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Human-induced changes in the composition of fish communities in the African Great Lakes

JOHN F. CRAIG

Craig Consultancy, Whiteside House, Dunscore, Dumfries DG2 0UU, Scotland, UK

Contents

Introduction

The aim of this review is to explore the extent of knowledge of fish species composition changes in the African Great Lakes, and to examine whether there is sufficient knowledge to enable differentiation between the effects of overexploitation and the introduction of exotic fish. Other human-induced effects, such as pollution, have a significant effect on the fish faunas of the lakes but will not be discussed in detail here. For the purposes of this study the term 'African Great Lakes' incorporates both natural and man-made lakes. Some of the latter – Cahora Bassa, Kainji, Kariba and Volta – have a surface area comparable in size to some of the natural Great Lakes (Tables 1a–g and Figure 1). The natural Great Lakes include those of the rift valleys, Albert (Mobutu), Edward–George, Kivu, Malawi (Nyasa), Tanganyika and Turkana (Rudolf), the inter-rift, Kyoga and Victoria, and several others including Bangweulu, Chad and Chilwa. Many of the natural lakes have unique fish faunas in which the majority of species, in particular members of the Cichlidae, are endemic. Man-made lakes have been populated mainly by indigenous riverine fishes. Fishing pressure has increased in all these lakes, natural and man-made, due to human population increase. They all have important fisheries which supply necessary protein to the people around their shores and beyond.

In some natural lakes, such as Lake Chad, the fish are still strongly influenced by inflowing streams and there is little distinction between riverine and lacustrine fish communities. Many of the non-cichlids have to return to the rivers to spawn. Lake Chad, Turkana and Albert have low levels of endemicity and fewer cichlid species than Lakes Malawi, Tanganyika and Victoria. The degree to which cichlids, in particular the haplochromine species, have evolved within the natural African Great Lakes is quite remarkable. Lake Victoria has over 300 cichlid species (Witte and Oijen, 1990) of which only about seven are non-endemic, and Lake Malawi has an estimated 500 cichlid species of which only about five are non-endemic.

For some time the haplochromine species of Lakes Victoria and Malawi were aggregated as *Haplochromis* species flocks since all the taxa involved were placed in this genus (Greenwood, 1974). Later Greenwood (1979, 1980), after considerable studies on the morphology of the fish, changed his mind because he did not think that he could establish the monophyletic origin of Lake Victoria *Haplochromis* species and considered the genus itself not to be a natural one. He came to a similar conclusion, that the flock was polyphyletic, for Lake Malawi haplochromines (Greenwood, 1983a, b). However, Hoogerhoud (1984) doubted a generic distinction and demonstrated continuous morphoclines on the basis of different characters. Studies by Sage *et al.* (1984), using starch gel electrophoretic techniques on the proteins, and by Meyer *et al.* (1990), examining the base pairs of mitochondrial DNA from various Lake Victoria *Haplochromis* species, indicated that the *Haplochromis* species flock within Lake Victoria was indeed monophyletic. Its morphological diversification has occurred over a very short period of time. The age of the lake is estimated to be between 250000 and 750000 years, and the origin of the flock less than 200000 years (Meyer *et al.*, 1990). The haplochromine flocks of Lake Victoria and Lake Malawi appear to be closely related, more so than they are to those of Lake Tanganyika. Recent studies (Meyer *et al.*, 1990) indicate that explosive evolutionary radiation has taken place from a single common ancestor within each lake.

The fairly constant environment of the littoral leads to the development of stable fish populations which are territorial with no requirement to migrate and which have low

Table 1a. A summary of data on the Great Lakes of Africa (Nile drainage, natural lakes)

	Lake Albert (Mobutu)	Lake George	Lake Edward (Idi Amin)
Country	Zaire and Uganda	Uganda	Zaire
Location	1°50′ N 30°40′ E	0°02′ N 30°25′ E	0°25′ S 29°40′ E
Area (km^2)	6800	270	2325
Maximum (mean) depth (m)	58 (25)	3.0 (2.5)	117 (34)
Conductivity (μohm cm^{-1} at 20°C)	730	200	840
pH	8.9–9.5	8.5–9.5	8.7–9.3
Secchi depth (m)	2.0–6.0	0.4	1.8–3.0
Primary productivity (gC m^{-2} $year^{-1}$)	970	1500	1569
Approx. no. fish families	14	8	8
Non-cichlids (endemic) no. of species	37 (2)	17 (2)	17 (2)
Cichlids (endemic) no. of species	9 (4)	60 (59)	60 (59)
Successful introductions	None	None	None
Main commercial species	*Alestes (A. baremose), Hydrocynus, Lates macrophthalmus* (lives offshore), *Bagrus, Oreochromis niloticus, O. leucostictus, Sarotherodon galilaeus, Tilapia zillii* and *Citharinus citharus*	*Oreochromis niloticus, Bagrus docmac, Clarias lazera* and *Protopterus aethiopicus*	See Lake George data
Landings (tonnes $year^{-1}$)	12548 in 1963; 12532 in 1988	12031 in 1963; 5936 in 1988	See Lake George data
Fishing gears used	Gill nets, beach seines, longlines, rod and line	Gill nets for cichlids (minimum size limit 5 inches), baited longlines for predators	As for Lake George
Notes	Fish species similar to riverine fish	Kazinga Channel outflow joins Lake Edward	

Table 1a *continued*

	Lake Victoria	Lake Kyoga	Lake Turkana (Rudolf)
Country	Uganda, Kenya and Tanzania	Uganda	Kenya and Ethiopia
Location	0°50′ S 32°50′ E	1°30′ N 32°45′ E	3°30′ N 36°05′ E
Area (km^2)	68000	2700	7200
Maximum (mean) depth (m)	79 (20)	8 (6)	120 (31)
Conductivity (μohm cm^{-1} at 20°C)	96	245–365	3000–3500
pH	7.1–9.0	7.2–9.0	9.4–10.0
Secchi depth (m)	1.3–8.2	0.9	–
Primary productivity (gC m^{-2} year^{-1})	950	–	259–6220
Approx. no. fish families	12	as for Lake Victoria	15
Non-cichlids (endemic) no. of species	38 (16)	as for Lake Victoria	35 (6)
Cichlids (endemic) no. of species	300 (293)	as for Lake Victoria	12 (11)
Successful introductions	*Lates niloticus;* tilapias: about 4 non-indigenous tilapine species introduced, from 1951 onwards, from Lake Albert into Uganda, Kenya and Tanzania waters, including *Oreochromis leucostictus, O. niloticus, Tilapia rendalli* and *T. zillii*	*Lates niloticus;* tilapias: about 4 non-indigenous species introduced from 1951 onwards, including *Oreochromis leucostictus, O. niloticus, Tilapia rendalli* and *T. zillii*	None
Main commercial species	1971, *Oreochromis, Bagrus, Clarias, Haplochromis* and *Protopterus;* 1990, *Lates niloticus, Rastrineobola argentea* and *Oreochromis niloticus*	as for Lake Victoria	*Lates niloticus, Sarotherodon niloticus, Citharinus* and *Alestes*
Landings (tonnes year^{-1})	110000 in 1968; 296000 in 1985	4500 in 1956; 160000 in 1977; 68000 in 1988	2045 in 1968; 3510 in 1974
Fishing gears used	Gill nets, beach seines, longlines, trawling, ringnets and Danish seines	Gill nets, beach seines, longlines	Gill nets, beach seines and traditional methods
Notes	Overfishing within both shallow inshore areas and river mouths Generalized water budget: rainfall on lake surface, 1260 mm; inflows, 330 mm; evaporation, 1310 mm; outflow (R. Nile), 280 mm	In the last decade there has been a steady drop in the water level (1.5 m) which has caused a reduction in the breeding and nursery areas	Similar fish fauna to Lake Albert, basically Nilotic; 12 species riverine and confined to the region of the Ono Delta Seasonality leaves growth checks on bony structures in many fish *Lates longispinus*, a dwarf and offshore-living species, comparable to the offshore form of *Lates* in Lake Albert Semi-desert region influenced by River Ono in Ethiopia.

Table 1b. A summary of data on the Great Lakes of Africa (Zaire drainage, natural lakes).

	Lake Bangweulu	Lake Kivu	Lake Mweru
Country	Zambia	Zaire and Rwanda	Zaire and Zambia
Location	10°55′ S 30°10′ E	1°45′ S 28°55′ E	8°50′ S 28°50′ E
Area (km^2)	2072	2700	5200
Maximum (mean) depth (m)	10 (2.5)	489 (240)	37 (12)
Conductivity (μohm cm^{-1} at 20°C)	14–35	1240	70–150
pH	7.0–8.3	6.5–9.5	6.6–9.3
Secchi depth (m)	0.8–1.05	2.5–9.3	0.76–1.2
Primary productivity (gC m^{-2} $year^{-1}$)	270	240 to 540	–
Approx. no. fish families	11	16	16
Non-cichlids (endemic) no. of species	59 (3)	9 (0)	83 (4)
Cichlids (endemic) no. of species	9 (1)	8 (7)	11 (1)
Successful introductions	None	*Limnothrissa miodon* and *Stolothrissa tanganicae* from Lake Tanganyika (latter was not successful) from 1958 to 1960	None
Main commercial species	Cichlids, mormyrids, clariids, bagrids, mochochids, characids	*L. miodon*	*Tilapia, Auchenoglanis, Chrysichthys, Gnathonemus* and *Mormyrus*
Landings (tonnes $year^{-1}$)	12000–15000	–	12445 in 1968
Fishing gears used	Gill nets	Artisanal–light attraction and lift nets	Gill nets
Notes	Natural shallow lakes, swamps and seasonally inundated floodplains	Success of introduction due to lack of predators and the abundance of pelagic plankton Residence time of water, 110 years; refill time (runoff alone), 190 years	

Table 1b *continued*

	Lake Tanganyika
Country	Burundi, Tanzania, Zambia and Zaire
Location	5°15′ S 29°40′ E
Area (km^2)	33000
Maximum (mean) depth (m)	1470 (570)
Conductivity (μohm cm^{-1} at 20°C)	566–620
pH	8.6–9.2
Secchi depth (m)	3.3–22
Primary productivity (gC m^{-2} $year^{-1}$)	1040 (290 – Hecky and Fee, 1981)
Approx. no. fish families	14
Non-cichlids (endemic) no. of species	75 (52)
Cichlids (endemic) no. of species	165 (164)
Successful introductions	None
Main commercial species	*Limnothrissa miodon, Stolothrissa tanganicae, Lates mariae, L. microlepis, L. angustifrons* and *L. (Luciolates) stappersi*
Landings (tonnes $year^{-1}$)	73000
Fishing gears used	Commercial purse seines; artisanal beach seines, handlines, longlines, weirs and gill nets
Notes	Benthic fish population occurs down to 200 m depth on the extensive shelf areas at the south and comprise about 60 species *Chaoborus*, the lakefly is not present in Lake Tanganyika as it is in Lake Malawi Generalized water budget: rainfall on lake surface, 900 mm; inflows, 530 mm; evaporation, 1350 mm; outflow, 80 mm Residence time of water, 430 years; inflow to volume ratio, 1:1500; refill time (runoff alone), 1000 years

Table 1c. A summary of data on the Great Lakes of Africa (Chad drainage, natural lake).

	Lake Chad
Country	Chad and Nigeria
Location	13°55′ N 13°40′ E
Area (km^2)	10000–25000
Maximum (mean) depth (m)	12 (variable)
Conductivity (μohm cm^{-1} at 20°C)	40–88
pH	7.1–8.3
Secchi depth (m)	0.15–1.27
Primary productivity (gC m^{-2} $year^{-1}$)	370
Approx. no. fish families	25
Non-cichlids (endemic) no. of species	84 (8)
Cichlids (endemic) no. of species	9 (1)
Successful introductions	None
Main commercial species	*Lates niloticus, Hyrocynus vittatus, Alestes baremose*
Landings (tonnes $year^{-1}$)	22400
Fishing gears used	–
Notes	The lake has been subjected to serious droughts as it lies just south of the Sahara and has oscillated in size over the years Fish biomass has varied as a result of lake size from 30 to 5620 kg ha^{-1} Fish species strongly influenced by inflowing rivers into which many fish enter to spawn Lake now almost dried up due to climatic conditions

Table 1d. A summary of data on the Great Lakes of Africa (Chilwa drainage, natural lake).

	Lake Chilwa
Country	Malawi
Location	15°30′ S 35°30′ E
Area (km^2)	Chilwa basin 7500
Maximum (mean) depth (m)	2.5 (variable)
Conductivity (μohm cm^{-1} at 20°C)	1000–1250
pH	7.6–8.7
Secchi depth (m)	–
Primary productivity (gC m^{-2} $year^{-1}$)	–
Approx. no. fish families	3
Non-cichlids (endemic) no. of species	8 (0)
Cichlids (endemic) no. of species	5 (0)
Successful introductions	None
Main commercial species	*Clarias mossambicus, Barbus paludinosus* and *Sarotherodon shiranus chilwae*
Landings (tonnes $year^{-1}$)	100–9800; depends on water level
Fishing gears used	Gill nets, beach seines
Notes	In times of drought fish take refuge in lagoons and streams; *C. mossambicus* can withstand desiccation and high conductivity Generalized water balance, 1961–71: rainfall, 893 mm; inflow, 410 mm; evaporation, 1303 mm

Table 1e. A summary of data on the Great Lakes of Africa (Zambezi drainage, natural and man made lakes).

	Lake Malawi (Nyasa) – natural	Lake Cahora Bassa – man made*	Lake Kariba – man made
Country	Malawi and Mozambique	Mozambique	Zimbabwe and Zambia
Location	10°45′ S 34°30′ E	16°00′ S 31°00′ E	17°15′ S 27°55′ E
Area (km^2)	30800	2665	5364
Maximum (mean) depth (m)	756 (426)	156 (21)	120 (29.2)
Conductivity (μohm cm^{-1} at 20°C)	220	112–132	80
pH	7.7–8.6	7.0–8.2	6.8–8.0
Secchi depth (m)	17	–	1–12
Primary productivity (gC m^{-2} $year^{-1}$)	252	–	620
Approx. no. fish families	11	14	16 (total no. species 40)
Non-cichlids (endemic) no. of species	45 (28)	50 (–)	40
Cichlids (endemic) no. of species	500 (495)	11 (–)	40
Successful introductions	None	*Limnothrissa miodon* by natural migration down the River Zambezi	*Limnothrissa miodon* and *Stolothrissa tanganicae* from Lake Tanganyika (latter was not successful) from 1967 to 1968
Main commercial species	*Haplochromis* spp., *Oreochromis* spp., *Rhamphochromis* spp.	*Hydrocynus vittatus*, *Labeo* spp., *Limnothrissa miodon*, *Clarias gariepinus*, *Oreochromis mortimiri*, *Distichodus schenga*	*Hydrocynus vittatus*, *Limnothrissa miodon*, *Clarias gariepinus*, *Tilapia rendalli* and *Serranochromis*
Landings (tonnes $year^{-1}$)	12445 to 30000	–	500 in 1974 to 24000 in 1985
Fishing gears used	Commercial ringnetting, midwater and demersal trawling; artisanal gill nets	Gill nets	Artisanal gillnet fishery and commercial/industrial pelagic fishery with lights and lift nets
Notes	*Haplochromis* spp. make up 72% of the nearshore catch *Chaoborus*, the midge larvae, is found in the pelagic zone Generalized water budget: rainfall, 1000 mm; inflows, 490 mm; evaporation, 1300 mm	Fishing density in 1984: 0.46 fishermen km^{-2}; critical density, 1.5 km^{-2} Dam closed in 1974 Outflow to volume ratio, 2:1 *Values taken from middle Zambezi	Dam closed 1958 Generalized water budget: rainfall on lake surface, 5.0 km^3; inflows, 60.9 km^3; evaporation, 8.6 km^3; outflows, 46.6 km^3; outflow to volume ratio, 1:3

Table 1f. A summary of data on the Great Lakes of Africa (Niger drainage, man made lake).

	Lake Kainji
Country	Nigeria
Location	10°00′ N 4°35′ E
Area (km^2)	1280
Maximum (mean) depth (m)	50 (12.3)
Conductivity (μohm cm^{-1} at 20°C)	73
pH	6.0–8.0
Secchi depth (m)	0.1–3
Primary productivity (gC m^{-2} $year^{-1}$)	890
Approx. no. fish families	22
Total no. of species	101 Similar species to Lake Volta
Successful introductions	None
Main commercial species	*Sarotherodon galilaeus* (dominant in the catch), *Lates niloticus, Bagrus bayad, B. docmac, Oreochromis niloticus, Tilapia zillii, Hydrocynus forskahlii* and *H. brevis*
Landings (tonnes $year^{-1}$)	4500–6000
Fishing gears used	Cast nets from the shore and from canoes
Notes	*H. forskahlii* feeds on clupeids and *H. brevis* feeds on cichlids Most mormyrids declined or disappeared after filling although a few species increased after the initial decline Yield of 35 kg ha^{-1} $year^{-1}$ similar to that of the floodplains Dam closed 1968 Generalized water budget: rainfall, 660–1352 mm; inflow 80000×10^6 m^3; evaporation, 1500–2000 mm; outflow to volume ratio, 4:1 – high compared to other reservoirs, cf. Volta, Kariba

Table 1g. A summary of data on the Great Lakes of Africa (Volta drainage, man made lake).

	Lake Volta
Country	Ghana
Location	7°10′ N 0°30′ W
Area (km^2)	8845
Maximum (mean) depth (m)	75 (18.6); drawdown of 3m
Conductivity (μohm cm^{-1} at 20°C)	–
pH	–
Secchi depth (m)	–
Primary productivity (gC m^{-2} $year^{-1}$)	930
Approx. no. fish families	26
Total no. of species	122
Successful introductions	None
Main commercial species	*Alestes, Citharinus, Distichodus, Labeo, Lates niloticus, Sarotherodon galilaeus, Oreochromis niloticus* and *Tilapia zillii*
Landings (tonnes $year^{-1}$)	Between 1971 and 1984, 36–42000
Fishing gears used	Gill nets
Notes	Pelagic clupeids (*Pellonula afzeliusi* and *Cynothrissa mento*) underexploited and tilapias overexploited Mormyrids virtually disappeared after filling Akosombo Dam closed in 1964 Outflow to volume ratio, 0.25:1

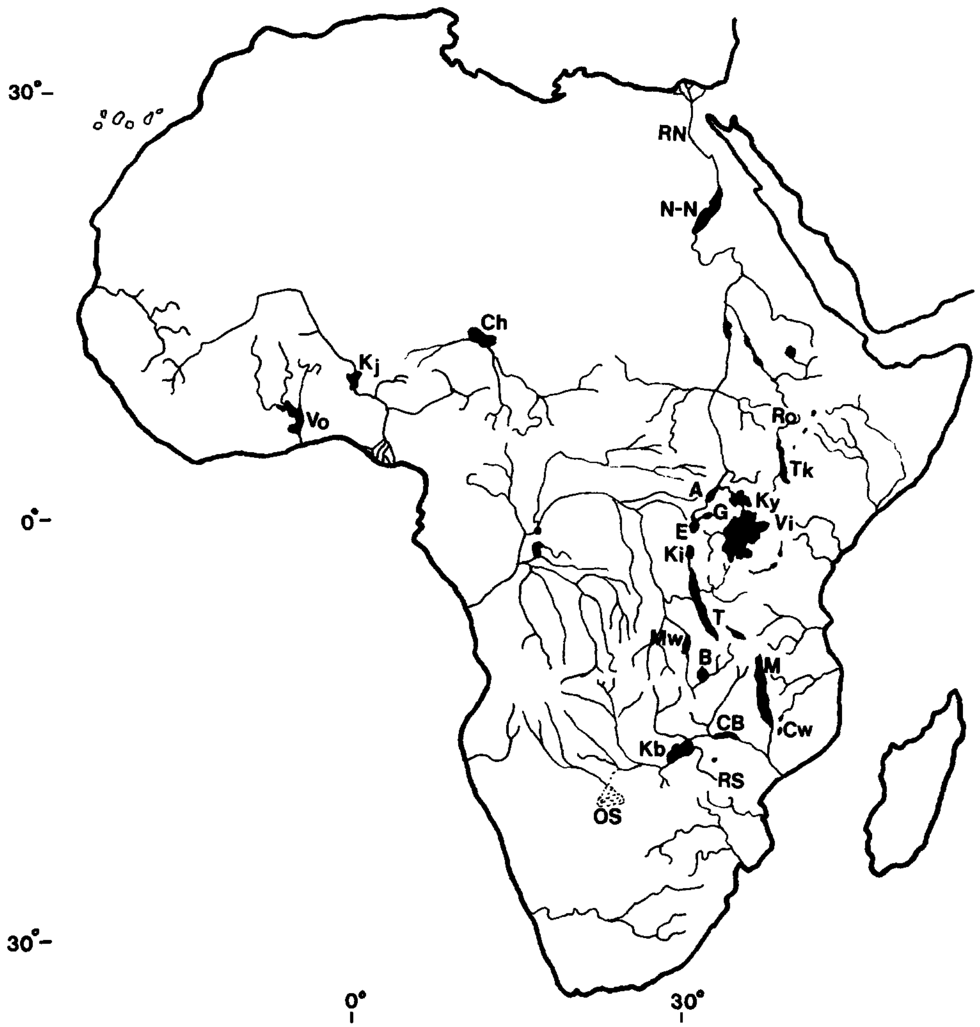

Fig. 1. Main lakes, reservoirs and river systems of Africa (equal area projection). Lakes: A, Albert; B, Bangweulu; CB, Cahora Bassa; Ch, Chad; Cw, Chilwa; E, Edward; G, George; Kb, Kariba; Ki, Kivu; Kj, Kainji; Ky, Kyoga; M. Malawi; Mw, Mweru; N-N, Nasser-Nubia; T, Tanganyika; Tk, Turkana; Vi, Victoria; Vo, Volta. Rivers: RN Nile; RO, Ono; RS, Sanyati. OS, Okavengo Swamp.

fecundity and exhibit parental care. Although many of the cichlids are confined to inshore areas, in Lake Victoria they also occupy (occupied) open offshore areas (Kudhongania and Cordone, 1974a) and there is (was) a plankton-feeding cichlid fauna (van Oijen *et al.*, 1981; Witte, 1981; Goldschmidt *et al.*, 1990; Witte and van Oijen, 1990). Lake Malawi also has a well-developed plankton-feeding cichlid fauna. However, the diversity of fish is comparatively simple in the pelagic zone compared with that in the very complex littoral. Predation in the open water may lead to selection of uniformity whereas in the rocky littoral with prey cover it may lead to species diversity (Lowe-McConnell, 1987).

In Lake Tanganyika the family Centropomidae is represented by four endemic species of *Lates*. These predators include *L. mariae* found in the benthic zone, *L. angustifrons*, an inshore fish preferring rocky areas, and *L. microlepis* and *L. stappersi* occupying the offshore pelagic areas (Coulter, 1991). Other deep-living forms of this genus have evolved in Lakes Albert and Turkana. This family includes the Nile perch, *Lates niloticus*, a species widespread from West Africa to the Nile system, which has been at the centre of controversy over its introduction into lakes Kyoga and Victoria. The pelagic zone of Lake Tanganyika is occupied by two endemic clupeids, *Stolothrissa tanganicae* and *Limnothrissa miodon*, upon which the *Lates* species prey. These clupeids have been introduced into Lake Kivu and into the man-made Lake Kariba (from where they spread down the Zambezi to Lake Cahora Bassa), but only *L. miodon* succeeded in colonizing the lakes (Davies *et al.*, 1975; Spliethoff *et al.*, 1983; Marshall, 1985, 1988). Two small zooplanktivorous cyprinids are becoming important in the pelagic fisheries, *Engraulicypris sardella* in Lake Malawi and *Rastrineobola argentea* in Lake Victoria (Skelton *et al.*, 1991). Cyprinid *Barbus* species are other important food fish. Further fish of significant importance in the fisheries of some of the lakes include other cichlids (*Tilapia* and *Oreochromis*), characids (*Hydrocynus* and *Alestes*), the catfish families, bagrids (*Bagrus*), clariids (*Clarias*, *Xenoclarias* and *Dinotopterus*), schilbeids (*Schilbe* and *Eutropius*), mochokids (*Synodontis*) and malapterurids (*Malapterurus*), protopterids (*Protopterus*) and polypterids (*Polypterus*).

The fisheries of the African Great Lakes were originally subsistence fisheries confined mainly to shoreline areas and seasonally to the mouths of rivers where migratory fish were caught. Poisons and gears made from locally produced fibres, such as seines and scoops, basket traps and weirs, harpoons and lances, and hooks and lines were used (Jackson, 1971). Gill nets were introduced in 1905 into Lake Victoria (Graham, 1929). Commercial fisheries using trawls and purse seines have developed as the use of modern materials in the traditional gears. This change in the fishing methods, combined with a greatly increased human population around the lakes, has resulted in a rapid increase in the rate of exploitation. The knowledge required to manage these fisheries or the powers of enforcing regulations have not increased at the same rate. The difficulties are not easy to overcome since the fisheries are concerned with many species, hundreds in the case of haplochromines. Quick methods to estimate sustainable yields, such as the use of the relationships between catch and the morpho-edaphic index (MEI), the division of total dissolved solids by the mean depth of the lake (Henderson and Welcomme, 1974; Ryder, 1982), between catch and primary productivity, have helped, but lack the level of sophistication required. Development of methods based on length-frequency data shows more promise (Munro, 1983). However, even if management plans are produced, these may be difficult to implement owing to political, social or economic reasons. There is no doubt that heavy fishing affects the species composition of these multi-species communities, which in turn results in a change in yield. Changes, usually leading to an unpredicted state, have also been brought about by deliberate or accidental introductions of alien fish.

Data on catch species composition in lakes where alien fish introductions have been made, or in lakes where there has been extensive exploitation, are most available for Lakes Victoria, Kyoga, Kivu, Kariba, Cahora Bassa, Malawi and Tanganyika. The following synthesis is therefore concentrated mainly on these lakes.

Establishment of introduced species

MAIN SPECIES INTRODUCED

Although about 50 species of fish have been introduced to, or moved between the waters of Africa (FAO, 1985), many have not become established. Those that have become established and are important because of their effects upon the fish fauna of the African Great Lakes include the tilapias, *Oreochromis leucostictus, O. niloticus, Tilapia rendalli* and *T. zillii* and the Nile perch, *Lates niloticus,* in Lakes Kyoga and Victoria, and the clupeid *Limnothrissa miodon* in Lakes Kivu, Kariba and Cahora Bassa.

The decline in the fisheries of Lakes Victoria and Kyoga, due to overfishing, led to the introduction of exotic tilapias in the early 1950s and 1960s to augment the existing stocks (Welcomme, 1964, 1966; Ogari, 1990). The introduced tilapias eventually replaced the indigenous ones.

The Nile perch, which is indigenous to Lakes Albert, Chad and Turkana, was introduced first into Lake Kyoga, in the 1950s, as a pilot experiment to determine the advisability or otherwise of stocking Lake Victoria. It was intended that the Nile perch would prey on the small haplochromines which were not fished to their full potential, thus making this source of protein more readily available. It has been suggested that one reason for stocking with Nile perch was to improve the sport fishing (Barlow and Lisle, 1987; Achieng, 1990). Before the effects of introduction into Lake Kyoga could be measured the Nile perch had found its way into Lake Victoria, both by unofficial and by official means (Acere, 1985; Achieng, 1990). Nile perch took only about 10 years to become well established in Lake Kyoga and about 20 years in Lake Victoria. Harrison (1991) has found that the Nile perch from Lake Victoria differed taxonomically from other *Lates* taxa he collected, including the riverine *L. niloticus niloticus, L. niloticus rudolfianus, L. niloticus longispinus, L. albertianus* and *L. macrophthalmus.*

The introduction of *L. miodon* into Lake Kariba was intended to fill a vacant ecological niche for pelagic plankton-feeding fish created by the formation of the reservoir (Bell-Cross and Bell-Cross, 1971). The adult fish were airlifted from Lake Tanganyika during 1967–68. They quickly became established and started to breed, as illustrated by juvenile *L. miodon* found in the stomach of a tigerfish, *Hydrocynus vittatus,* in 1968. By the end of 1969 *L. miodon* could be found throughout the lake (Begg, 1976). This same clupeid had previously been introduced to Lake Kivu (1958 to 1960) for a similar reason to that in Lake Kariba, to establish a pelagic plankton-feeding fish population (Collart, 1960). *Stolothrissa tanganicae* was introduced together with *L. miodon* but did not become established. *L. miodon* was widespread in Lake Kivu by 1976 (Frank, 1977).

FACTORS AFFECTING ESTABLISHMENT

The reasons for success or otherwise of introduced fish are not clearly understood, even in countries where stocking, often indiscriminate, has taken place over many years (Welcomme, 1988). Major aspects which may influence establishment include physiological adaptation, competition, predation, reproduction and the availability of suitable food at each stage of the life cycle.

Physical factors

In many of the natural lakes the abiotic factors are fairly constant throughout the year, although well-marked seasonal cycles in the large lakes occur as a result of seasonal wind changes and reservoirs are greatly affected by river inflow and water draw-down. Since the introductions under examination were made within the African tropics, the introduced fish probably experienced temperature and daylength ranges similar in character to those in their natural habitat. The Nile perch occurs naturally in many waters in the Sondanian region and is apparently physiologically adapted to a wide range of conditions. The lower limiting temperature for this fish is about 10 °C and it requires a temperature above 24 °C to breed (Barlow and Lisle, 1987). It may be restricted by oxygen concentration (Fish, 1956) because mass kills have been observed in Lakes Albert and Victoria when the water has become anoxic (Hamblyn, 1966; Okedi, 1971; Ochumba, 1988; Ochumba and Kibaara, 1989). Although the endemic species of *Lates* in Lake Tanganyika are mainly pelagic and live in the oxygenated zones, *L. mariae*, a demersal form, has been caught at 120 m where there is no recordable oxygen (Coulter, 1966, 1967, 1968). The effects of water clarity are not apparent but may be important in highly active, visually feeding predators (Craig and Babaluk, 1989).

Competition

Competition with the indigenous fish may play a vital role in determining the success of an exotic. This is very difficult to determine in simple fish faunas and may be impossible in the diverse multi-species complexes of the African lakes. Evidence of niche overlap has been used to indicate the importance of competitive interactions, but it does not distinguish between competition and overlap in resource use (Holt, 1987). Some resources only may be shared, but this sharing may vary, for instance seasonally or between different stages in the life history. Habitat choice can be a response to features such as vegetation, temperature and the distribution of predators, food or competitors. Competition will not be important if the shared resource is in plentiful supply or if predators or other factors reduce the potential competing population. The clupeids may have become established in Lakes Kariba and Kivu because there were no other pelagic plankton-feeding populations to compete with them. This may be inferred here by the absence of a competitor but cannot be quantified. Competition for food is probably more important in pelagic communities than in littoral communities, where habitat may be of great importance. With time, interspecific competition may lead to niche differentiation and specialization, resulting in speciation. The specialized cichlids may not be able to compete against introduced more generalized cichlids. Fryer and Iles (1972) suggest that the tilapia, *Oreochromis niloticus*, introduced into Lakes Kyoga and Victoria, was a superior competitor to the endemic *O. variabilis* and *O. esculentus* as it had a wider food spectrum and could achieve a larger size for a given age, although little is known of the age of these fish. *Tilapia zillii* may have competed with *O. variabilis* for nursery areas (Fryer, 1961). The success of the introduced tilapias may have been due to competition, or in addition to or because of other factors, such as the low levels of the endemics brought about by overfishing before the exotics were introduced. The introduced species may have filled vacant niches where competition was lacking, such as *O. leucostictus* in pools and shallow areas behind papyrus beds, and *T. zillii* to feed on macrophytes. The Nile perch, another generalist feeder, may have become established because there was a plentiful supply of suitable food, mainly haplochromines, or the numbers of the other predators were reduced by overfishing and thus there was no competition for the resource. Another possibility is that the other predators were more specialized feeders and thus did not compete so well for a limiting resource. These factors can be inferred but not proven.

Predation

Exotic fish must be introduced in sufficient numbers or must be large enough to avoid predation to become established. The introduced fish may have to learn how to avoid newly encountered predators, or an introduced predator may have to learn to feed on new prey and compete with indigenous predators. It is apparent that these problems were overcome from the speed with which *L. miodon* and Nile perch became established in their new habitats. Mechanisms to avoid predation include schooling, body shape and colour, spines, oral incubation and the guarding of eggs and young.

Reproduction

Reproduction plays a major role in determining the establishment of an introduced species. The success of reproduction depends not only on the number of eggs produced, which is related to fecundity, size of female and number of batches laid, but more importantly on the survival of the eggs and young to an age when they themselves reproduce. The species exhibiting a generalist mode of reproduction that can be altered in response to changing environmental conditions will probably be the most successful in colonizing a new habitat. The tilapiine species introduced into Lakes Kyoga and Victoria, in particular *O. niloticus*, are more fecund and grow to a larger size than the endemic *Oreochromis* species (Fryer and Iles, 1972). Nile perch are highly fecund, laying between two million (at 77 cm SL) and 17 million (at 173 cm SL) eggs per female fish (Ogutu-Ohwayo, 1988a). Length at first maturity varies between lakes and is usually smaller in males. Females mature at 58 cm and males at 46 cm (SL) in Lake Victoria (Acere, 1985) compared with 82 and 59 cm respectively in Lake Turkana (Hopson, 1982). There are usually more males than females in a population albeit the larger fish are predominantly females. The Nile perch lays pelagic eggs in one batch, although the breeding season can be prolonged throughout most of the year if conditions remain favourable. Hatching occurs at an early ontogenetic stage (Hopson, 1969). In Lake Turkana pelagic post-larvae and inshore juveniles were caught throughout the year (Hopson, 1975). The Nile perch lives for up to 20 years (Ligtvoet and Mkumbo, 1990) so its lifetime production of eggs is phenomenal. This form of reproduction is probably ideal as a means for a population of introduced fish to become established, having no restrictions in spawning habitat or parental care and the potential to produce numerous eggs almost continuously.

The reproductive capacity of freshwater clupeids is more restrictive but apparently just as successful. Clupeids in the Volta system lay two to three batches of demersal eggs per year (Reynolds, 1974). In Lake Kivu *L. miodon* reproduces over an extended period, peaking during August to October with a least active period from March to May. Males mature at 61 mm and females at 62 mm (FL) (Spliethoff *et al.*, 1983). This is smaller (and probably younger) than those in Lake Tanganyika where they originated, 64 mm FL for males and 75 mm FL for females (Ellis, 1971), and where they spawn mainly in the rainy season (Coulter, 1991). In Lake Kariba hatching occurs from September to February, with little or no breeding in other months (Cochrane, 1984). The fish breed in shallow water and the young move into deeper water as they get older. The fish probably live for no longer than 1 year and they grow rapidly (Marshall, 1988). Data on fecundity and age of maturity do not appear to be available. Marshall (1987a) found that the growth and mortality rates of *L. miodon* in Lakes Kariba and Cahora Bassa were higher than in Lakes Kivu and Tanganyika. One suggestion he put forward for this was a life-history strategy related to the less stable environments of the man-made lakes, where the clupeids may have been selected for short life cycles and early reproduction. However, this goes against the present selection theory, in which a stable environment is thought to select for short life cycles and early reproduction (Sibly and Calow, 1986). It appears that *L. miodon* has adapted to the different conditions in the four lakes, ranging from the stable environment in Lake Kivu with no predation and stable hydrology to the extremely unstable one in Lake Cahora Bassa with high predation and extremely variable hydrology, by altering growth rate, maximum size, age (size) of reproduction and longevity.

Food and feeding

For a species to become established, upon introduction, suitable food must be available both spatially and temporally for all its life stages. Greater flexibility in the selection of prey items gives greater potential for success. Bourn (1974) recommended the three main commercial species of Lake Chilwa, *Barbus paludinosus*, *Clarias gariepinus* and *Oreochromis shiranus chilwae*, as potential candidates for introductions because of their plasticity in selecting food items, an ability developed through exposure to extreme habitat conditions in Lake Chilwa. *O. niloticus* is omnivorous and has a broad food spectrum, embracing phytoplankton, including bluegreen algae, detritus, and invertebrates such as *Caridina*, chironomids and gastropod molluscs (Balirwa, 1990). Juvenile Nile perch eat mainly invertebrates, but as sub-adults or adults they are usually piscivorous (Ogutu-Ohwayo, 1984; Ogari, 1985; Hughes, 1986). When Nile perch were introduced into Lakes Kyoga and Victoria the adults fed on the haplochromine cichlids (Gee, 1969; Okedi, 1971). As these became less available the Nile perch was able to adapt to other foods, including invertebrates, the cyprinid *Rastrineobola argentea* and its own young (Ogari and Dadzie, 1988; Ligtvoet and Mkumbo, 1990; Ogutu-Ohwayo, 1990a). Clupeids introduced into Lakes Kivu, Kariba and Cahora Bassa had little competition from other fish for the plankton. In the reservoirs (Kariba and Cahora Bassa) the indigenous fish were riverine and not suited to life in the pelagic zone. *Limnothrissa miodon* feeds on phytoplankton and zooplankton when young, but older fish feed on plankton, invertebrates and fish (including their own young) (Iongh *et al.*, 1983). *Stolothrissa tanganicae* has a similar diet when young but adults have a more restrictive diet and remain planktivores (Coulter, 1991). Dumont (1986) considers *S. tanganicae* to be in dynamic equilibrium with the endemic calanoid copepod *Tropodiaptomus simplex* in Lake Tanganyika, and for this reason not able to adapt to new habitats without this prey.

Effects of introductions on the fish community

The evidence for dramatic species changes in the African Great Lakes is overwhelming, but the causes are difficult to differentiate quantitatively. However, this has not stopped a number of authors from speculating and apportioning 'blame' between overfishing, the introduction of exotics and abiotic factors. Changes in the fish community have been studied from catch data, either from the fisheries or from experimental fishing, usually from the former. The quality of catch statistics may be very variable (FAO, 1983), and there are probably significant errors due to differences in methods of collection. It is very hard to establish an index of fishing effort, owing to the various gears used or to differences in construction within a single gear or just for lack of reliable records. For example gill nets may be hand-made of no standardized material or dimensions (Ligtvoet *et al.*, 1988). However, although the catch data may be suspect for estimating yield, they can be used to compare variation in species composition from year to year.

CLUPEID INTRODUCTIONS

The complexity of predator–prey systems can be illustrated in a 'simple' pelagic system, from the qualitative changes that have been recorded since the introduction of *L. miodon* into Lake Kariba, though an initial problem for understanding the ecosystem was the lack of information on the pre-impoundment ecology of the Zambezi River (Marshall, 1984). The population size of *L. miodon* in Lake Kariba is strongly influenced by abiotic factors, such as thermal stratification (Mtada, 1987) and nutrient input from rivers (Marshall, 1982), by predators and by fishing. The tigerfish (*Hydrocynus vittatus*) is a major predator in Lake Kariba. Since the introduction of *L. miodon*, the tigerfish population has increased in size and extended its habitat into pelagic areas (Machena, 1988). Other predators are present in the lake but there are few data about them. Marshall (1985) noted the increase in the tigerfish population in the eastern arm of Lake Kariba after the successful establishment of *L. miodon*. However, the number of tigerfish recruits started to decline, which Marshall (1985) considered was due to fishing pressures and changes to their breeding areas in inflowing rivers. The Sanyati River is the main breeding area for tigerfish from the eastern arm of Kariba, and 30% of this breeding area was drowned when the lake was formed. Marshall (1987b) later changed his mind on the main causes of the tigerfish decline and decided it was due to reduction in numbers of *L. miodon* brought about by overfishing.

INTRODUCTION OF NILE PERCH

The effect of predation by Nile perch on the species composition of Lakes Kyoga and Victoria has been estimated from a comparison between the stomach contents of the fish and the composition of catches (Ogari, 1985; Hughes, 1986; Kenya Fisheries Dept, 1988). Initially the adult Nile perch were piscivorous and their diet consisted mainly of haplochromine species (Gee, 1969; Okedi, 1971). The original fish community of Lake Victoria was dominated by several hundred species of haplochromines, catfishes (*C. gariepinus*, *Schilbe mystus* and *Bagrus docmac*) which preyed upon them, two endemic tilapiine cichlids and about 38 non-cichlids. Hughes (1986) found that by the mid 1980s the Nyanza Gulf (Kenya) region of Lake Victoria was dominated by Nile perch (80% of fish biomass), the other main species present being the zooplanktivore, *R. argentea*, and the introduced tilapia, *O. niloticus*. The diet of adult Nile perch at this time consisted mainly of *R. argentea*, juvenile Nile perch and *Caridina nilotica*, a prawn (Ogutu-Ohwayo, 1990a). Tilapiine species were rarely found in the stomachs of Nile perch (Okemwa, 1983). *O. niloticus* coexists naturally with Nile perch for instance in Lakes Albert and Turkana and may have developed methods of avoiding predation (Twongo, 1988). Ogari (1990) found that other predators in the Nyanza Gulf, such as *Protopterus aethiopicus* and *C. gariepinus*, which were once found in open water, were by the late 1980s confined to the swampy fringes of the lake with low oxygen concentration. This may be an area which the Nile perch cannot exploit due to its high oxygen demands. Other predators including *B. docmac*, and *Alestes* species and most haplochromines had disappeared or had diminished to very low levels.

A similar change in Lake Kyoga to that in Lake Victoria was found in the species composition of the lake and of the Nile perch diet (Ogutu-Ohwayo, 1988b; Twongo, 1988). Up to the early 1950s the lake contained, as well as haplochromines, in order of their importance to the fisheries: *O. variabilis*, *O. esculentus*, *P. aethiopicus*, *B. docmac*, *C. gariepinus*, *Barbus* species and *Schilbe mystus*. From 1958 Nile perch, *T. zillii*, *O. niloticus* and *O. leucostictus* started to appear in the catches after their introduction during 1954 to 1957. In 10 years the Nile perch population dominated the community, as it does now in Lake Victoria. However a stock survey of Lake Kyoga in 1985 indicated that the contribution of the Nile perch had declined. *O. niloticus* was then dominant (78.5%), compared with Nile perch (16.7%), *P. aethiopicus* (4.1%) and other species (0.7%) (Ogutu-Ohwayo, 1988b). These data indicate that the fish communities are not yet in a state of equilibrium, and the effects of cannibalism and the fishery in controlling numbers of Nile perch may be important.

Understanding the changes that have taken, and are taking, place in Lakes Kyoga and Victoria is complicated not only by the introduction of a predator but also by the introduction of tilapiine competitors, some of which may have formed hybrids with the native tilapiines (Welcomme, 1967, 1988). All the introduced species became distributed in suitable habitats around the lakes. Their growth to a large size, improved condition compared with fish in other lakes where they are endemic and their ability to breed throughout most of the year may be indicators of their competitive success. Further complications for understanding the dynamics of the fish community have been brought about by changes in other factors such as those leading to eutrophication in Lake Victoria (Ogutu-Ohwayo and Hecky, personal communication) and the rise in water levels in Lake Kyoga (Twongo, 1988).

Effects of fishing on the fish community

Changes in the fish community as a result of fishing can be caused by alterations in fishing gears, in mesh sizes and in fishing effort. As mentioned above, the effects of fishing can be compounded by other effects, such as the introduction of exotic predators and competitors and changes in abiotic factors, especially in complex multi-species communities such as in Lakes Kyoga and Victoria (Ogutu-Ohwayo, 1990b). Alteration in species composition itself brings about changes in fishing, putting different pressures on different species.

LAKE VICTORIA

Owing to the lack of regularly collected and recorded data from the African Great Lakes, only qualitative changes can be indicated. Most information comes from Lake Victoria; a study of the fishery there gives some indication of the effects of exploitation on fish species composition. A number of authors have recorded the effects of overfishing, from the decline of some species to the virtual disappearance of others (Graham, 1929; Beverton, 1959; Garrod, 1960, 1961a, 1961b; Cadwalladr, 1965; Jackson, 1971; Benda, 1979, 1981; Marten, 1979a). The effects of exploitation by the early subsistence fishermen were probably very slight. In 1905 gill nets made from cotton were introduced into Lake Victoria and a fishery for the endemic tilapias was established (Graham, 1929; Acere, 1988). Flax gill nets were first used in 1916. A decline in the catches of the endemic tilapiines was noted during the period 1905 to 1928 so mesh sizes were restricted to 127 mm or above and beach seines were banned in 1933. It was not possible to enforce these fishing regulations, and fishing effort increased during the 1940s with the use of undersized, illegal mesh sizes. Terylene and nylon nets were introduced in 1952 and outboard motors were employed from 1953. Overfishing and the sharp reduction in catch in the inshore areas resulted in the fishermen extending the geographical range of fishing effort. Since the use of a minimum 127 mm mesh gill net could not be enforced, the law was repealed in the states concerned during 1957 to 1961 although a strong case for its retention was made (Beverton, 1959; Garrod, 1961a). The endemic tilapia became severely reduced (Fryer and Iles, 1972), as did many non-cichlid species due to the use of small-meshed nets. In the 1960s the use of 38 to 46 mm mesh nets, an increase in the use of beach seines and the use of mosquito net seines (13 mm mesh) resulted in a further reduction of small fish, including haplochromines and the juveniles of haplochromines and other genera. During 1972 to 1973 a significant decline in *O. esculentus* was noted in Kenyan and Tanzanian waters of Lake Victoria. This was some time before the establishment there of Nile perch. At the same time an increase in the catches of large predators, *Bagrus* and *Clarias* was noted. Marten (1979b) recommended the use of large-mesh gill nets and an increase in hooks to capture these predators so that tilapiines would benefit from reduced predation. Fish that migrated into rivers to spawn had been heavily exploited for some time with traps. Since the 1950s the fishing pressure has been increased by the engagement of gill nets across the river mouths. A marked decline in the proportion of these migrating species in the lake community has been observed since the introduction of these gill nets (Cadwalladr, 1965). Experimental trawl fishing was introduced in the late 1960s (Kudhongania and Cordone, 1974b), and trawls were used on a commercial basis in the Mwanza area (Tanzania) from 1976. Trawling led to a reduction in the haplochromine stocks. The trawl fishery of the Mwanza Gulf was monitored by HEST (Haplochromis Ecology Survey Team) and TAFIRI (Tanzanian Fisheries Research Institute) (FAO, 1983), who noted a sharp decline in haplochromines (Barel *et al.*, 1991). Getabu (1988) and Goudswaard and Ligtvoet (1988) suggested that the Nile perch had the greatest impact on the haplochromines, although the effect of fishing was also significant. During 1973 to 1982 haplochromines in the Mwanza Gulf decreased as a result of fishing, as the Nile perch was then virtually absent from that area (Barel *et al.*, 1991; Witte *et al.*, 1992). Of further interest was the selective disappearance of large individuals and species of cichlid, a finding similar to that of Turner (1977a, b) for Lake Malawi. Haplochromines, greater than 150 mm and mainly piscivorous, disappeared (Goudswaard, 1988). Of 45 species caught in the Mwanza Gulf in 1977 to 1978, only 5 species were caught in 1984 to 1985. Those of about 100 mm in length and molluscivores were also disappearing. The adult size of several species was found to be reduced.

LAKE MALAWI

Studies of the impact of artisanal and commercial fishing in Lake Malawi have not yet been published. The artisanal fishery operates from dugout canoes and small plank boats within 2 km of shore (Alimoso *et al.*, 1990). Traditional gears are employed, including shore seines, gill nets, long lines and traps. The commercial fishery employs boats with diesel inboard motors and trawl nets or ring nets. In the south-west arm of Lake Malawi the number of cichlid species in the catches was reduced by about 20% as a result of trawling (Turner, 1977a). Large adult fish were caught owing to the selective nature of the cod end. Turner (1978) noted that fishing gear such as gill nets and long lines used in Lakes Victoria, Malawi and Tanganyika selected the larger fish and there was a shift towards the smaller species. In Lake Turkana a change in the species composition was also noted as a result of alterations in fishing gears and their selectivity (Bayley, 1977).

LAKE TANGANYIKA

Cichlids dominate the inshore areas of Lake Tanganyika (Ndaro, 1990), but there is no information concerning the effects of fishing on these communities. Coulter (1991) considers the benthic fishery to be insignificant on a lake-wide basis compared with the pelagic fishery for clupeids and *Lates* species. The scope for the development of the benthic fishery is limited and consideration should be given to conservation of its unique species diversity. Many cichlids are caught and exported for the aquarium trade, but Andrews (1990) believes that this practice poses little threat to their survival.

Most attention has been paid to the pelagic fish community of Lake Tanganyika. Industrial fishing for pelagic fish started in 1962 in Zambian waters and the artisanal fishery was expanded after 1957 (Pearce, 1990). Both fisheries use lights to attract clupeids to purse or beach seines respectively and *Lates* species are caught in these nets. The initial effect of intensive mechanized fishing was a steady reduction in all *Lates* species but an increase in clupeids (Coulter, 1991). In the second phase the small pelagic *L. stappersi* increased considerably but fluctuated inversely in abundance with *Stolothrissa tanganicae.* So the system became reduced to a single prey and predator system of *S. tanganicae* and *L. stappersi* interacting under intensive fishing pressure (Roest, 1988; Chitamwebwa, 1990; Pearce, 1990). A decline in the clupeid fishery has been observed in recent years, probably the result of fishing to very low levels of stock biomass and not the result of predation. Marked seasonality in the vertical mixing of the lake results in cycles of nutrient input, plankton production and fish production (Coulter, 1988). The cycles result in an increase in clupeid production about every 6 years. The years that favour clupeid production are also suitable for juvenile *L. stappersi.* It takes 2–3 years for these juvenile *Lates* to become adult, which accounts for a time lag in abundance cycles reflected in the catches of the two species (Coulter, 1991). The present fishery has more effect on *S. tanganicae* than on *L. stappersi.* An examination of the fishery has clearly shown the change from a stable fish community based on a predator and prey system to an unstable one based more on competitive effects (Coulter, 1991). However, the data presented so far do not give a clear indication of the effects of overfishing, predation and nutrient input.

LAKE KARIBA

In Lake Kariba, nutrients in inflowing rivers influence the production of the clupeids, as well as fishing and predation by tigerfish. The abundance of tigerfish will in turn be influenced by the availability of *L. miodon* and by fishing pressure. The tigerfish may prey on other important species and control their relative numbers (Takano and Subramaniam, 1988), but little is known about the dynamics of these other species (Machena, 1988). The inshore fishery may be constrained by low fish biomass, especially along the exposed rocky shorelines (Marshall and Langerman, 1988).

CONCLUSIONS

In Lake Malawi, stocks of fish can recover quickly from excessive fishing if the effort is reduced (Tweedle and Magasa, 1989). A successful species is able to ensure the continuity of its existence regardless of its population size. Success is related to the species' ability to overcome adversity and is indicated by population growth potential and surplus production (used in exploitation). The potential is associated with stock and recruitment, and some species with a low level of variance in recruitment may be less responsive and therefore more sensitive to perturbations (Garrod and Horwood, 1984). Therefore regardless of the life history strategies utilized by a species, it is the flexibility to alter life history traits that will determine its success. The indications are that many of the endemic species of the African Great Lakes do not have this flexibility and are thus very vulnerable to exploitation (Ligtvoet and Witte, 1991; Wanink, 1991). Without careful control of exploitation based on a quantitative knowledge of the biology of the species, reduction in the species composition to a few flexible species, exotic or indigenous, is inevitable.

Conservation of unique faunas

Extensive changes have already taken place in Lakes Kyoga and Victoria, and so the threats of overexploitation as a result of poor management and the presence of exotics are no longer threats to the composition of the fish fauna, but actual events. There appears to be no hope of restoring the fish species diversity in these lakes. The fish community in Lake Victoria is still in a very unstable condition, and although increased yields have been obtained after the Nile perch became established and this fish is now very acceptable as a food fish (Reynolds and Greboval, 1988; FAO, 1990), it is not possible to predict the future of the fish fauna or the fisheries.

In Lake Malawi some change to species composition has occurred as a result of fishing methods, but not on the scale of the changes in Lake Victoria. A greater threat to the fauna of Lake Malawi, and to any other lake where the practice may be contemplated, is the introduction of exotics. This is mainly because no predictions can be made as to the changes that might occur. The lack of understanding of dynamics of the system prevents forecasts of species changes or fishery yields. Some time ago Turner (1982) suggested that clupeids might be introduced from Lake Tanganyika into Lake Malawi. This was based on his observation of the presence of *Chaoborus* in Lake Malawi and absence from Lake Tanganyika. He inferred that the clupeid fishes of the latter were more efficient zooplanktivores than the fish in Lake Malawi, and that by introducing clupeids into Lake Malawi better use would be made of the plankton, resulting in increased fish yields. This suggestion provoked much response (Hecky, 1984; Barel *et al.*, 1985; Eccles, 1985).

The introductions of new fish species into Lakes Kyoga and Victoria provide an illustration of the potential impact of introducing new fish species into other Great Lakes and have been used as a warning to portray the threat to the endemic fish faunas. While this is appreciably true, some questions such as 'What are the benefits of their conservation?' need to be considered. The people living around the lakes are poor and depend on the fisheries as a source of income and food. Concern about the conservation of the biodiversity in these lakes should not overlook the nutritional requirements of these people. Fish introductions may remain an option in maintaining production in some of African Great Lakes if no immediate alternative for providing protein to the local people is available (Ogutu-Ohwayo, personal communication). However, Lake Tanganyika, which has the richest fauna of any lake on Earth (Coulter, 1991), merits special conservation status; its faunas, and that of Lake Malawi – already recognized as of 'World Heritage' status – are of worldwide concern and great importance for studies of evolutionary mechanisms.

In Lake Tanganyika the main fisheries are for pelagic fish in open water, whereas the main diversity is in the littoral. It is in the littoral where human-induced changes, including pollution (sedimentation following deforestation, agricultural chemical runoff, urban waste and so on), are most potent.

Mitigating measures for fish species conservation

As outlined above, the unique faunas of the Great Lakes of Africa have undergone changes as a result of exploitation and introductions (Coulter *et al.*, 1986; Barel *et al.*, 1991). The degree of these changes has depended on the extent of the perturbations, although this has not been easy to estimate. In theory it may be easier to overcome the problems of excessive and selective fishing than to deal with unwanted species by appropriate management policies. However, socio-economic factors normally override biological and conservation ones, so biological mismanagement continues. In addition, many management policies are often extremely difficult to enforce.

PROPOSED MEASURES

The following mitigating measures to conserve remaining cichlids in Lake Victoria were suggested by Ribbink (1987) and Bruton (1990). Ribbink submitted that the situation might be redeemed, but Bruton took the more realistic view that the situation was irreversible and the measures were those to prevent or reduce any further damage.

Captive propagation

This has also been proposed by Reid (1990) who has established an aquarium for cichlid fish at the Horniman Museum, London. Small-scale breeding experiments have also been established at the Universities of Leiden, The Netherlands, Bielefeld, Germany (which have now ceased) and the New England Aquarium, Boston, USA. Reid (1990) refers to plans by the American Association of Zoological Parks and Aquaria to develop a captive breeding programme, involving 30 species of Lake Victoria cichlids, to be carried out in the laboratory and in the field. But these measures can have very little impact due to the scale of the issue and also to the problems of re-introductions. States around the lake would have to develop extensive culture facilities for success, and these might be used instead as aquaculture systems rather than for conservation of rare species.

Reduction of Nile perch stocks

This would require selective fishing for large fish. However, increased fishing pressure on the larger members of a predatory stock can elevate the rate of predation. The removal of the largest members often results in an increase in the number of smaller, younger fish (the biomass remaining constant). These fish have a faster growth rate and greater consumption rate per unit mass than fish that have nearly reached their maximum size. The complete removal of an introduced species is probably not possible. It might also not be acceptable on economic grounds.

Closure of haplochromine fishing

Large-scale industrial haplochromine fishing is no longer of economic importance.

Creation of conservation areas

The Kenyan Government has designated an aquatic nature reserve at the Dairy and Mfangano Islands (Reid, 1990). Underwater reserves have been established in Lake Malawi (at Cape Machem, now a World Heritage site) and in Lake Tanganyika (Sumbu National Wildlife Park), but further areas are required (and planned for Lake Tanganyika). The development of underwater conservation areas should be linked with tourism so that income is generated for the local people. Experience has already been gained from the establishment of terrestrial national parks. They would be difficult to establish in Lake Victoria because of turbidity and schistosomiasis.

CONCLUSIONS

Planning should be associated with rational exploitation and maximum production of fish. Fishing should be directed towards those species that can withstand exploitation such as the Nile perch, *O. niloticus* and the pelagic cyprinids. Fishing pressure should be reduced or stopped on those species that are particularly vulnerable, such as those fished at river mouths on spawning migrations (e.g. *Labeo victorianus*). More development should go into the artisanal fisheries. Commercial fisheries, such as ring netting, should be carefully regulated. Four further proposals may help to conserve the African Great Lakes fish stocks:

1. the development of other sources of protein which can be utilized by the majority of people;
2. the education of fishermen and fisheries extension workers on the importance of the fisheries and the dangers of overexploitation;
3. research into the basic biology of many of the species;
4. the continuation and further development of negotiations between riparian states.

Through these negotiations strict guidelines can be developed for the best exploitation of the lakes and for regulations to prohibit unauthorized release of exotics. Since many of the lakes are bordered by more than one state, this last proposal is particularly important so that agreement can be reached before any major changes occur to their faunas.

Need for appropriate information

Apart from a few notable exceptions, such as for the pelagic systems of Lakes Kariba and Tanganyika, many of the factors determining changes in the fish species composition of the African Great Lakes are not yet understood and inferences have been at best qualitative and commonly subjective. There appear to be few quantitative data available which can be used to separate different factors such as overfishing, predation and competition from exotic fish, and for incorporation into predictive models. Ideally it should be possible to develop models of predator and prey relationships so that the effects of predatory pressure on or by introduced fish can be predicted. These models require an understanding of the population dynamics of both the predators and prey, as well as data on prey preferences and consumption rates and how these alter as the fish grow. There are indications that the introduced Nile perch population may decline in Lake Victoria as it did in Lake Kyoga. Is this due to shortage of food, cannibalism or changes in abiotic factors such as those leading to anoxia?

The information on competition between different species is particularly poor. Speculation on potential competition can only be based on the assumption of a shared resource that may be limiting. Due to the complex nature of the fish fauna of the African lakes it may not be possible to quantify competitive effects.

The effects of fishing may be easier to determine than those arising from the introduction of exotics. Elucidation would require close scrutiny of catch and effort data, which are not available in the published literature but may be forthcoming from relevant government and research institutions. It appears that some of these data may be suspect owing to the nature of their collection. There is a need for continuity in the collection of accurate and uniform data on catch statistics (FAO, 1988). This would involve an extensive education programme for those collecting the data in the field and for the local people who do the fishing. A centralized repository for information with an appropriate data base should be established. This base could be shared between riparian states of a particular water body. Data are required on stock definition, stock size and vital parameters such as length/age of maturity, mortality rates, fecundity and growth. Information on genetic stock identification and hybridization is scarce.

There is a lack of basic biological data on both exploited and unexploited species. These include food and food chains, consumption rates, reproduction and the survival of young stages, competition and predator–prey relationships, behaviour and physiological adaptations to abiotic factors. Further investigations of young stages should include growth associated with food supply and vulnerability to predators.

It is essential that a greater understanding is achieved for successful management and conservation of the lakes. A closer study of the investigations already under way should help to improve understanding of the trophic dynamics of African lakes and indicate the direction of future research.

Summary

Large natural African lakes contain unique and diverse fish faunas which have evolved within each lake in a comparatively short period of time. Members of the family Cichlidae are particularly diverse, although there is strong evidence to show that the haplochromines in Lake Victoria, and possibly Lake Malawi, are monophyletic. The unique faunas in Lakes Victoria and Kyoga have been subject to perturbations from the introduction of exotic fish, and the faunas in these and other lakes have been disturbed by fishing activities and other human endeavours.

Factors governing the establishment of exotic species are not clearly understood. The exotic fish must be physiologically adapted to their new environment, able to compete successfully both for habitat and for food at each stage of their life history, able to avoid predation and must have a suitable reproductive potential. Although about 50 species of fish have been introduced into African inland waters, including reservoirs, only comparatively few, in particular Nile perch (*Lates niloticus*), various cichlids (especially tilapias) and clupeids (*Limnothrissa miodon*), have been successful in establishing themselves. Those that have become established have had obvious but unquantifiable impacts on the indigenous faunas.

It is difficult to differentiate between the effects of fishing and of the presence of alien fish on the fish species composition of the lakes (Witte *et al.*, 1992). Many of the lakes were overfished before introductions were made, with a resultant decline in some species, especially the larger ones, and the virtual disappearance of others. Some lake fish faunas,

such as those of Lakes Kyoga and Victoria, which have been subjected to the perturbations described above, continue to change rapidly (Ogutu-Owayo, 1990b).

There is a fundamental need to collect biological information on the fish communities of African lakes for effective management, resulting not only in the conservation of unique fish faunas but also the production of sustainable fish yields for the people relying on this source of protein. This information is required before any more introductions of exotic fish are made.

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