lake Victoria haplochromines: comparison of cichlid species flocks in African lakes. pp. 155–167. *In:* A.A. Echelle & I. Kornfield (ed.) Evolution of Fish Species Flocks, University of Maine Press, Orono.

Witte, F. & P. Goudswaard. 1985. Aspects of the haplochromine fishery in southern Lake Victoria. pp. 81–88. *In:* CIFA Report of the Third Session of the Sub-Committee for the Development and Management of the Fisheries of Lake Victoria, Jinja, Uganda, 4–5 October 1984. FAO Fish. Rep. no. 335, FAO, Rome.