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SHORT ARTICLES AND REVIEWS

THE CHANGING ECOSYSTEM OF LAKE VICTORIA, EAST AFRICA

ROSEMARY LOWE-McCONNELL

(Dr R. H. Lowe-McConnell, Streatwick, Streat Near Hassocks, Sussex BN6 8RT, England.)

(This article is based on a talk given at the FBA's Scientific Meeting on "Freshwater biodiversity and water quality", September 1992.)

Introduction

Dramatic changes are occurring in the Lake Victoria ecosystem. Two-thirds of the endemic haplochromine cichlid species, of international interest for studies of evolution, have disappeared, an event associated with the sudden population explosion of piscivorous Nile perch *(Lates:* order Perciformes, family Centropomidae) introduced to the lake some thirty years ago. The total fish yield has, however, increased 5-fold from 1970 to 1990, but this yield is now dominated by just three fish species: the introduced Nile perch *(lates niloticus,* see below*), Nile tilapia *(Oreochromis niloticus),* and a small endemic pelagic cyprinid *(Rastrineobola argentea);* these three have replaced a multispecies fishery. Contemporaneously the lake is becoming increasingly eutrophic with associated deoxygenation of the bottom waters, thereby reducing fish habitats. Conditions appear to be unstable. There is now an urgent need for intensive limnological studies to understand the relationships between these events, and to learn from this unintended large-scale field experiment how to manage the lake to avoid further loss of biodiversity and destruction of fisheries.

[*The Nile perch in Lake Victoria are usually referred to as *Lates niloticus* but the exact taxonomic status of these fish and some related species has been called into question (Harrison 1991). In this account I shall simply use the generic name *Lates.* The fish is very large and fecund, reaching sexual maturity after about 2 years and producing several million eggs at each spawning. It may live for 20 years; in Lake Victoria body weights of 35-50 kilograms are common and a fish of 1 79 kg has been recorded (Achieng 1990).]

Limnological and fisheries research on Lake Victoria have had close connections with the Freshwater Biological Association, so it seems opportune to report here on the present state of the lake. The first research station on Lake Victoria, the East African Fisheries Research Organization laboratory based at Jinja, Uganda, where the Nile flows out of the lake (Fig. 1), was planned by Dr E. B. Worthington while Director of the FBA. As a member of the 1927-28 Survey of Victoria Nyanza and its fisheries (Graham 1929), Dr Worthington knew Lake Victoria very well. A founder member of the FBAs staff, R.S.A. Beauchamp, became EAFROs first Director (from 1947 to 1961). The composition of staff at EAFRO was based on the FBA plan, with a chemist, algologist, invertebrate zoologist and fish biologists. The close connection with the FBA continued for many years; various members of the FBA staff joined or visited EAFRO (including myself and Jack Tailing), and Geoffery Fryer from EAFRO joined the FBA staff (Fryer & Tailing 1986).

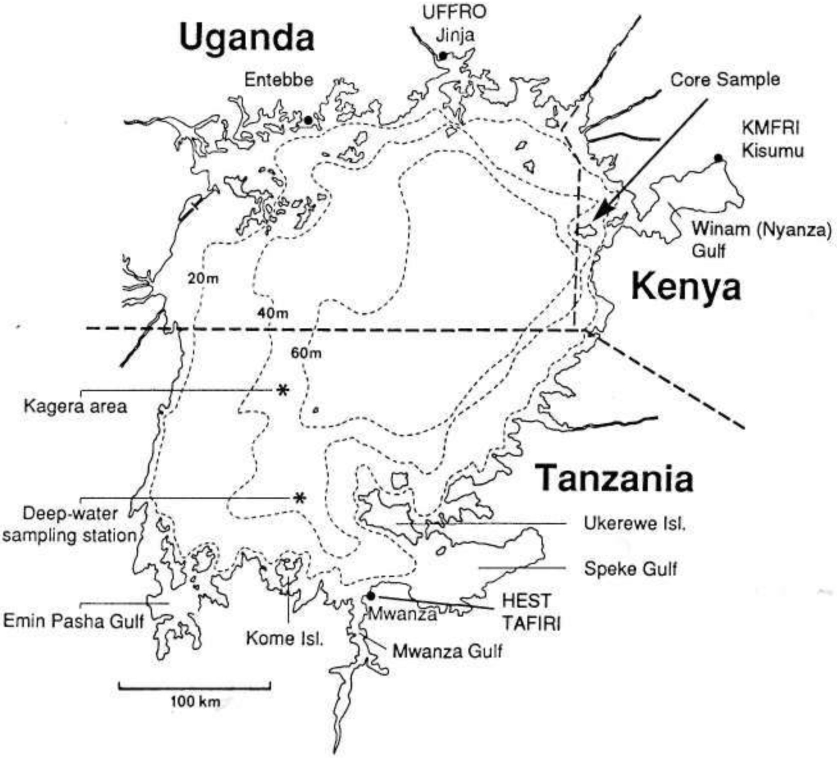

FIG. 1. Main study sites in Lake Victoria: UFFRO (formerly EAFRO), Jinja Uganda; KMFRI Kisumu Kenya; TAFIRI and HEST Mwanza Tanzania, with additional sampling by HEST in the Speke Gulf, Emin Pasha Gulf, the Kagera area and a deepwater station north of Kome Island. LVRCP core sample from 55 metres water-depth outside Winam (Nyanza) Gulf.

To assess the present drastic changes to the limnology and fish fauna of the lake, comparisons with past data are needed, and much of the basic work was done by scientists working from this EAFRO laboratory. Research has been continued by limnologists of the national fisheries research institutions: UFFRO (Uganda Freshwater Fisheries Research Organization, as EAFRO became), KMFRI (Kenya Marine & Fisheries Research Institute) based at Kisumu, and TAFIRI (Tanzanian Fisheries Research Institute) at Mwanza. Their work has been supported by development agency projects and limnological institutes and universities in Europe and North America, notably by HEST, the Haplochromis Ecology Survey Team from the University of Leiden (Netherlands) which worked from Mwanza in 1977 to 1991, and by Canada's Freshwater Institute and the University of Michigan based at UFFRO. Israel's Kinneret Laboratory and the New England Aquarium, Boston, USA, have also provided support as part of an international Lake Victoria Research and Conservation Project (LVRCP) based at KMFRI in Kisumu, Kenya. There is now a vast bibliography dealing with many aspects of research on this lake (Crul et al. 1993); here it is possible to cite only a few papers, choosing those with reference lists for further reading (Greenwood 1981; Meyer et al. 1990; Ogutu-Ohwayo 1990; Lowe-McConnell 1993).

The lake setting

The equatorial Lake Victoria is the world's third largest lake and largest tropical one (68,800 square kilometres in area - approximately the size of the Irish Republic). Saucer-shaped, with a maximum depth only 79 metres and a mean depth of 40 metres, it is noted for its spectacular flocks of endemic cichlid fishes (ca. 300 taxa). The lake also supports fisheries vital to the welfare of millions of people in the three riparian countries: Tanzania, Uganda and Kenya. The present Lake Victoria represents a drowned topography, probably formed by the coalition of small lakes on westward-flowing rivers which crossed the basin some 750,000 years ago, though much of it may have dried out about 14,000 years Before Present (Stager et al. 1986). The lake now drains via the small Lake Kyoga to Lake Mobutu (Albert) in the Nile system, but the Murchison Falls below Kyoga have prevented most nilotic fish species (including *Lates* and the tiger fish *Hydrocynus)* from gaining access to the lakes upstream of these falls (Worthington 1937, 1954). A much older lake (the Miocene L. Karunga), was situated in the northeast of the present Victoria basin but this dried up and an earlier fauna became extinct (including *Lates karungae* known from fossils). The present Lake Victoria has several large gulfs fringed with papyrus and swamp.

Deposits of soft flocculent algal-detritus, a metre or so deep, cover much of the lake bottom; firmer, sandy bottoms occur off the more exposed western shores, and there are a few rocky islands. Most inflowing rivers are slow-flowing, many seasonal, reflecting the equinoxial rains at the north end of the lake, but there is a more clearly defined single wet season at the southern end. Most of the annual intake of water comes from rain falling onto the lake surface, where temperatures remain at ca. 23-26°C throughout the year. Hydrological cycles are wind-driven; southeast tradewinds blow up the lake between June and August.

In 1969-71 trawl surveys were carried out in the open lake under the auspices of UNDP/FAO (United Nations Development Program/Food & Agriculture Organization) based at EAFFRO Jinja (Kudhongania & Cordone 1974a,b). Commercial exploitation and mechanized fishing increased greatly in the 1980s, including trawl fisheries for haplochromines in Tanzanian and Kenyan waters (Barel et al. 1991). From 1977, HEST carried out trawl surveys from Mwanza, where HEST monitored the appearance in 1982 and subsequent population explosion of Nile perch and its dramatic effect on the endemic haplochromines. In 1989 the LVRCP studied the effects of eutrophication and deoxygenation in Kenyan waters; they worked in close association with R. Hecky of the Canadian Freshwater Institute and UFFRO staff.

Changes to the fish fauna

Two special events have had profound long-term effects on the lake: (1), introductions of several exotic fish species, i.e. tilapias and *Lates,* between 1953 and 1962 and (2), exceptionally high lake levels due to high rainfall, from 1961 to 1964; this helped the introduced tilapias to get established (Welcomme 1966) and also accelerated eutrophication and other limnological changes (Hecky 1992, 1993). The rapidly increasing human populations led to rising demands for fish. Overfishing occurred because the scientists' advice to prevent this was ignored. To counter the declining tilapia catches the exotic *Tilapia zillii* was introduced (from Lake Albert, via Uganda dams) as a "complementary" species. With *T. zillii* came other exotic tilapias, *Oreochromis leucostictus* and *O. niloticus,* which had also been stocked in these dams. These exotic tilapias have now replaced Victoria's two endemic tilapia species, and *O. niloticus,* which coexists with *Lates* in other lakes where both are indigenous, is now the dominant tilapia in Lake Victoria's catches.

More controversial was the introduction of *Lates,* despite scientific advice against such an action (Fryer 1960). The fish came from Lake Mobutu (Albert), with a few stocked later from Lake Turkana (Rudolf). A few *Lates* were discovered in Lake Victoria near Jinja in 1960 (possibly these had escaped from stocked dams though it now seems that some were introduced clandestinely about 1954), so deliberate introductions were made near Entebbe in 1962. For about 20 years, *Lates* populations increased gradually and then suddenly irrupted in the Winam (Nyanza) Gulf, Kenya, in the mid 1970s. *Lates* arrived in numbers at the south end of the lake in 1982 and abundant 10-cm juveniles appeared here in 1985, indicating that *Lates* were spawning in the Mwanza area.

HEST monitored the changes in haplochromines as the *Lates* populations increased. Of the 123+ species caught at their sampling stations, ca. 80 had disappeared from the catches after 1986. Extrapolation of the Mwanza Gulf data to the entire lake would imply that approximately 200 of the 300+ endemic haplochromine taxa (recognized but not all formally described) have disappeared or are threatened with extinction (Witte et al. 1992a,b). The large haplochromine species vanished first (many may have been selected out by trawling), then rare species and those with most overlap in habitat with *Lates.* Least affected were haplochromines living in rocky areas or in very shallow water with plant cover. Haplochromines had been estimated, from early trawl surveys, to make up ca. 80% of the demersal fish biomass (of more than 200 kg per hectare) in sublittoral areas (Kudhongania & Cordone 19.74a,b). The disappearance of this huge biomass was thought by the HEST team to be a major cause of cascading changes in the ecosystem (Goldschmidt et al. 1993). These haplochromines were mostly detritivorous and phytoplanktivorous fish (an estimated 40% of the biomass in the sublittoral, 6-20 m deep), particularly important as primary and secondary consumers, whereas the currently dominant *Lates* (now more than 90% of the demersal fish biomass and estimated at less than 100 kg per hectare in the sublittoral)

Numbered groups in Fig. 2 *(opposite page)* comprise the following species. (1) Piscivores: *Bagrus docmak, Clarias gariepinus, Schilbe mystus,* and haplochromines (black). (2) Insectivores: *Alestes* spp., *Barbus* spp., Mormyridae, *Synodontis afrofischeri,* and haplochromines (black). (3) Zooplanktivores: *Rastrineobola argentea,* and haplochromines (black). (4) Molluscivores: *Barbus altianalis, Synodontis victoriae,* haplochromines (black), and *Protopterus aethiopicus.* (5) Algivores: *Oreochromis variabilis* and *O. esculentus.* (8) Detritivorous and phytoplanktivorous haplochromines (black). (11) Introduced piscivorous Nile perch *{Lates)* adults, and (12) juveniles. (13) The endemic cyprinid *Rastrineobola argentea.* (14) Introduced Nile tilapia *Oreochromis niloticus.*

[Other non-fish groups depict (6) chironomids and *Chaoborus* spp, (7) zooplankton, (9) molluscs, (10) phytoplankton and detritus, (15) chironomids, (16) prawns *(Caradina nilotica).]*

Fig. 2 is reproduced with permission from Witte et al. 1992a *(Proceedings of the 7th International Ichthyological Congress, 1991 (The Threatened World of Fish),* published in *Netherlands Journal of Zoology, 42, 214-232).*

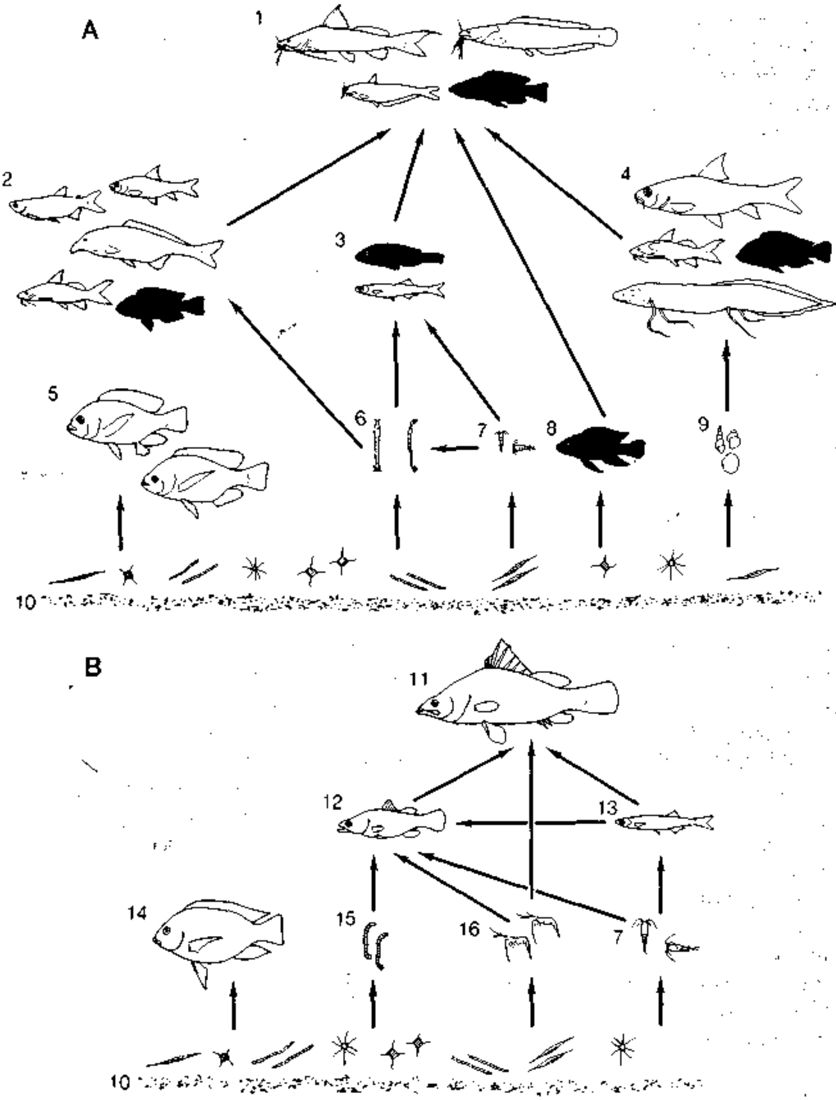

FIG. 2. The fish fauna and simplified food webs in the Mwanza Gulf sub-littoral zone (6–20 m deep) during the 1970s before the arrival of *Lates* (A), and in 1989 after the *Lates* irruption (B). Only those organisms known to form a major component of the diets of the main fish species are depicted. In the 1970s haplochromines (coloured black in A) dominated both the biomass and number of species in all groups except the piscivores.

and the pelagic cyprinid *Rastrineobola argentea,* are mainly tertiary and secondary consumers (Witte et al. 1992a; Goldschmidt et al. 1993).

At the south end of the lake, changes in the haplochromine fauna coincided with the arrival of *Lates* in the area, leading HEST to conclude that they were responsible for the main faunal changes (Witte et al. 1992a,b). Changes in the species and their food webs in the Mwanza area sublittoral (6-20 m deep) were summarised by HEST, comparing conditions in the 1970s, before the *Lates* irruption, and 1989 after it (Fig. 2). In the 1970s haplochromines dominated both in biomass and numbers of species in all trophic groups except the piscivores. By 1989, *Lates* had replaced piscivorous catfishes and haplochromines. Detritivorous/phytoplanktivorous haplochromines appear to have been replaced by the atyid prawn *Caridina nilotica,* and after the decline of the zooplanktivorous haplochromines, numbers of the cyprinid *R. argentea* increased greatly. *Oreochromis niloticus,* a more generalised feeder than the indigenous tilapias, replaced these. After the haplochromine decline, *Lates* fed mainly on *Caridina,* Odonata (dragonfly) nymphs, *Rastrineobola* and juveniles of its own species.

Limnological changes to the lake

Concern for the deteriorating state of the lake, its loss of biodiversity and signs of collapse of the indigenous fisheries, led to a workshop on "Biodiversity, Fisheries and the Future of Lake Victoria", held at UFFRO Jinja, in August 1992. This was organized by the New England Aquarium, Boston, USA in collaboration with KMFRI, and was funded by the US National Science Foundation. About 40 participants focused on limnology, fish biology and conservation, and socioeconomics, policy and management, aiming to set up testable hypotheses, recommendations and research agendas (Kaufman 1992; New England Aquarium 1993). The many contributions to this meeting indicated that environmental changes in the lake basin were basically due to the increase in human populations, with intensification of land use and increased run-off of nutrients into the lake. There is also some urban and industrial pollution, mainly in the gulfs near the growing townships of all three riparian countries. Clearing riparian vegetation has removed plants which acted as natural filters, removing nutrients from waters draining to the lake (reforestation of lake shores would help). Climatic cycles leading to high lake levels (most marked in 1961-64) drowning riparian bush and swamps, contributed to accelerated eutrophication, Between the 1960s and 1990s, a 3-fold increase has been detected in the nutrient concentrations in rain falling over the lake; this may be the result of increased burning of bush and grasslands in countries round the lakes.

In 1990, the LVRCP group based in Kisumu brought in sophisticated equipment including a hydroprobe for physical and chemical measurements, a remote-operated *vehicle* (ROV) *for underwater* video observations, and a bottom-deposit corer. The latter allowed sedimentation rates and plankton changes over the past 90 years to be deduced from cores taken from Kenyan waters (55 m deep) in the main lake. This team worked in close cooperation with algologists at UFFRO (Hecky 1992, 1993). These studies showed that eutrophication had started in the 1920s (a time of land clearance for estates) and accelerated greatly in the early 1960s when marginal vegetation and swamps were flooded, washing much decaying plant material into the lake. Overfishing and poor fisheries management have also contributed to environmental changes; lack of unified statistics in the three countries, particularly the absence of records of "fishing effort" for the recorded weights of fish landed, makes it impossible to assess whether the increased fish landings are due to increased fishing effort or to increased biological productivity.

Data on eutrophication come mainly from Hecky (1992, 1993), UFFRO plankton samples (Mugidde 1993), and from a bottom-deposit core in Kenyan waters. These all indicate changes in lake structure and function between the 1950-1960s and the 1990s. Secchi-disc values are now one quarter of Worthington's (1930) values. The core data show that phytoplankton changes started in the 1920s and accelerated in the 1960s: the diatom *Melosira* and chlorophytes decreased in both inshore and offshore samples and there was a great increase in nitrogen-fixing cyanobacteria. The algal biomass has increased 3- to 5-fold and algal productivity has doubled. Algal blooms are now more often associated with fish kills (Ochumba 1990). Deposition of silica and phosphorus has increased. The modern chemical and algal conditions appear to have been established by the 1970s, before the *Lates* irruption (Hecky 1992).

Data on recent oxygen changes come mainly from Kenyan waters (LVRCP studies). Compared with observations made by Tailing (1966) the hypolimnion oxygen has greatly decreased and is now less than 1 milligram of oxygen per litre in water over ca. 50% of the bottom during the season of stratification; wind-mixing in June-August no longer takes oxygen to the bottom. The depth of the oxycline now varies between 5 and 50 metres in Kenya's Nyanza Gulf, and appears to remain at 20-30 metres depth in the open lake "throughout the year". In November-June, sporadic upsurges of the oxycline (to 5 m) have led to fish kills (Ochumba 1990) and to fish movements inshore where they may be more vulnerable to fishermen's nets - a possible reason for the greatly increased catches here in the past few years. A video operated on ROV dives (5 in Winam Gulf, 5 in Kenya open lake) revealed large numbers of dead individuals of the small pelagic cyprinid *Rastrineobola,* in water with less than 3 milligrams of oxygen per litre, but it recorded carpets of live *Caridinia* prawns below the oxycline.

Effects on fisheries

By 1990 the Lake Victoria commercial fishery was based on three species: exotic *Lates* (ca. 60%), Nile tilapia *O. niloticus* (14%), and increasing amounts of the small endemic cyprinid, *R. argentea* (18%). Subsistence fishing still takes some other species. The change from the haplochromine-dominated fishery in the 1960s to the /.afes-dominated one twenty years later is shown clearly for Nyanza Gulf catches (Fig. 3). Over the lake as a whole, catches increased 5-fold between 1970 and 1990, from 106,500 tonnes to 561,700 tonnes (Greboval & Fryd 1993), but it is not known how much this was due to increased fishing effort or to other factors. These could include an increase in biological productivity of the lake, or the cropping of r-selected species *(Rastrineobola* and *Lates)* which have a higher turnover production rate than the small-brood /(-strategy haplochromines (Witte et al. 1992b). HEST's evidence suggests that *Lates* were mainly responsible for the fish faunal changes at the south end of the lake. But in Ugandan waters lack of effective management, overexploitation with destructive fishing gear, and interspecific competition among the tilapias, were considered to be more important in the decline of Ugandan fisheries than predation by *Lates* (Kudhongania et al. 1992).

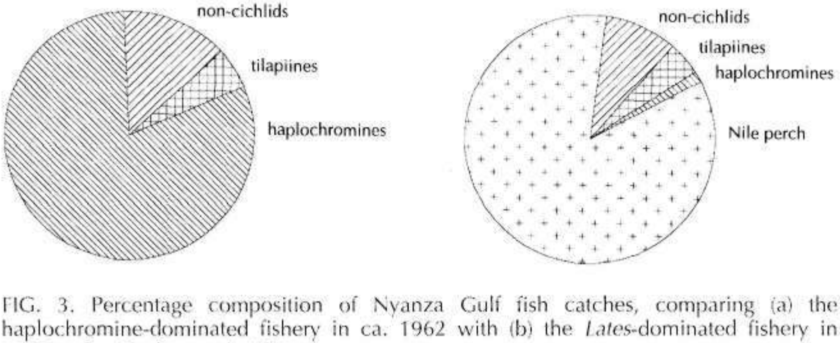

FIG. 3. Percentage composition of Nyanza Gulf fish catches, comparing (a) the haplochromine-dominated fishery in ca. 1962 with (b) the *Lates*-dominated fishery in 1982. (After Coulter et al. 1986).

Hypotheses

What are the interrelationships between the fish faunal changes and the eutrophication which has apparently led to permanent deoxygenation of the bottom waters? And why the sudden irruption of *Lates* twenty years after the introduction of this species to the lake?

The HEST team suggested that the removal of the large piscivorous haplochromines (by trawling and predation by *Lates)* might have allowed greater survival of juvenile *Lates.* They later considered that cascading effects, resulting from the removal of the vast biomass of detritivorous/phytoplanktivorous haplochromines which formerly turned over the soft bottom deposits, contributed to eutrophication and deoxygenation of the bottom waters (Goidschmidt et al. 1993). The LVRCP Kisumu team stressed that the removal, by *Lates,* of so many phytoplanktivorous fishes (including the endemic tilapias) has contributed to algal blooms; algal mats then sink and their decomposition leads to deoxygenation of the bottom waters. Algological and bottom-core studies have, however, shown that eutrophication started - and accelerated - before the *Lates* irruption, probably influenced mainly by land-use changes around the lake. Hecky (pers. comm. 1992) suggested that the consequent deoxygenation of bottom waters might have led benthic haplochromines to move inshore, thus providing more food for *Lates.*

Future prospects?

Lates cannot now be eradicated from the lake, but there is a distinct possibility - indeed a likelihood if management is not improved - that *Lates* populations will crash. This would have very serious socioeconomic consequences for the riparian countries. *Lates* were at first disliked but are now regarded by local people as the "saviour" since the enhanced catches lead to more jobs. However, so much of the catch is now processed for export that riparian people with little money have less protein than formerly. Also, the processing facilities under construction could take more than the estimated total population of *Lates,* which could easily be overfished, and there are already some signs of this; furthermore they are now cannibalising their own young.

The few haplochromines which have survived need protection, by preventing fishing in inshore waters and between rocks, where some small species still survive, although there is a temptation to catch them for bait for line fishing (Kaufman & Ochumba 1993). The original haplochromine complex of numerous species with highly specific habitat ranges (as discovered by the HEST team) was involved in very tight cycling of nutrients. There was an amazing number of piscivorous species (over 30 described species and numerous other taxa recognised but not formally described, Witte & van Oijen 1990), feeding mostly on other haplochromines, especially on their young stages. This complex has now been lost. However, it seems highly improbable that the high yield of the present fisheries could have been obtained by a carefully controlled fishery of haplochromines, because their specific habitats and low fecundity make them very sensitive to fishing pressure (Barel et al. 1991).

Lake management urgently needs a unified Lake Victoria Fisheries Commission, to unify statistics and legislation in the three riparian countries. If the *Lates* population crashes, there may be pressure for further fish introductions. We would need to know a great deal more about the limnology of the lake before attempting any such remedy. Using bays of the lake for culture of tilapias and other species already in the lake would be more advisable.

Acknowledgements

I wish to thank Trevor Furnass (IFE) for kindly preparing the text-figures, and the authors and publishers for permission to reproduce Figure 2.

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