

RECENT RESEARCH IN THE AFRICAN GREAT LAKES:
FISHERIES, BIODIVERSITY AND CICHLID EVOLUTION

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Abstract

The East African Great Lakes are now well known for (1) their *fisheries*, of vital importance for their rapidly rising riparian human populations, and (2) as *biodiversity hotspots* with spectacular endemic faunas, of which the flocks of cichlid fishes unique to each of the three largest lakes, Tanganyika, Malawi and Victoria, offer unique opportunities to investigate how new species evolve and coexist. Since the early 1990s research involving over a hundred scientists, financed by many international bodies, has produced numerous reports and publications in widely scattered journals. This article summarizes their main discoveries and examines the status of, and prospects for, the fisheries, as well as current ideas on how their rich endemic fish faunas have evolved. It first considers fisheries projects in each of the three lakes: the deep rift valley lakes Tanganyika and Malawi and the huge Victoria, all of which share their waters between several East African countries. Secondly it considers the biodiversity surveys of each lake, based on underwater (SCUBA) observations of fish ecology and behaviour which have revealed threats to their fish faunas, and considers what conservation measures are needed. Thirdly, using the lakes as laboratories, what have the international investigations (including DNA techniques and follow-up aquarium experiments) now revealed about the origins and relationships of their cichlid species flocks and mechanisms of evolution?

Introduction

The African Great Lakes, especially Tanganyika, Nyasa/Malawi and Victoria, are now well known from a voluminous literature as hotspots of biodiversity, the flocks of endemic cichlid species, with their spectacular adaptive radiations to use all kinds of foods, providing unique material for evolutionary studies. The lakes also support fisheries vital for the rapidly growing riparian human populations. As a young fisheries research officer I spent happy years (1945-54) studying these beautiful lakes for the East African Fisheries Research Organisation. Fifty years later I am naturally curious to know: (a) how their fisheries have developed, (b) whether their

faunas are still as diverse, and (c) what advances have been made in understanding the origin and evolution of their most remarkable endemic cichlid fish faunas. Others might also find it useful to have this overview as many recent findings are published only in journals and reports **with** restricted distributions.

This review concentrates on the state of the fisheries, conservation of biodiversity, and cichlid evolution in the three lakes on which I worked for many years. These are the very **old** deep rift-valley lakes Tanganyika and Malawi and the huge saucer (69 000 km², < 90 m deep) of Lake Victoria, its equatorial waters shared by Tanzania, Uganda and Kenya (Fig. 1). These lakes have been the main focus of recent research as they have the most important fisheries, on which the rising human populations (now estimated at some 287 million around these lakes) rely for their protein. They also have the most diverse faunas (now threatened by anthropogenic impacts), and in them the most spectacular flocks of endemic cichlid species have evolved, which provide unique material for scientific studies of worldwide interest on the evolution of new species and their co-existence (Fig. 2). For reasons of space, little can be included about studies on the smaller African lakes, though these too support fisheries and are helping to reveal cichlid relationships throughout the region. For example, in many satellite lakes swamps have provided refuges for certain species (e.g. papers by Chapman et al. 1996, 2003), and in the Lake Rukwa drainage (Seegers 1996) and in Cameroon crater lakes cichlid species appear to have evolved sympatrically (some useful references are given in Lowe-McConnell 1991, 1995, 2000; Leveque 1997, 2001; Turner et al. 2001, Crisman et al. 2003).

In 1987 I was 'volunteered' to be Convenor of the African Great Lakes Group of the International Limnological Society (SIL), formed at SIL's New Zealand Congress in response to George Coulter's concern that drilling for oil had started on the shores of Lake Tanganyika; such drilling could endanger priceless fauna, fisheries and water supplies for the four riparian countries, Burundi, Tanzania, Zambia and Zaire (now Democratic Republic Congo). The Group's first task was to organize an 'International Symposium on Resource Use and Conservation of the African Great Lakes', on Lake Tanganyika at the University of Burundi, Bujumbura in 1989. With the kind co-operation of Frits Roest of the Fisheries Unit of IAC in Wageningen, Netherlands, this symposium was attended by over 100 people from 21 countries (including many African participants). It provided the first opportunity for people of many disciplines to discuss fish stocks and fisheries, water quality and vulnerability to pollution, the

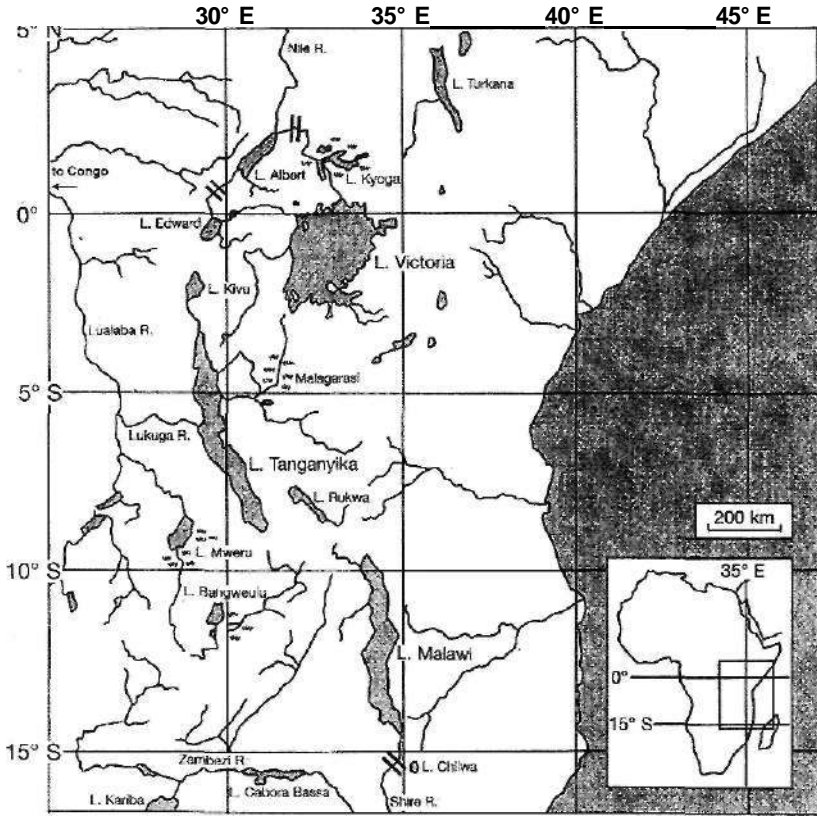
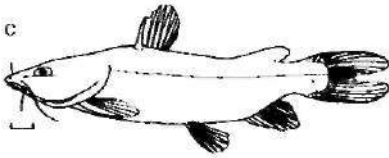
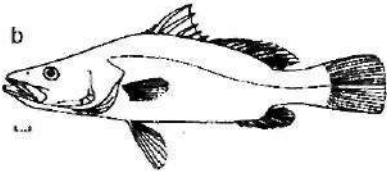


FIG. 1. The Great Lakes of eastern Africa - Victoria, Tanganyika and Malawi (also called Nyasa in Tanzania and Niassa in Mozambique) - with associated river systems, indicating barriers (waterfalls and rapids) important in the isolation of the various basins. Reproduced with kind permission of Kluwer Academic Publishers, from Lowe-McConnell (1996): *Environmental Biology of Fishes*, vol. 45, p.220. Fig. 1 (with minor modification).

Non-cichlids



Cichlids

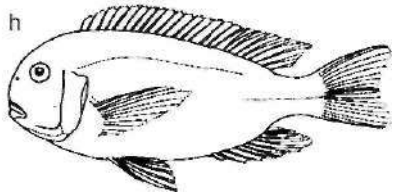
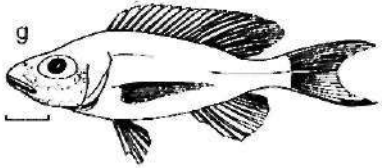
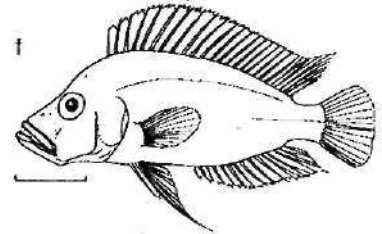
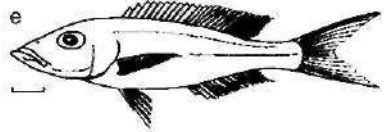


FIG. 2. Representatives of Lake Tanganyika's 23 families of non-cichlids and 12 tribes of cichlids (scale bars = 20 mm). Non-cichlids: a) zooplanktivorous clupeid; b) piscivorous *hates*; c) carnivorous bagrid catfish; d) omnivorous clariid catfish; Cichlids: e) piscivorous *Boulengerochromis*; f) carnivorous crevice-feeder *Lamprologus*; g) bottom-sand sifter *Trematocara*; h) algal-grazing *Petrochromis*. Modified, with kind permission of Kluwer Academic Publishers, from Lowe-McConnell (1996): *Environmental Biology of Fishes*, vol. 45, p.221, Fig. 2.

scientific value of the lakes and conservation measures (IAC 1990a, b; Lowe-McConnell et al. 1992). A subsequent conference in Bujumbura concentrated on 'Conservation and Biodiversity of Lake Tanganyika' (Cohen 1991). The widely circulated recommendations from these two meetings were then used to apply for international funds for fisheries and biodiversity projects.

Sources of information

The 1990s saw a veritable explosion of research. It had already become clear that all three lakes were facing serious anthropogenic threats caused by the rapid rise in human populations, leading to overfishing and pressures on biodiversity from sedimentation and pollution resulting from changes in land use in the lake basins. Large projects and workshops (listed in Appendix 1) included the FAO²/FINNIDA³ Lake Tanganyika Research Project (LTR), financed by Finland and executed by FAO, which examined the sustainability of Lake Tanganyika's commercial pelagic fisheries; the UK/SADC survey which explored the offshore waters of Lake Malawi for new pelagic fish stocks; and a Lake Victoria Fisheries Research Project (LVFRP) financed by the EU⁵ which examined the prospects for Victoria's fisheries, much changed since the establishment of the predatory Nile perch (*Lates niloticus*), introduced to the lake in the mid-1950s.

International interest in conservation of biodiversity was stimulated by the Biodiversity Convention signed at the Rio Earth Summit in 1992. This enabled United Nations agencies to set up projects using GEF⁶ funds for biodiversity studies on lakes Tanganyika and Malawi and for a Lake Victoria Environmental Management Project (LVEMP). In addition to the very numerous reports and widely scattered scientific papers from these projects, ongoing research on all three lakes also contributed abundant new information. In particular, from the clear waters of Lake Tanganyika, Japanese and African scientists, organized since 1977 by H. Kawanabe of Kyoto University, used SCUBA to observe the ecology and behaviour of the numerous endemic cichlid species cohabiting in the lake's highly diverse rocky shore communities (Kawanabe et al. 1997). In Lake Victoria, Leiden University's Haplochromis Ecology Survey Team (HEST) from The Netherlands, together with the Tanganyika Fisheries Research Institute (TAFIRI), continued research initiated in 1977 in Tanzanian waters at the

Food and Agriculture Organization of the United Nations
Finnish International Development Agency
Southern African Development Community
European Union
Global Environmental Facility

south end of the lake (producing a number of PhD theses which include their published papers, e.g. Wanink 1998; Seehausen 1999). Looking for cichlid refuges from the Nile perch, HEST discovered a whole new group of 100+ species of rock-dwelling cichlids, analagous to those of lakes Malawi and Tanganyika (Seehausen 1996). Following heavy exploitation of Nile perch in this area, they found resurgence of some haplochromine populations (Seehausen et al. 1997b; Witte et al. 2000) and also discovered that eutrophication has led to cichlid hybridization which appears to have affected cichlid speciation (Seehausen et al. 1997a). On Lake Malawi, studies continued on niche overlap in cohabiting cichlids (Genner et al. 1999a, b, c), on the effects of trawl-fishing which is landing a high proportion of as yet undescribed cichlid species (Turner 1994b, 1995), and most recently a huge multiauthored survey of the trophic ecology of the demersal fish community (Irvine et al. 2002). Aquarists have also published much valuable information on cichlid ecology in these lakes, from underwater observations using SCUBA (e.g. Konings & Diekhoff 1992; Konings 1995).

Furthermore, in the 1990s several specialist groups organised workshops and symposia producing good review papers (see Appendix). These included a 1992 workshop in London on 'The Impact of Species Changes in African Lakes'. Stimulated by the effect of introduced Nile perch (*Lates niloticus*) on the fishes and limnology of Lake Victoria, this meeting also considered Lake Kivu and the man-made Lake Kariba, in both of which clupeids introduced from Lake Tanganyika had come to support valuable fisheries (Pitcher & Hart 1995). Another symposium, held in Jinja 1992, looked at 'Biodiversity, Fisheries and the Future of Lake Victoria' (Kaufman 1992). In 1993, IDEAL⁷ organised a conference at Jinja on 'The Limnology, Climatology and Paleoclimatology of the East African Lakes' (Johnson & Odada 1996). Also in 1993, the Speciation in Ancient Lakes (SIAL) group (initiated from Belgium museums), held a stimulating workshop on 'Speciation in Ancient Lakes' (published as *Archiv fur Hydrobiologie*, vol. 44), with useful review papers (e.g. Cohen 1994; Coulter 1994; Martens et al. 1994). From this group's next gathering - 'International Conference on Ancient Lakes' (ICAL), held on Lake Biwa in Japan in June 1997 - two volumes were produced: 'Ancient Lakes; their Cultural and Biological Diversity' (which contained papers on conservation issues, Kawanabe et al. 1999), and 'Ancient Lakes: Biodiversity, Ecology and Evolution' (published as *Advances in*

International Decade of East African Lakes; supported by the US National Science Foundation and Swiss National Climate programme to focus on bottom sediments, and hence ages, of the Rift Valley lakes

Ecological Research, vol. 31). In November 1993, PARADf held a symposium in Senegal on 'Biological Diversity of African Fresh and Brackish Water Fishes' (organised by Christian Leveque; Teugels et al. 1994). This was followed by a PARADI/FISA⁹ symposium in 1998 in Grahamstown, South Africa on 'African Fish and Fisheries - Diversity and Utilization' (Skelton & Teugels 2001). Great Lakes of the World (GLOW; a group started in North America), at its GLOW II workshop in Sligo, Ireland, in July 2000, considered 'Sustainability of Great Lakes: is it a scientifically sound and practical concept' (Allison 2002). GLOW III in Arusha, Tanzania in 2002, which compared 'Great Lakes of the World: Climate, Food-webs, Biodiversity and Integrated Management', included eight African lake papers (published in a special issue of *Aquatic Ecosystem Health & Management*, vol. 6 (3), 2003). Another international conference on 'Lake Victoria 2000: a New Beginning', sponsored by many organizations interested in the lake's future, was held in Jinja, May 2000 (see Balirwa et al. 2003).

Conservation Biology in 1993 (vol. 7) included a special section (10 papers) on the Great Lakes of Africa. Invited reviews also appeared in *Environmental Biology of Fishes* (e.g. Witte et al. 1992; Fryer 1996; Lowe-McConnell 1996; Ogutu-Ohwayo et al. 1997) and in *Environmental Conservation* (Worthington & Lowe-McConnell 1994). Hull International Fisheries Institute's symposia have also included African lake papers (Cowx 1996, 2002). A UNESCO¹⁰ hydrology project produced helpful monographs on the limnology and hydrology of all three lakes (Crul 1995, 1997, 1998), and SIL published a review of limnology in Malawi (Msiska 2001). Tailing & Lemoalle (1998) summarised much limnological work for these three lakes. There are also many papers on the management of fisheries and biological diversity of these lakes (e.g. nine papers in Ribbink 1999; Molsa et al. 1999; Geheb & Sarch 2002; Allison 2002; van der Knapp et al. 2002). The bibliography is now so enormous that here it is only possible to cite recent reviews with good bibliographies and to comment on the main findings of the large projects, the bulky reports of which are not readily available for consultation. References are also given to important papers in scientific journals for readers to consult these for further details.

Poissons Africains: Role et Applications de la Diversite Biologique; instigated from ORSTOM (L'Institut Francais de Recherche Scientifique pour le Developpement en Cooperation), Paris to unite francophone and anglophone scientists
Fisheries Society of Africa
United Nations Educational, Scientific and Cultural Organization

FISHERIES PROJECTS

Lake Tanganyika

The very ancient and beautiful 650 km long Lake Tanganyika, lying between the mountainous walls of the rift valley, is the second deepest lake in the world (1,470 m), but being permanently stratified, its deoxygenated waters below ca. 200 m are out-of-bounds for the fishes. In this lake, unlike most other African lakes, the main commercial fisheries exploit pelagic species, using traditional (scoopnet, gillnet, beach seine), artisanal (lift nets) and industrial (purse seine) nets with lights at night to attract the fish (Coulter 1991). The catch is of endemic zooplanktivorous clupeids, *Stolothrissa tanganicae* and *Limnothrissa miodon*, and their endemic centropomid predators, mainly *Lates stappersi* and the larger *L. microlepis* (with *Lates mariae* and *L. angustifrons* as more benthic predators). Fish stocks are shared by the four riparian countries. *Stolothrissa*, the main catch in northern waters with a life cycle of about one year and very fecund, has a high turnover rate. The catches correlate negatively with those of its main predator, *L. stappersi*, with which it has an intricate predator-prey relationship. Juvenile *L. stappersi* are zooplanktivorous. This species is increasingly important in southern waters.

FAO catch statistics for both Burundi and Zambia show a decline in fish landings from 1957 to 1989, despite a large increase in fishing effort (Roest 1992). Analyses of 37 years of monthly catch records (1956-1992) from Burundi's purse-seine fishery have shown a downward trend of 1.6% per year in total catches, which explains why these industrial fisheries, with their higher overhead costs, have now been phased out (van Zweiten et al. 2002). When the catch rates of the industrial fisheries in Burundi were analysed, these pelagic fisheries showed great fluctuations not only in catch, but also of interannual variability, seasonality and short term persistence. Basic uncertainty, as variance not explained by trends or seasonality, comprised 75% of the variance in total catch rates. The Burundi catch records also showed intriguingly significantly higher (kg/vessel) monthly mean catch rates of small fish between 1964-1977 compared with the two adjacent periods (1959-64 and 1977-92, which were not significantly different from each other), perhaps due to climatic effects?

Comprehensive analyses indicated that the large changes in catch rates are mainly environmentally driven, and so are of little use for prediction of future catches until more is known of the effects of long-term meteorological changes. Plisnier et al. (1999) concluded that the annual limnological cycles in Lake Tanganyika appear closely linked to climatic conditions. Production in these African lakes is wind-driven with the

south-east trade winds blowing May-September, affecting both lakes Tanganyika and Malawi (the effect of shifts in the position of the InterTropical Convergence Zone on the lake levels and limnology of Lake Malawi had already been noticed by Eccles, 1984). In the mid 1990s the Lake Tanganyika survey found an increase in air temperature and a general decrease in wind speeds compared with earlier studies, the upper part of the lake being on average 0.34°C warmer in 1993-94 compared with 1947 and 1956-57. Two other recent studies consider climatological and limnological data (Verburg et al. 2003; Verschuren 2003) and historical records combined with paleolimnological data from carbon isotopes in sediment cores (Livingstone 2003; O'Reilly et al. 2003). Both studies stress the ecological consequences of the observed warming of Lake Tanganyika's surface waters and decreased wind speeds in reducing vertical mixing and thereby primary production, leading to declining fish production in this deep tropical lake. O'Reilly et al. (2003) conclude that the regional impact of global climate change on this very deep lake is larger than that of local anthropogenic activity or overfishing.

The FAO/FINNIDA Lake Tanganyika Research project, conceived by Professor O. Lindqvist of Kuopio University, Finland, was a lakewide project to investigate the limnological processes governing pelagic fish production and to see if further fisheries could be developed and managed on a sustainable basis. Financed mainly by Finland, this six year project (1992-1998) based at its headquarters in Bujumbura (ably coordinated - despite Burundi's civil war - by George Hanek of FAO) worked from the fisheries laboratories: at Kigoma (in Tanzania), Uvira (Congo), and Mpulungu (Zambia). Plans and results were also discussed at two international symposia held in Finland at Kuopio University (Molsa 1995; Lindqvist et al. 1999). Over a hundred investigators were involved: studies included meteorology (with three thermistor chains anchored far offshore), hydrodynamics, limnology, plankton and fish samples collected over three years (1995-1997), with twenty lakewide cruises for hydroacoustic and limnological studies from the research vessel *RV Tanganyika Explorer*.

From earlier studies, Lake Tanganyika's overall fish yield had appeared too high for the oligotrophic nature of its waters (Hecky 1991). The LTR project discovered 'missing' primary production deeper than previously sampled (30-40 m or deeper), the phytoplankton showing strong photo-inhibition especially on a sunny day. Secondly, while LTR findings agreed that the southern end of the lake functions as the main wind-driven engine causing upwellings and nutrient inputs from deeper waters, the hydrodynamic modelling revealed a much more complicated picture, with a highly mosaic pattern of upwellings and downwellings occurring all over the lake, even short-term high wind (of a few hours) mixing down to 90 m. This dynamism and turbulence also resulted in a deeper productive layer

and enhanced encounter rates between zooplankton and its food, with no long-term refuges for the pelagic organisms. The relatively simple pelagic system (only 2-3 crustacean zooplankton species and generally three fish species) should mean efficient utilization of primary and secondary production by the pelagic fish stocks. Langenberg et al. (2002), when comparing data from the two ends of this long lake, observed pronounced variability of thermal structure in time, depth and region, stressing the consequences of hydrodynamic processes on the lake's productivity.

Great fluctuations in production were shown from year to year (possibly over periods of several years, as mentioned above), but in the mid-1990s, the LTR team estimated primary production to be 426-662 g C m⁻² (47-128% higher than previously published values) with bacterioplankton amounting to ca. 20% of this primary production. Zooplankton biomass (1 g C m⁻²) and production (23 g C m⁻² yr⁻¹) were 50% lower than earlier reported (suggesting that carbon transfer efficiency was low, in contrast to earlier speculations). Fish production estimates were based on hydroacoustic assessment of pelagic fish biomass, with growth rates obtained from length frequency analyses checked against daily increment rings on fish otoliths. Planktivorous fish biomass (0.4 g C m⁻²) and production (1.4-1.7 g C m⁻² yr⁻¹) also indicated a low carbon-transfer efficiency from zooplankton into planktivorous fish production (not unexpected with high metabolic losses due to high temperatures and the probably high costs of predator avoidance). In the mid 1990s the total fisheries yield of Lake Tanganyika was estimated to be 0.08-0.14% of pelagic primary production (not dissimilar to some other lakes, Sarvala et al. 1999). Lake Tanganyika's pelagic fish production thus appears to be 650-750 kg ha⁻¹ yr⁻¹ (65-75 g m⁻² yr⁻¹) (compared with ca. 80-130 kg ha yr⁻¹ in Lake Malawi: Allison 1995, 1996), and Tanganyika's pelagic fish biomass 19-35 g m⁻² or 600 000 - 1 000 000 tonnes (compared with an estimated 6.6 g m⁻², 160 000 t in Lake Malawi).

Bioenergetic calculations (Sarvala et al. 2002), using diet data from fishes of different sizes and from different regions of the lake, indicated that food requirements of the planktivorous fish were 25-38% of the zooplankton production, but there were very high predation pressures (73-104%) on shrimps and >100% on prey fish. The annual catches of *Stolothrissa* varied for different regions but averaged 25% of estimated production for the whole lake. For *Limnothrissa* this ratio was lower in Tanzanian and Zambian waters than in the Congo and Burundi, but for the whole lake averaged 30%. The catch/production ratio for *hates stappersi* was very high (94% lakewide average). These figures suggested that the present clupeid fishery is operating on a sustainable basis but that the *hates* populations are clearly overfished.

Over fifty traditional and artisanal fishing gears used in the inshore

waters of Lake Tanganyika were described and illustrated in the Fishing Practices Special Study of the UNDP¹ /GEF Lake Tanganyika Biodiversity Project (LTBP) described below (Lindley 2000).

Management, both for fisheries and conservation of Tanganyika's biodiversity (LTBP, see below) presents special problems (Coulter & Mubamba 1993; Lindqvist et al. 1999; Molsa et al. 2002; Reynolds et al. 2002).

Lake Malawi

For zoogeographical reasons Lake Malawi, which drains to the Zambezi, lacks clupeids and *hates* in its fish fauna, and cichlids support the main commercial fisheries. When I studied these in 1945–47, tilapia, particularly the three endemic *Oreochromis* species, were caught in large beach seines, open-water ring nets and gillnets. The fishery for these has now almost collapsed (FAO 1993; Turner 1994b, 1995), as have the fisheries for the potamodromous fishes (such as *Labeo mesops*) and other large species, including the large endemic *Bathyclarias* species and *Bagrus* (Turner 1994b). Commercial trawling for smaller cichlids, including 'over a hundred' haplochromine species, many not yet named scientifically, was developed in the 1980s in the relatively shallow waters at the south end of the lake (Turner 1994b, 1995; Banda et al. 1996). Numerous studies on both the rock-dwelling cichlids (known locally as 'mbuna'), using SCUBA, and trawl-caught fishes continue to be made from the Malawi Fisheries Department headquarters at Monkey Bay. This laboratory has also been used as a base by many visiting scientists (listed by Tweddle 1991). The colourful mbuna are exported as aquarium fishes and many species are now bred in tanks at Senga Bay (by Stuart Grant) to reduce pressure on the wild stocks. The thriving aquarium fish trade was valued at US \$276 000 for the year 1994 (Msiska 2001).

In the 1990s it was estimated that 70% of Malawi's animal protein came from fish. Since then there has been a huge increase in the human population (reaching 11 million in 2000; United Nations, 2000) and in fishing effort, with a 20% increase in the number of artisanal fishing vessels - dug-out canoes and plank boats. More than 53 000 people are now involved in catching and harvesting fish with an estimated 20 000 employed in ancillary industries (Allison et al. 2002). Malawi's total annual fish catch (all waters, but mainly Lake Malawi) varied from 75 000 t to 58 000 t in 1990-1994 (Msiska 2001). Lake Malawi fisheries caught an estimated 35-40 000 t annual yield; the artisanal fishery yields have been approximately stable for the last 15 years, lake-wide, and largely dependent on small low-value zooplankton-feeding cichlids (utaka) and

cyprinids (usipa), whereas yields of the higher value catfish and tilapias (chambo) have declined and now comprise less than 20% of the total catch (Irvine et al. 2002).

Seeking new sources of fish for the rapidly rising human population, in 1987 the UK financed an ODA¹²/SADC project to assess the 'Fishery Potential and Productivity of the Pelagic Zone of Lake Malawi/Niassa'. Directed by Andy Menz, this five year survey became operative in 1990 at Senga Bay north of Monkey Bay (Fig. 1), with a research vessel able to cope with the stormy open waters of this lake, the well-equipped *RV Usipa*, a 15 m long catamaran. The final report (Menz 1995) is a compendium of detailed information about the limnology and newly-discovered pelagic fish fauna. The great surprise was to find that these open waters had been colonised by cichlids, mostly species new to science and mainly of zooplanktivorous *Diplotaxodon* spp. and piscivorous *Rhamphochromis* spp., living at characteristic depths (as determined by fleets of gillnets set from the surface to 300 m deep - the lower limit of fish being at 250 m) (Menz 1995; Thompson et al. 1996). In contrast, the expected 'utaka' zooplanktivorous cichlids (apart from one species *Copadichromis quadrimaculatus*) were confined to places where concentrations of zooplankton made feeding easy, in nutrient-rich waters rising around seamounts ('virundu'), and adults of the expected 'usipa' (*Engraulicypris sardella*, a small endemic pelagic cyprinid) were found mainly in more inshore waters, though their pelagic larvae were widely distributed in the open lake.

These new pelagic cichlids, and the little yet known of their biology, were described by Turner (1996a). Their main food sources are the copepod *Tropodiptomus cunningtoni*, the late instars and pupae of the lake fly *Chaoborus edulis* and the pelagic usipa larvae. These cichlids have the unusual ability (for a cichlid which has a closed swim bladder) of making vertical migrations upwards, from day-time preferred depths, at night following their prey. By day, survey gillnets at 200-220 m, just above the oxygen boundary, caught *Diplotaxodon* 'bigeye' (later found to be several species, Turner 1996a) and *Synodontis njassae*. Above this, at 50-200 m, lived *D. 'elongate'* (= *D. limnothrissa*) and *Rhamphochromis ferox*; the top 100 m was inhabited by *Copadichromis quadrimaculatus*, *Engraulicypris sardella* and *Rhamphochromis longiceps*. Most species moved up at night, though the extent of the upward movement varied according to species and possibly according to the phase of the moon. A characteristic of these offshore cichlids was how little of the secondary crustacean zooplankton is consumed directly by them, and also their ability to switch prey to utilise whatever items were most readily available,

including usipa and lakefly larvae. The surprisingly abundant endemic *Synodontis njassae* catfishes were found to be feeding on the same organisms and able to migrate from the oxygen limit (250 m) to surface waters nightly.

Bioacoustic studies indicated total ichthyomass in the offshore regions to be an estimated 168 400 tonnes. Gillnet studies showed the dominant taxa to be *Diplotaxodon limnothrissa* (estimated 87 000 t) and *D. 'bigeye'* (32 700 t), *R.longiceps* (11 300 t) and *R.ferox* (5,500t), *C. quadrimaculatus* (8,700t), other cichlids (3,400 t), together with *S. njassae* (13 400t), *E. sardella* (51000t) and *Opsaridium* (a potamodromous cyprinid predator, 1,300 t). From the five acoustic surveys, in combination with trawling surveys, Allison (1996) assessed the fishery potential of the ca. 24 000 km² lakewide pelagic zone; these indicated a lakewide mean pelagic fish biomass of ca. 6.6 g wet weight m⁻² (in fair agreement with predictions based on biomass size distribution theory of 6.2-8.8 g m⁻²). Fish production, estimated from primary production using size spectrum models, was of the order of 8-13 g m⁻² yr⁻¹, mainly of zooplanktivores. By comparison, the production of clupeids in Lake Tanganyika was 65-70 g m⁻² yr⁻¹.

Production in Lake Malawi's pelagic zone is driven by the south-east tradewinds ('mwera') that normally blow from May to September causing mixing of nutrient-rich hypolimnion water into the photic zone (Patterson et al. 2000). Seasonal plankton samples collected through two full years (1992 and 1993), showed how the seasonal variation in wind-mixing was closely followed by peaks in primary production, then peaks of *T. cunningtoni* dominant in the zooplankton, and of usipa larvae lakewide. These all showed clear seasonal patterns with higher values centred on the middle-to-late part of each year. This coincidence of high production at the three trophic levels indicated food limitation and rapid carbon transfer up the food chain as far as the secondary consumers. The biomass of all fish species combined showed no seasonal pattern, as the populations consisted of adult fish of several year-classes.

Overall, biomass values for all planktonic organisms were higher in 1993 than 1992, suggesting that the observed higher primary production in 1993 led to an increased transfer of carbon up the food chain and indicating that the standing biomasses of these groups, as well as their production rates, are strongly controlled by their food supply (for details of the spatial and temporal patterns of zooplankton standing biomass and production, see Irvine & Waya 1999). But the fairly rapid response of predator populations to increases in their prey showed that predators are also important in determining the standing biomass of prey organisms. Thus it appears that in Lake Malawi while production is largely set by food availability, biomasses are controlled by both food supply and predation.

Usipa (*E. sardella*) production was greater in 1993 than 1992, and these short-lived usipa, which are important predators on zooplankton, showed a marked seasonality in production. The interaction between predation and food limitation may account for the high annual variability seen in the landings of usipa by the artisanal fishermen, and might explain why strong usipa recruitment (as reported by Lewis & Tweddle 1990) is relatively infrequent.

The SADC Survey answered two outstanding questions concerning the integral value of the lake fly and the inadvisability of introducing clupeids from Lake Tanganyika (as had once been suggested, but countered by Eccles 1985). The survey found that more than half the adult fish production in the pelagic ecosystem is sustained by consuming *C. edulis* and *E. sardella* larvae, rather than by feeding directly on herbivorous zooplankton (Allison et al. 1995a, b). This extra step in the food chain means that the conversion of primary production to fish production is less efficient than in a system with a shorter food chain (an estimated 0.3% of primary production to fish production in L. Malawi, compared with 3.3% in Lake Tanganyika, Allison 1995). But elimination of this extra step by introduction of a specialist zooplanktivorous fish was not thought to be feasible (or advisable) as zooplankton densities are too low. This extra step serves to concentrate the scarce food resources into a form exploitable by fishes, making the sparse zooplankton available to cichlids which hunt by sight. Furthermore, in L. Malawi every niche appears to be already filled by species that have evolved within the lake. As Irvine (2000) has stressed, any fish introduction that effectively redirected production from *C. edulis* into fish could have disastrous consequences on deep water and demersal stocks of fish that feed on *C. edulis* and this would cause serious disruption to ecosystem functioning, biodiversity, fish stocks and ultimately protein availability for human consumption. Ideas on utilising these offshore pelagic fishes were explored at a workshop on the ODA Ncheni Project held at Senga Bay in February 1997, with useful papers on implementation of possible recommendations (Turner 1997). As yet, we know little of their breeding biology and growth rates.

Concerning Lake Malawi's other fisheries, what has happened to the chambo (tilapia) fishery? Prior to 1986 chambo had dominated the fisheries, with beach seines, gillnets and open-water ringnets competing for the same three endemic species of *Oreochromis*. Of the formerly important fishing grounds only the south-eastern arm still retained a viable fishery in 1986 and this appeared to be fully exploited. Fisheries Department statistics have since shown a switch from large-meshed to small-meshed gears, both in the artisanal fishery - from gillnets and chambo (tilapia) seines to small-meshed kambusi, chilimila and nkatcha seines - and in the mechanised industry. Catch data summarised by the FAO Chambo survey

(1993) showed that in the SE and SW arms and Lake Malombe (a small lake on the outflowing Upper Shire river into which some brooding female tilapia move from Lake Malawi), artisanal fisheries were increasingly dominated by small-meshed seines, some lined with mosquito-netting. Juvenile tilapia concentrate in shallow water so are particularly vulnerable to these beach seines. Overfishing was most serious in L. Malombe and the Upper Shire, where since 1980 the number of small-meshed seines had increased tenfold and the catch become almost entirely of small haplochromines (Tweddle et al. 1995). A decline in the populations of larger species (including the larger non-cichlids) led to a decrease in the effectiveness of gillnets and chambo seines, many of which were then fitted with smaller meshes and re-targeted on haplochromines (Turner 1995). The collapse of the tilapia stock was attributed to excessive use of the small meshed seines in Lake Malombe together with excessive effort in the chambo fisheries on the main lake.

Is the trawl fishery for haplochromines sustainable? Haplochromine cichlids are 'K selected' fish, mouth-brooding very small broods of young, so cannot recover fast if overfished; moreover many species appear to have limited ranges. Since the mid 1970s they have been exploited by three trawling techniques: semipelagic trawling (catches dominated by *Diplotaxodon limnothrissa*); demersal single-boat trawling (catches dominated by large demersal species, especially *Lethrinops microdon*), and demersal pair-trawling (fishing an entirely different community, mainly of small undescribed species characteristic of soft bottoms in water less than 40 m deep). All techniques took substantial catches of pelagic *Rhamphochromis* (ca. 15 species). Turner (1995) considered the demersal trawling in 50-70 m water to be severely overexploiting the fish stocks and the shallow water catches showed marked changes in abundance of different taxa, with decline in the larger species and changes in community structure (Turner 1995; 1997). Comparing 1971-73 and 1991-92, surveys showed declines in eight of the ten guilds of haplochromine cichlids, especially of the larger piscivores, molluscivores and arthropod feeders. In 1994 four demersal stock assessment surveys in the southern arms of the lake showed cichlids made up 80-90% of the catch and comprised perhaps more than 100 species (Banda et al. 1996). Most species were caught in a narrow depth range, with the most marked change in fish community around 50-70 m, coinciding with the thermocline and limits of the euphotic zone. Turner (1996a) has listed the cichlid species caught in the 1992 trawl surveys, dominated by small haplochromine cichlids, many of them sediment feeders.

The Final Report of the four-year EU sponsored survey of 'The Trophic Ecology of the Demersal Fish Community of Lake Malawi/Niassa, Central Africa' (covering March 1998 to February 2002, Irvine et al. 2002), is a

compendium of new information on the taxonomy and genetics, fisheries assessment and trophic modelling of these benthic fish, mainly small haplochromines. Data coordinated by Ken Irvine (of Trinity College, Dublin), were gathered by a consortium of six European and three African partners (the Brussels and Tervuren Museums in Belgium; Universities of Hull, East Anglia, Southampton in UK; Department of Fisheries and University of Malawi; Tanzanian Fisheries Research Institute; with some participation from Fisheries Institute Mozambique). From its base at Senga Bay, extensive lakewide research cruises were made in the *RV Usipa*, trawling fish down to 125 m and collecting benthos samples down to the oxygen boundary at 200 m depth. Their separate tasks included measuring primary photosynthetic and microbial production, investigating the diversity, structure, seasonality and production of the invertebrate communities, fish taxonomy (including genetic structure of populations), fishery assessment (by trawl and frame surveys), growth rates of demersal fish, fish diet analysis (including stable isotope work) and trophic modelling. The findings of the project strongly indicated that the southeast arm, where most of the work was based, is under severe fishing pressure that requires immediate management strategies to minimize further deterioration. Increasing levels of fishing (as is likely under current pressure on stocks and lack of enforcement capacity) will cause further change in both species composition and trophic structure, although fish yields may continue to increase, particularly if fishing is expanded into areas such as the deep water demersal and offshore pelagic zones.

This project found that diversity and densities of benthic invertebrates declined with increasing depth; molluscs and insects abundant at 10 m were absent from sediment samples at 30 m (probably affected by oxygen availability). Taxa found at 125 m included high numbers of bivalves, nematodes and chironomids. The diversity of the fish fauna is even greater than previously thought, with numerous species of the deep water *Lethrinops* complex and a whole new suite of ca. 47 species of *Placidochromis*. Diet analysis showed ten main trophic guilds, with the bulk (58%) of the biomass concentrated at trophic level 3.0, in which a number of fish groups feed on the benthic invertebrates. They also consume lakefly (*C. edulis*) larvae, and are then subject to predation by a large number of piscivorous fish species. The apex predators are *Bagrus meridionalis* and clariids, with some of the large cichlid piscivores. For many taxa there appears to be a high proportion of trophic-equivalence within the demersal fish community - 'at least 40% of species within the Lake Malawi demersal fish community are trophic analogues' according to Allison & Darwall (2002). While this suggests that elimination of species will result in subsequent replacement by functional analogues, these

analogues could also be highly important for the maintenance of ecosystem function through provision of a buffer against environmental change.

The relationships between organic matter, invertebrates and bacteria in the bottom sediments of Lake Malawi suggest that benthic invertebrates are essential to the processing of detrital carbon and that a shift in the degree of anoxia within the lake, affecting their distribution, could severely alter the cycling of carbon (Buat et al. 2002).

Perhaps the most surprising finding was that the demersal system appears to rely most heavily on biomass imported from the pelagic through the consumption of copepods by fish migrating vertically to feed in the pelagic, as well as through the fall out of diatoms which are consumed by fish sifting them from the sediment ooze. Lake Malawi appears to be much more efficient than previously supposed, as the demersal fish community is able to make direct use of pelagic production previously thought to be exported to detritus. Calculated from trophic models, mean transfer efficiencies between trophic levels are slightly higher in Malawi (14%) than in Lake Victoria (11%) (and significantly lower, only 4.7%, in the artificial impoundment of Lake Kariba) (Allison & Darwall 2002; Darwall & Allison 2002).

A key to Lake Malawi's invertebrate genera was made available for field work. Reference collections have been left at Senga Bay, and also in Tanzania and at the J. L. B. Smith Institute Grahamstown (South Africa). Taxonomic work is continuing at the two Belgium Museums, where a book on Lake Malawi's cichlid diversity, identification, distribution and taxonomy is in preparation at Tervuren (Snoeks ed. in preparation).

The combined Malawi fisheries exploit in excess of 300 species of fish, growing to and breeding at different sizes and at different times of year, complicating conservation measures. So the best strategy appears to be to establish well-monitored unfished reserves over various types of bottom. Management of Malawi's offshore fishes was discussed by Turner (1997), Turner et al. (2002), Darwall & Allison (2002) and also in three papers in Geheb & Sarch (2002), including Allison et al. on 'Conflicting agendas in development and management'. Fishery impacts and management scenarios have also been assessed using the ECOSIM computer program (Allison & Darwall 2002).

Lake Victoria

In the shallower and turbid waters of Lake Victoria, with its many gulfs and bays, much of the shoreline is swampy, the lake bottom covered with algaecious mud and detritus. Here the first commercial fishery used gillnets for tilapia and about a dozen large non-cichlid species. An experimental trawl fishery in the 1960s showed the main fish biomass to consist of

haplochromines of many species and trophic groups. By the 1990s the Lake Victoria ecosystem was much changed and the fishery had become much simplified (as discussed in many chapters in Pitcher & Hart 1995; Witte & van Densen 1995; Johnson & Odada 1996; Jackson 2000). There had also been a significant increase in release of nutrients from atmospheric and catchment sources which, together with in-situ nitrogen fixation by cyanobacteria, had enhanced eutrophication. The average open-water chlorophyll concentration had increased 2-5 fold, with light transparency reduced fivefold (Mugidde 1993). There had been declines in hypolimnetic oxygen (anoxia below 40 m seasonally) and vertical mixing rates had changed profoundly. Annual wind-mixing no longer brought saturated oxygen levels from surface to bottom. There had also been an increase in water temperatures.

These dramatic changes in the biological, chemical and physical characteristics of the lake are believed to have resulted from the interaction of several factors: effects of the introduction of Nile perch in the mid-1950s, climate change and increased human activities in the watershed (Ogutu-Ohwayo et al. 1997). HEST stressed the effects of the drastic changes in the food web, following the loss of ca. 200 endemic haplochromine species - previously 90% of the biomass and including phytoplanktivore-detritivores which turned over bottom deposits. Lehman et al. (1998) concluded that virtually every recent change in Lake Victoria can be ascribed to consequences of altered mixing state, the lake presenting an example of ecosystem response to climatic forcing functions and eutrophication. From their palaeolimnological data, Verschuren et al. (2002) concluded that landscape disturbance, rather than food-web alterations or climate change, is the dominant cause of the ongoing eutrophication.

In the 1960s Victoria's fisheries based on indigenous species sustained a production of ca. 100 000 tonnes a year, though there were already signs of over exploitation. After 1979 catches were augmented by the exploding Nile perch (*Lates*) population and by the early 1990s the fisheries produced over 500 000 t annually. But these fisheries were much simplified and dominated by three species: the introduced Nile perch and Nile tilapia (*Oreochromis niloticus* - which had replaced the endemic *O. esculentus*) and dagaa (the small endemic cyprinid *Rastrineobola argentea*). The Nile perch became the mainstay of the fishery, attracting very large numbers of fishers; boats on the lake increased from 22 700 in 1990 to 42 500 in 2000. Nile perch processing factories developed to absorb ca. 122 000 t wet fish annually and the combined exports from the region were worth ca. US\$ 220 million annually (LVFRP 2001).

In the 1970s adult Nile perch, feeding on the abundant haplochromines, grew very obese (Jackson 2000). In Kenyan waters in 1983, Hughes (1992)

found that males matured when 50-55 cm total length (TL) (thought to be two years old), females when 80-85 cm TL (four years old). The large fish were mostly females, suggesting a possible sex change from male to female (as known in *hates calcarifer*). By 1999 Mkumbo et al. (2002) found that in Tanzanian waters, the maturation size of females had fallen from 95-100 cm TL in 1988 to 70-78 cm TL, and in trawl catches 80% of the fish were immature, implying over fishing (see below).

Research essential for sustainable fisheries was financed by the EU as a Lake Victoria Fisheries Research Project (LVFRP - Phase II 1997-2001), for which a consortium from Europe, led by UNECIA¹³ Ltd (headed by HIFI¹⁴) worked in collaboration with the fishery research institutes of Uganda, Kenya (KMFRI¹⁵) and Tanzania (TAFIRI). LVFRP's headquarters was at FIRRI¹ at Jinja, Uganda, where they assisted the newly established Lake Victoria Fisheries Organisation (LVFO) to develop a management framework for the fisheries. The LVFRP involved stock assessment, research on fish biology and on the social and economic impacts of management strategies on the fishing communities. Data amassed were used for the preparation of a Lake Victoria Fisheries Management Plan (Bwathondi et al. 2001).

Fish stocks were assessed by lakewide acoustic surveys combined with trawl and gillnet fishing. Bottom trawl and gillnet catches and biological sampling of commercial catches were used to determine fish stomach contents and food webs for the main fish species. Bottom trawl surveys (November 1997-September 2000) gave an average catch of 195 kg per hour (substantially less than the 800 kg per hour recorded during a similar type of survey ca. 1970). About 70% by weight of the Nile perch was of immature fish. Fishes were most abundant in areas between 10 m and 30 m deep (above the deoxygenated bottom water). Acoustic surveys showed the total biomass index did not change much over the two years of the programme (August 1999-Sept 2001), but the Nile perch biomass index decreased from 1.58 to 0.89 million tonnes over two years and the biomass of small pelagics (mainly dagaa) increased. Combined trawl and acoustic data, gave abundance estimates for the three full years which indicated that Nile perch stock continued to fall and by September 2001 had declined to 540 000 tonnes. Since then the Nile perch fishery has declined so much that some of Uganda's fishers have migrated to lakes Kyoga and Albert and there have been some violent conflicts over fishing areas in Lake Victoria (Cowx, personal communication 2003).

Universities of Northern England Consortium for International Activities
Hull International Fisheries Institute
Kenya Marine Fisheries Research Institute
Fisheries Resources Research Institute; formerly EAFRO (East African Fisheries Research Organisation)

Acoustic indices were also determined for other categories of fish and *Caridina nilotica*. This prawn had become very abundant in the lake and now has a key role as food for Nile perch and other commercial fishes (Budeba 2003). In the shallow coastal areas, up to 25 m deep, the all-species standing crop was four times higher than in offshore waters deeper than 40 m. When the lake was stratified, echoes were negligible below the thermocline or oxycline. Small pelagics were observed in substantial quantities in the upper waters throughout the lake (Tumwebaze et al. 2002). Gillnet surveys showed higher catches in bottom set nets, but on average 50% by weight of the fish live in midwater more than 5 m above the lake bed. In shallow bays gillnets took 10 fish taxa, with the tilapia *O. niloticus* nearly 50% of the total weight, followed by haplochromines (19%) and Nile perch (17%).

Catch assessment data were of poor quality, but current landings were estimated at ca. 260 000 t, largely because of the high contribution of dagaa. Commercial catches of Nile perch from gillnets, longlines, beach seines and mosquito seines all showed a downward trend (in kg per boat-day) from 1989-1998. The Nile perch fishery exhibits classic indicators of overfishing: reduction in age/length at maturity, reduction in catch per unit effort (especially taking into account higher fishing pressure), reduction in mesh size of nets used, and an increased proportion of immature fish (less than 50-70 cm) in the catches. Trawl data also suggested that the proportion of mature adult fish in the stocks is now very low. There is still much to learn of the behaviour of Nile perch in this lake, its spawning behaviour, breeding and nursery grounds.

The exploitation of Nile perch is primarily driven by export markets, through the processing factories. In 1999 factory capacity in the three riparian countries was over 213 000 t, despite Nile perch annual landings from the lake being ca. 231 000 t (in 2000) with an estimated Maximum Sustained Yield of 213 000 t (LVFRP 2001). LVFRP therefore recommended that the industrial processing factories should adopt a slot size limit, taking only 50-85 cm total length Nile perch, and that no more factories should be licensed. Despite this recommendation, Uganda has since licensed some new factories. There are recent reports that Nile perch taken from Lake Victoria are now being grown in ponds in China (Cowx, personal communication), which may affect future exports from East Africa.

Of the other species, *O. niloticus* tilapia catches rose when larger meshed gillnets were used for Nile perch, but these also now show signs of overexploitation (Goudswaard 2002b; LVFRP 2001). The *Rastrineobola* (dagaa) stocks are also exhibiting signs of overexploitation, damaged by small meshed seine nets fishing the inshore breeding grounds, so it is recommended that fishing should be 80-100 m offshore (Wanink 1999).

Plans for future research and management of Lake Victoria and its basin, and how to combine fisheries development with conservation of the lake's biodiversity, were discussed at an International Conference 'LV 2000: a New Beginning', held at Jinja in May 2000. Two decades after the rise of the Nile perch this had shown signs of being overfished and some of the indigenous species that were in retreat - or even thought extinct - are now re-emerging. Data on the resurgence of the endemic haplochromine species (see below) suggest that heavy fishing of Nile perch may enhance biodiversity. This has renewed interest in management options that promote both sustainability of the fishery and conservation of biodiversity (as discussed by Balirwa et al. 2003). A resurgence of some haplochromine species following heavy fishing of Nile perch, has also been studied in the small satellite Lake Nabugabo on the northwest coast of Lake Victoria (Chapman et al. 1996, 2003; Schofield & Chapman 1999).

Another large international project LVEMP (Lake Victoria Environmental Management Project), funded by the World Bank, started in July 1997 and is still in progress. This deals with aspects such as water quality, wetlands, and the severe invasion and biological control of water hyacinth (*Eichhornia crassipes*) using the weevils *Neochitina eichhorniae* and *N. bruchi* (many papers, abstracts in LVEMP 2001). The effects of water hyacinth on the fisheries were also discussed by Njiru et al. (2002) and Balirwa et al. (2003).

Sadly it seems clear that whether Lake Victoria will keep its very lucrative fisheries depends on greed and political interests, which are determining what happens to the fisheries, not the unheeded advice from fishery biologists. Fisheries management - 'pitfalls and building blocks' towards management of Lake Victoria's fisheries, fishers' attitudes towards management and co-management, and conflicts among resource users - were discussed by Crean et al. (2002), van der Knapp et al. (2002) and in three papers in Geheb & Sarch (2002).

In a useful discussion on maximization of yields from these and other African lakes (twenty lakes classified as 'hates lakes', 'clupeid lakes' or 'cichlid lakes') Turner (1996b) concluded that while fisheries based on large predators may be more profitable, at least in the short term, fisheries based on small species have given higher yields, and the decision on whether to manage African lakes in a way which maximizes yields or profits is essentially political.

BIODIVERSITY: THREATS, REFUGES AND CONSERVATION

Lake Tanganyika: biodiversity

Tanganyika faces a variety of threats including pollution, sedimentation and over-fishing or fishing with destructive gears, activities resulting from socio-economic conditions in the riparian countries (Cohen 1991; Cohen et al. 1996). In 1995 UNDP/GEF financed a five year project on 'Pollution Control and other Measures to Protect Biodiversity in Lake Tanganyika' (LTBP). The international tender was won by a UK-based consortium consisting of the Natural Resources Institute (NRI, Greenwich), the Marine Resources Assessment Group (MRAG of Imperial College London) and the Institute of Freshwater Ecology (IFE, now Centre for Ecology and Hydrology) for a coordinated approach to the sustainable management of L. Tanganyika in collaboration with the national institutions.

To achieve this five 'Special Studies' were first made of biodiversity, pollution, sedimentation, fishing practices and socio-economics, each with a team to collect data on the current state of biodiversity and threats against it. The Special Study reports were then used to develop a Strategic Action Programme, designed to feed back information on the lake's resources with a prioritised list of management interventions, to the local communities. The project also included an Educational Programme and, finally, a draft Legal Convention to bind the four riparian countries to manage the lake's resources sustainably. But civil war and political changes in the riparian countries presented difficulties to the signing of this legal agreement (West 2001).

The Biodiversity Final Technical Report (Allison et al. 2000) had four key objectives: (1) to review current levels of biodiversity, achieved by an initial literature survey followed by underwater surveys for which African counterpart crews were first trained to use SCUBA techniques; (2) mapping the distribution of major underwater habitat types; (3) suggesting priority areas for conservation, based on existing knowledge and recommendations from the special study programmes; (4) developing a sustainable biodiversity monitoring programme for future use. The chosen conservation areas were underwater extensions to four existing national parks around Lake Tanganyika: in the Ruzizi Delta, off the Gombe Chimp reserve and Mahale Mountains National Park in Tanzania, and Nsumba Bay Park in Zambia. The Biodiversity team reviewed the concepts and conditions that led to the choice of survey methodology and its validation. Their extensive archive and database summarised current knowledge on Lake Tanganyika's biodiversity from the literature survey and results of the team's underwater surveys in 1997-1999. The report concluded with a summary of recommendations for conservation, management action,



Lake Tanganyika. *Above:* Burundi fishing beach, showing canoes piled with artisanal lift nets ready for nocturnal fishing, using lamps to attract the pelagic fish. *Below:* The pelagic fish catch (clupeids and juvenile *Lates stappersii*) on drying racks, which can be covered in rain storms, on a Burundi beach. (Photographs courtesy of F. C. Roest)



George Coulter, a pioneer of Lake Tanganyika's fisheries research, backed by Burundi's industrial purse seine boats; note (on left) the lamps used to attract the pelagic fishes in this nocturnal fishery.

George Turner and Rosanna Robinson preparing cichlid species for taxonomic study on Malawi's research boat off Monkey Bay, 1991.



Tony Ribbink using SCUBA to collect mbuna cichlids off Cape Maclear's rocky shore, Lake Malawi.

Scientists representative of the numerous people, of many nationalities, who have contributed to these African lake studies. (Photographs by R. Lowe-McConnell)

monitoring and research priorities. Teams from all four riparian countries participated in the design and testing of the survey methods to ensure a high level of ownership and understanding of survey methodology to be used in future surveys.

As most taxa are not sufficiently well known taxonomically to form the basis for large-scale survey activities, the main techniques were standardized protocols for sampling the very diverse fish community and molluscs as total biodiversity surrogates. Three fish-survey techniques were developed, two SCUBA based (stationary visual census and rapid visual census) and standardized gillnet surveys for use where crocodiles and hippopotami endangered SCUBA divers. Shannon-Wiener estimates of diversity were preferred to Simpson's index. Habitat surveys established that the areas adjacent to the existing terrestrial protected areas contain the full range of littoral habitats (emergent and submerged macrophytes, stromatolite reefs, shell beds and all combinations of hard and soft substrates). Of the described lacustrine fish species, 73% were found in waters adjacent to existing national parks. The highest number of species was found in the sub-littoral down to 40 m. A high percentage of this biodiversity was ubiquitous, though a limited number of fish taxa had spatially restricted distributions in the lake (and mollusc distributions appear much more complex; E. Michel, personal communication 2003). Fish communities on rocky substrates were more diverse than those on sandy ones, and pristine habitats had higher diversities than areas close to population centres subject to disturbance from fishing, pollution and sedimentation.

This survey had a strong technical focus, providing essential baseline information for a first management plan for the lake. It stressed the importance of joint planning with cooperation between different disciplines and management. It also emphasised the need for a critical analysis of the costs and benefits of conservation to ensure that the benefits of conservation flow to those who live around the lake, while some way should be found for costs to be born by all who value its diversity.

Coexistence in Lake Tanganyika's biodiverse fish communities: SCUBA studies of cichlid resource partitioning

The partitioning of Lake Tanganyika's littoral/sublittoral zone resources by trophic radiations, feeding behaviour and by selection of breeding sites and territoriality, has been explored since 1977 by Japanese and African teams (Hori et al. 1993; Nakai et al. 1994; Kawanabe et al. 1997). The interrelationships between species (mainly cichlids) in the diverse and crowded littoral zone are well illustrated by its exceedingly complex food web: Fig. 3, from Hori (1997). Their initial census of a 20 X 20 m quadrat in water 1–11 m deep off the rocky northwest coast of Lake Tanganyika

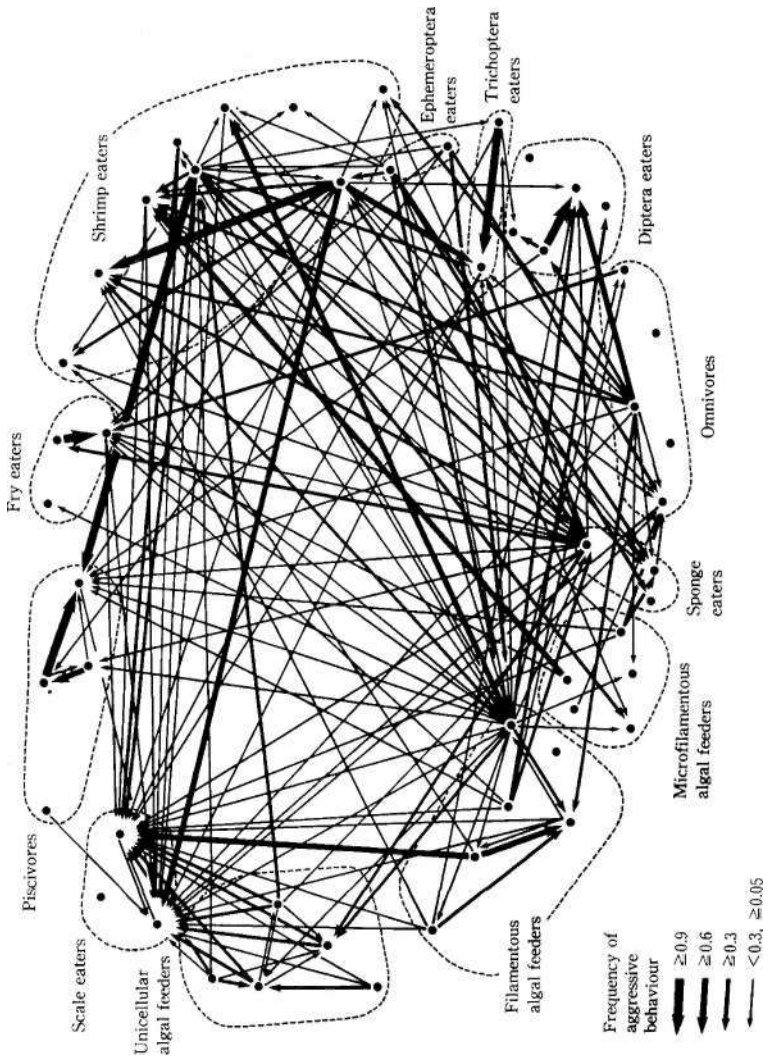


FIG. 3. The complexity of interactions between species (mainly cichlids) within and between food habit groups observed in the rocky littoral zone of central Lake Tanganyika. The dots within the circles defining each of the 12 food habit groups represent each fish species belonging to the group (for details, see Hori 1997). Reproduced with kind permission from Hori (1997).



Above: *Neolamprologus brichardi*, one of Lake Tanganyika's 250+ endemic cichlid species, a planktivorous substratum spawner. Below: *Haplochromis callipterus* from Lake Malawi, a mouth-brooding cichlid showing the male's 'egg-mimic' spots on the anal fin. (Photographs courtesy of P. A. Morris, *above*, and G. F. Turner, *below*)



Above: One of the world's largest cichlids - Lake Tanganyika's endemic *Boulengerochromis microlepis*, a substratum-spawning piscivore of which the juvenile stages live among water plants. Below: Endemic *Rhamphochromis* cichlid species from the open waters of Lake Malawi. (Photographs courtesy of P. A. Morris, above, and F. C. Roest, below)

found ca. 7000 individuals of ca. 38 species, mainly cichlids, packed at ca. 17 individuals m⁻². Renewed censuses here and at other sites showed that species numbers remained remarkably constant over ten years, although the same species were not always present. Analyses of distributions within the quadrats according to depth, substrate type and feeding habits, showed the presence of twelve feeding guilds: for example, 15 species of algal grazers (18% of total abundance) on rocks in shallow water, 8 species of zoobenthos-feeders (ca. 4%), 6 species of piscivores (ca. 4%), 2 species of planktivores living gregariously over rubble, and 7 species of omnivores. Each feeding guild at one site, composed of congeners and related genera, included species with similar food habits but which collected food by different foraging methods, showing how behaviour differences are of primary importance for coexistence (as discussed by Lowe-McConnell 1994b). For example, among 13 cohabiting lamprologine species - 7 benthivores, 4 piscivores and 2 planktivores - the predators utilising the same kinds of food items caught their prey by different hunting methods. Cases of commensalism which aided coexistence were also discovered. For example, among 18 cohabiting algivorous species, the filamentous algae-feeding *Tropheus moori* and unicellular-algal-feeding *Petrochromis polyodon* live in a symbiotic association as dominant species with overlapping feeding territories, tolerating one another but aggressive to other algivorous species.

In the very crowded littoral zone, breeding sites are a critical resource influencing mating and parental care systems. There is intense competition for breeding sites, both among mouth-brooders and substratum-spawning lamprologines. Removing territorial males showed sites are very species-specific (as has also been found in Lake Malawi), thereby reducing interspecific competition but leading to intense intraspecific competition. Many unusual breeding behaviours have evolved in Tanganyika (including 'sneaking' and 'floating' males), even 'farming out' broods with other species. Tanganyika is unique in having substratum-spawning cichlids (a third of its cichlid species) as well as mouth-brooders (as discussed further below) and also species showing intermediate types of parental care (Konings & Dieckhoff 1992; Kwanabe et al. 1997).

Lake Malawi: threats to biodiversity

The GEF/SADC Lake Malawi Biodiversity Conservation Project (1997-2000, funded primarily through the World Bank) was requested by the three riparian countries, Malawi, Tanzania and Mozambique, to develop a strategy for the conservation of biodiversity and sustainable use of the lake's resources, principally fishes. Directed by Tony Ribbink, this involved limnological, systematic, ecological and conservation work by

more than 30 scientists and technicians based at the Senga Bay headquarters. By mid-1999 well equipped laboratories had been set up in all three territories and the project had trained more than 50 people in environmental education, monitoring, development of databases and community programmes. Limnological work on lake and catchment was led by Harvey Bootsma and Bob Hecky, supported by the Canadian International Development Agency CIDA (Bootsma & Hecky 1998). Taxonomic studies by Jos Snoeks, Ben Ngatunga and team were used towards an interim identification guide to the fishes of Lake Malawi and a taxonomic revision (Snoeks, in prep.). GIS studies were run by the Canadian Centre for Earth Observational Sciences.

The team's research focussed on providing fisheries managers with the maximum amount of information on life histories of the main demersal cichlid species. The multi-authored *Fish Ecology Report* (Duponchelle & Ribbink 2000) was based mainly on data from June 1998-July 1999, with cooperation from the Malawi Fisheries Department and collaboration with the Ecology Team of the EU project on 'The Trophic Ecology of the Demersal Fish Community of Lake Malawi/Niassa' mentioned above (Irvine et al. 2002). The GEF/SADC Fish Ecology report discussed the project's response to the main threats to fish diversity, fishing activities and increasing loads of sediments and nutrients from agricultural activities in the lake basin. Changes in a multi-species community in response to fishing pressure, difficulties of managing a fishery based on several hundred species, and the role of sanctuaries in their conservation were described by Ribbink (1999), who has also discussed the lake's fisheries in a socio-economic context (Ribbink et al. 2001). Lake Malawi already has a National Park at Cape Maclear, gazetted in 1980 to 'preserve a sample of the Lake Malawi biome with particular reference to its rocky lake shore and its specialist cichlid communities'. Created a World Heritage Site by UNESCO, this includes an underwater nature trail which attracts tourists (Lewis et al. 1986).

Lake Victoria: response to Nile perch predation, refuges, effects of eutrophication

The changing ecosystem of Lake Victoria (Goldschmidt et al. 1993; Goldschmidt 1996; Witte et al. 1999; and Lowe-McConnell 1994a, 1996, 1997) has provided a large scale (though unintentional) experiment on the environmental factors affecting cichlid communities (Wanink & Witte 2000a) which has attracted a huge amount of research. To what extent was the loss of an estimated 200 species of endemic haplochromines due to *hates* predation, overfishing, or associated limnological changes, including eutrophication and deoxygenation of the bottom waters? Other species were



Lake Malawi. *Above:* The rocky shore at Cape Maclear, frequented by mbuna cichlids and now a World Heritage Site with an underwater nature trail. *Below:* A typical long sandy beach, used for the artisanal seine-net fishery, viewed from the Senga Bay laboratory headquarters from which the pelagic, benthic, and biodiversity surveys described in this article were made. (Photographs by R. Lowe-McConnell)



Above: Ring-netting in the open waters of Lake Malawi, removing the catch, mostly of pelagic cichlids, from the net. *Below:* Piles of cichlids, many new to science, from the *RV Ethelwynn Trewavas* experimental trawl catch off Monkey Bay, SE arm of Lake Malawi, in 1991. (Photographs courtesy of G. F. Turner, *above*, and M. E. Varley, *below*)



also affected, including tilapia (Goudswaard et al. 2002b) and lungfish (Goudswaard et al. 2002a).

In the 1990s HEST's research in Victoria's Tanzanian waters included a survey of littoral habitats, seemingly refuges from *hates* predation. Here, while sampling 36 new sites to study distributions of the remnant cichlid fauna, they discovered over a hundred undescribed cichlid species, two thirds of them from rocky shores (Seehausen et al. 1997b; Seehausen et al. 1998a). The clearer water round the rocks permitted SCUBA explorations of the ecology of these 'mbipi' cichlids, comparable with Lake Malawi's rock-dwelling 'mbuna' and the cichlids on Tanganyika's rocky shores, revealing most remarkable examples of parallel evolution in morphologies and life styles in the three lakes (Seehausen 1996, 1999).

These littoral faunas were being threatened by fishing practices (including use of fish poisons), invasion of water hyacinth (*Eichhornia crassipes*) and eutrophication, and since 1990 another 13 cichlid species have disappeared from littoral habitats, together with some from the upper littoral. However, on the deeper sub-littoral mud bottoms (sampled in 1987-1990: Witte et al., 1992), individual and species numbers increased (although nowhere near to levels found earlier in the 1980s before the upsurge of Nile perch, *Lates*). The interesting thing was how this sub-littoral fauna differed from the well-studied *pre-Lates* fauna. It was now dominated by previously unknown species (some possibly hybrids), and some known species had made dramatic habitat shifts (Seehausen et al. 1997b).

This led HEST into intensive research of why some species had recovered while comparable species had vanished, and an examination of factors leading to differential extinction (Witte et al. 2000). Predictions about survival and recovery had to take account of not only the effects of the decline in the now heavily-fished *Lates* populations, but also that surviving species were having to cope with other environmental changes since the late 1980s, with eutrophication, algal blooms, decreased water transparency and low oxygen concentrations. So HEST made a comparative study of a pair of related species, of which one had disappeared and the other survived, to try to identify what factors determined susceptibility to extinction.

The chosen pair (*H. heusinkveldi* which disappeared and *H. pyrrhocephalus* which recovered) were zooplanktivores which were morphologically similar except for male breeding colour and formerly had nearly identical distributions. A preliminary comparison suggested that differences in functional morphology of the visual apparatus and respiratory adaptations and/or aspects of their life history might be involved. HEST discovered marked differences in the retina of the eye between these two species, such that the survivor (*H. pyrrhocephalus*) was

likely to have a higher sensitivity to light (particularly red light) than the vanished species, having a retina structure which seemed advantageous for visual observation of prey, predators and mates in areas where eutrophication caused a decrease in light penetration. They suggested that this might also explain why spawning activities in the surviving species may have been less constrained by water transparency, as their earlier observations had shown that most haplochromines in the sublittoral area of the Mwanza Gulf spawn in the dry season when water transparency becomes temporarily high, whereas in the clear shallow waters of sandy and rocky habitats most species spawn throughout the year. Laboratory experiments confirmed that turbidity constrains colour vision and interferes with mate choice based on male colouration which maintains reproductive isolation between sympatric closely related species (Seehausen et al. 1997a, 1998b, 2003). Additionally, between 1978 and 1999 the average number of secondary gill lamellae in *H. pyrrhocephalus* (the survivor) increased by ca. 25%, possibly a response to increased hypoxia. This species also showed increased fecundity between 1983 and 1988. Furthermore, *H. pyrrhocephalus* had changed its feeding habits from zooplankton to eat more large prey, including shrimps, fish and even molluscs (Katunzi et al. 2003).

Rapid morphological changes in gill structure were later found in the small cyprinid dagaa (*Rastrineobola*) in this area (Wanink & Witte 2000b). These had shifted niche and increased greatly in numbers following the decline of the zooplanktivorous haplochromines, and were now supporting an important fishery. Would this be affected by the resurgence of the zooplanktivorous haplochromines, which had now become commoner here than detritivorous/phytoplanktivores (Wanink & Witte 2000a)?

LAKES AS LABORATORIES: CICHLID EVOLUTION

The endemic cichlid fish of Lakes Malawi, Tanganyika and Victoria are textbook examples of explosive speciation and adaptive radiation (Coulter 1994). To answer the question 'How many species of cichlid fishes are there in African lakes?', Turner reviewed discoveries of new species and flocks and appraised the evidence on species richness from recent studies of polymorphism and assortive mating, using behavioural and molecular methods (Turner et al. 2002). Many haplochromine taxa, including those which occur sympatrically and do not interbreed in nature, produce viable fertile hybrids in aquaria, and laboratory experiments indicate the importance of mate preference (mainly female choice of male colours) for speciation. Overall estimates of species numbers in Lake Malawi and Victoria are very dependent on the assigning of species status to allopatric populations differing in male colour. Testing their specific status is now in



Lake Victoria. Above: Preparing fishing gear at the Fisheries Research Laboratory, Jinja, Uganda (formerly the East African Fisheries Research Organization, EAFRO, later Uganda's Fisheries Resource Research Institute, FIRRI). Below: A lively fishing village near Kisumu, on the Kenyan waters of Lake Victoria. (Photographs by R. Lowe-McConnell, *above*, and F. C. Roest, *below*)



Above: Gillnets drying and fish being unloaded at an artisanal fishing beach near Kisumu on Lake Victoria. *Below:* A typical gillnet catch, mostly of introduced Nile tilapia (*Oreochromis niloticus*) and Nile perch (*Lates niloticus*), both species introduced into Lakes Victoria and Kyoga in the mid-1950s. (Photographs courtesy of F. C. Roest)

progress in aquaria at the University of Hull in collaboration with other institutions.

Origins and relationships of the cichlid flocks

Nishida's (1997) molecular phylogeny (Fig. 4) indicated that Tanganyika has half a dozen ancient cichlid lineages (derived from the Congo basin and not found in Lakes Malawi or Victoria), mostly corresponding with the tribes of Tanganyika cichlids proposed by Poll (1986). The implications of these lineages for the origin and evolution of the Tanganyika cichlid fauna suggest that Tanganyika's cichlids are a polyphyletic conglomerate with many ancestral lineages resulting from eight or so invasions into the lake or proto-lakes. The Lamprologini, the largest tribe (60+ very morphologically and ecologically diverse species), are all substratum-spawners. Groups that seem to have been relatively recent intruders into the Tanganyika basin, such as the Haplochromini and Tilapiini lineages, have radiated little in the lake, whereas most of the older lineages (except *Boulengerochromis*) have undergone extensive radiations. The old lineages Bathybatini, Trematocarini and *Boulengerochromis* have specialised for deep or open-water habitats, consistent with the hypothesis that they are long-standing lake inhabitants.

The interlacustrine difference in level of ecological diversification in the haplochromini assemblage in Lake Tanganyika, compared with those in Lake Victoria and Malawi, intrigued Nishida. In these other lakes almost all cichlids are haplochromines and they show a wide array of trophic radiation from algivory to piscivory, whereas the 'H-lineage' in Tanganyika has no piscivores (except the scale-eating Perissodini), the piscivores here being mainly lamprologines, bathybatines and *Boulengerochromis*. In spite of being the oldest of the three lakes (ca. 20 my), Tanganyika now has the least number of cichlid species (Table 1), possibly due to extinctions caused by successive encounters of different species assemblages which have radiated independently (in Lake Victoria the recent disappearance of many haplochromine cichlids following the introduction of predatory Nile perch *Lates* has demonstrated this process vividly). Nishida concluded that the mouth-brooding habit in the Tanganyikan cichlids must have arisen in four or five separate lineages from substrate-spawning lineages. Nearly two thirds of Tanganyika's cichlid species are mouth-brooders - a habit which appears to be a useful adaptation for the proliferation of cichlid species in lacustrine environments.

The genetic composition of different lineages varies greatly; Tanganyika's *Tropheus* lineage of six species was found to contain twice as much genetic variation as the entire morphologically highly diverse

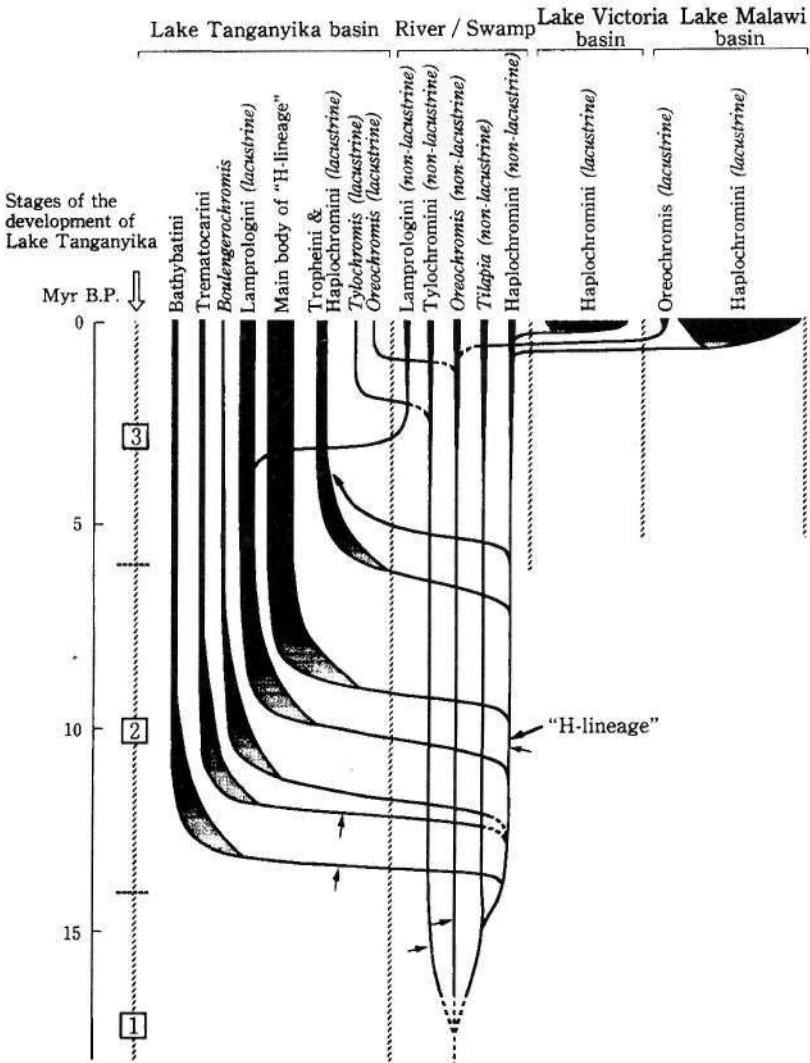


FIG. 4. A schematic representation of the evolutionary scenario of cichlid fishes in Lake Tanganyika and other East African waters on the basis of a synthesized phylogeny (for details, see Nishida 1997). Reproduced with kind permission from Nishida (1997).

Table 1. Indigenous fish species richness in East African lakes. Species numbers from Snoeks (2000). *Cichlids mostly haplochromines except in Tanganyika. ¹ denotes former drainage.

	Cichlid species*		Non-cichlid species		Estimated age of lake	Drainage
	No.	% endemic	No.	% endemic		
Tanganyika	250	98	75	59	20 my	Congo
Malawi	ca. 800	99	45	29	ca. 2 my	Zambesi
Victoria	ca. 500	99	45	16	400 000 y refilled 14 600 y	Nile
Edward/George	60	92	21	5		Nile
Albert	11	36	37	5		Nile
Turkana (Rudolf)	8	50	36	17		(Nile) [†]

cichlid lineage of L. Malawi, and six times more variation than the L. Victoria flock. But although highly variable in colouration, the *Tropheus* group has not undergone appreciable morphological change (Snoeks et al. 1994)

Mitochondrial DNA studies of the phylogeny of the Tanganyika flock and its relationship with other Central and East African cichlid faunas have excited other groups of biologists (Meyer 1993). Salzburger et al. (2002) found that all the haplochromines that they analysed from surrounding rivers and lakes seem to have evolved within the radiating Tanganyikan lineages and then secondarily colonised surrounding rivers and other lakes (though some may have evolved in the Tanganyika basin before the lake became a hydrologically and ecologically closed system). They therefore suggested that the current diversity of Central and East African haplochromines represents a relatively young and polyphyletic fauna that evolved from, or parallel to, lineages now endemic to Lake Tanganyika.

For Lake Malawi haplochromines, mitochondrial DNA studies suggested that, in addition to the two major mbuna and non-mbuna groups, *Rhamphochromis*, *Diplotaxodon*, *Copadichromis mloto* and *Astatotilapia calliptera* appear to be separate lineages (in addition to *Serranochromis robustus* and the tilapia lineages in this lake). The *Rhamphochromis* lineage appears to be more basal than *A. calliptera* (formerly believed to be the most basic). The mbuna group appeared to be paraphyletic, and the *Copadochromis* genus polyphyletic and in need of taxonomic revision (Meyer et al. 1996).

For the Lake Victoria species flock, Seehausen et al. (2002), using nuclear DNA instead of mitochondrial DNA and with a wider coverage of riverine species for analyses of the Lake Victoria-Edward flocks, concluded that these haplochromines revealed unexpected genetic variation

and had a Congolese-Nilotic origin, derived from the morphologically and ecologically diverse *Thoracochromis* from the Congo and Nile (and not from the phenotypically conservative East African *Astatotilapia* as formerly believed). This implied that the ability to express much of the morphological diversity found in the Lake Victoria flock may long predate the origin of the flock, and that its diversity is considerably older than the 15 000 years since Lake Victoria started to refill. Their data did not confirm strict monophyly of either Victoria or Malawi species flocks, and raised the possibility that the flocks may have arisen from hybrid swarms (now under investigation).

In the mid 1990s, bottom cores from deep waters indicated that Lake Victoria had virtually 'dried up' about 14 700 years ago, suggesting that its spectacular flock of ca. 500 haplochromine species had evolved at an unprecedentedly fast rate (Johnson et al. 1996). Fryer (2001) questioned the complete drying up, suggesting from non-cichlid evidence that some swampy lake areas probably persisted (as found in the Bangweulu swamps). But Seehausen's (2002) analysis of speciation rates concluded that the patterns of fish radiation in Victoria are compatible with the Pleistocene desiccation and 14 600 year history for its cichlid species flock. Recolonization would probably have come through interconnecting channels from the deeper Lake Edward lying in the western Rift Valley.

The origin, age and mechanism of diversification of Lake Victoria's species-flock is still being debated. Adopting a comprehensive phylogeographic approach - with phylogenetic analyses of ca. 300 mitochondrial DNA sequences of East African cichlids from waters of the East Coast ichthyological region, taken to include Lakes Victoria, Edward, George and also Kivu - Verheyen et al. (2003) concluded that the Lake Victoria cichlid flock was derived from the geologically older Lake Kivu (Kivu drained northwards before the formation of the Virunga Volcanoes reversed its drainage to Lake Tanganyika). They suggest two seeding lineages may have already been lake-adapted when they colonised Lake Victoria. They also consider that the most recent desiccation of Lake Victoria did not lead to complete extinction of the endemic cichlid fauna and that the major lineage diversification took place ca. 100 000 years ago. The molecular clock used suggested that the vicariance event that split the Lake Victoria and Lake Kivu faunas must have occurred less than 41 500 to 30 500 years ago (an age estimate that they stated fell within the range of the highest geological estimates for the eruption of the Virunga Volcanoes that separated Lake Kivu from the northern Rift Valley lakes; but these volcanoes are now reliably estimated at 200 000 years old or older - see Rogers et al. 1998). As they pointed out, closely related lineages will not necessarily have similar speciation rates, and it appears that the youngest and largest basin, Lake Victoria, provided more

opportunities that facilitated speciation. If descendents of Kivu haplochromines colonized Lake Victoria, this idea parallels the idea that descendents of Lake Tanganyika cichlids appear to have colonized river systems and other lakes; both these deep lakes acting as evolutionary reservoirs because of their relative stability, conserving lineages that seeded the neighbouring rivers and lakes at a later time. Based on phylogenetic criteria these two lake faunas should be given a high priority in conservation programmes.

Kocher (2003), commenting on the above papers, has drawn attention to differences between gene trees and species trees, and stresses that these African lake cichlids still represent the fastest known rate of vertebrate speciation, whether they shared an ancestor 10 000 or 100 000 years ago. As Kaufman (2003) puts it, the complexity of these high-diversity biotas has developed in two interacting ways. Multiple invasions contribute composite biota, while reiterative evolutionary bursts within clades over time produce manifold species flocks that sum surviving taxa over successive radiations. Lake Victoria's haplochromines are a manifold species flock, closely related phylogenetically to what may be a simple flock in Lake Kivu, a manifold flock in Lake Edward, and a subassemblage of Victorian species in Kyoga. The Lake Tanganyika fish fauna has examples of both manifold evolution and development of a composite biota. Reality is probably much more complex than one would imagine from prevailing publications.

Mechanisms of cichlid speciation

Based on SCUBA studies in Lake Malawi, the stenotopic and philopatric characteristics of the rocky shore cichlids (mbuna) led to the development of intralacustrine allopatric speciation explanations. But it is more difficult to see how such explanations apply to the very numerous non-mbuna species living sympatrically over the soft bottoms without obvious barriers to distribution, and to the pelagic species recently discovered in the open lake (Turner 1994a, 1999, 2000).

Diversification of trophic structures and behaviour has promoted the co-existence of sympatric species (as so amply demonstrated by the Japanese-led SCUBA teams working in Lake Tanganyika), but Turner argued that trophic diversification is unlikely to have played a significant role in speciation. Many sibling species do, however, differ in male colour and form of display structures (platforms, bowers), which suggests that sexual selection, through female mate choice, may have played an important role in speciation, a mechanism that could operate in both sympatric and allopatric models (Seehausen & van Alphen 1998; Seehausen 2000). Laboratory experiments on mate selection are progressing well at Hull

University (UK) using Malawi and Victoria cichlids with polymorphic male colour forms (Turner & Seehausen, personal communication).

Progress on two long-standing issues: niche overlap and sympatric speciation?

Niche overlap ?

Over fifty years the question of how the co-habiting, closely related cichlid species on the rocky shores in each of the three lakes seemingly contradict Gause's edict (that closely related species cannot continue to coexist sympatrically) has attracted numerous studies on resource partitioning. First interpreted in terms of trophic overlaps - e.g. among the algal-grazing rock-dwelling cichlids in Lake Malawi, where in addition to SCUBA behaviour observations and stomach content analyses, increasingly sophisticated approaches include isotopic signatures (Bootsma et al. 1996) - these studies have indicated that some species do share the same food resource (Genner et al. 1999a). Cichlids are, however, flexible in behaviour, being able to change foods according to resource abundance (see Seehausen & Bouton 1997; Katunzi et al. 2003); and slight differences in preferences may have been of use in the past (see Kuusipalo 2000). The Japanese SCUBA observations in Lake Tanganyika have shown that breeding sites, rather than food, may be limiting for many littoral cichlids (both among substratum-spawners and some mouth brooders), and for some species they found interactions between territoriality for food resources and breeding sites.

In Lake Victoria, the HEST group looked at resource partitioning in relation to differences in available resources on neighbouring small rocky islands. Diets were most diverse in the assemblage with the lowest density, though in this particular assemblage factors other than competition for food were probably more important in regulating density (Bouton et al. 1997). They also examined fluctuations in diet overlap in relation to seasonal changes in food supply and found overlap to be highest in periods of food abundance. HEST also tested to what extent island populations of three *Neochromis* species appear anatomically adapted to exploit locally abundant resources (Bouton et al. 1999), followed by experimental evidence for adaptive phenotypic plasticity in response to different foods (Bouton et al. 2002).

Sympatric speciation ?

Microallopatric speciation has long been held to account for speciation among the rock-dwelling mbuna of Lake Malawi, but for open-water species and demersal dwellers over soft bottoms, seemingly without

barriers, this has presented a problem (Turner 1994a). The alternative possibility of sympatric speciation has long been discussed (and derided by Barlow 2000, reviewed by Lowe-McConnell 2002). DNA studies of population structure have now indicated sympatric speciation of some pelagic cichlids in Lake Malawi (Shaw et al. 2000). Furthermore, the laboratory evidence of mate selection by female cichlids, in species from Lake Malawi and Lake Victoria, now provides a mechanism whereby sympatric speciation can explain the rapid speciation in many of these endemic cichlids (Seehausen & van Alphen 1999; Seehausen et al. 1999; Turner & Seehausen, personal communication).

CONCLUSIONS

For the impressive international investment in these large projects on all three African great lakes, what has been achieved? We now know that stocks of the main commercial fish species have declined markedly in all three lakes, basically due to anthropogenic threats caused by the steep rise in human populations which have led to overfishing and changes in land use in the lake basins, causing eutrophication, sedimentation and pollution. The industrial fisheries have declined, though artisanal fisheries have continued to grow. In Lake Malawi a whole new suite of pelagic cichlids has been discovered in the open waters, the last as yet unexploited resource in this lake. In Lake Victoria the fisheries that were rejuvenated by the introduction of exotic Nile perch, producing valuable exports for the riparian countries, are now perilously near to collapse. In addition to practical and scientific results all the projects have been of high educational value, particularly in training indigenous fishery biologists to continue the research and survey work on sound lines.

We now have a much better understanding of the biological events controlling fish production in these lakes, and know that conditions are very dynamic. In Lake Tanganyika, in addition to overfishing, changes in catch rates of pelagic fish seem to be environmentally driven by events outside the lake system, which complicates predictions of future catches. But it is clear that in all the lakes socio-economic and political conditions in the riparian countries will probably have the decisive role in the sustainability of the fisheries, and that community co-management is vital for any fishery management measures. The decision to try to manage the lakes in a way that maximizes yields or profits is essentially political.

The biodiversity survey of Lake Tanganyika amassed a huge database and mapped underwater areas for its management plan, based on extending protected areas into the lake from the existing land-based National Parks. Malawi's biodiversity survey paid particular attention to the effects of land use in the lake basin; and for Lake Malawi we also have a study of the

trophic ecology of the demersal fish community. In Lake Victoria, a suite of a hundred previously unknown cichlid species, comparable to the mbuna cichlids in Lake Malawi, have been discovered in rocky shore refuges. The Lake Victoria fisheries survey found reasons for the probable imminent decline of the Nile perch fishery, which has become so important for the economies of the riparian countries. What can be done to halt this decline? The resurgence of some indigenous fishes has stressed the urgent need to conserve stocks of these in some protected areas of the lake, so that further resurgence can occur as the Nile perch population declines.

Of greater (worldwide) significance, the huge scientific value of these lakes as laboratories, offering unique opportunities to study evolutionary processes, has been most amply demonstrated. Scientists from numerous international institutions have cooperated with local personnel, leading to considerable advances in understanding the origins and mechanisms of evolution of the unique cichlid species flocks and of how they continue to coexist in such very complex communities. But there is still a great deal of work left to do.

Acknowledgements

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Appendix: projects and symposia

Lake Tanganyika

- 1992-1998 FAO/FINNIDA: Lake Tanganyika Research Project (LTR).
Production and Potential for Optimal Management of Pelagic Fisheries.
References: Molsa (1995); Lindqvist et al. (1999).
- 1995-2000 UNDP/GEF: Lake Tanganyika Biodiversity Project (LTBP).
Pollution Control and other Measures to Protect Biodiversity.
References: Allison et al. (2000); West (2001).
- 1977-ongoing, Japan: Ecology and Behaviour of Littoral Cichlid Fishes.
Japanese/African SCUBA observations.
References: Kawanabe et al. (1992); Kawanabe et al. (1997).

Lake Malawi

- 1990-1995 UK/SADC: The Fishery Potential and Productivity of the
Pelagic Zone of Lake Malawi/Niassa.
Reference: Menz (1995).
- 1997-2000 SADC/GEF: Lake Malawi/Nyasa Biodiversity Conservation
Project. Conservation of biodiversity and sustainable use of resources.
References: Bootsma & Hecky (1998); Duponchelle & Ribbink (2000);
Ribbink et al. (2001).
- 1998-2002 EU: The Trophic Ecology of the Demersal Fish Community of
Lake Malawi/Niassa. INCO-DC: International Cooperation with
Developing Countries.
References: Irvine et al. (2002) (coordinator, Trinity College Dublin);
Buat et al. (2002).

Lake Victoria

- 1995-2001 EU: Lake Victoria Fisheries Research Project (LVFRP).
Fisheries, socio-economic research and management plan.
References: Final Report (LVFRP 2001); Lake Victoria Management
Plan (Bwathondi et al. 2001); van der Knapp et al. (2002).
- 1977-ongoing, University of Leiden Haplochromis Ecology Survey Team
(HEST):
Effects of introduced Nile perch on cichlid ecology (Tanzanian waters).
References: numerous papers in scientific journals (see et al. 1992,
1999,2000)

Symposia which included African Great Lakes

- 1989 SIL Symposium on Resource Use and Conservation of the African Great Lakes, Bujumbura.
Reference: Lowe-McConnell et al. (1992).
- 1991 Limnology and Fisheries of Lake Tanganyika, Burundi.
Reference: Cohen (1991).
- 1992 The Impact of Species Changes in African Lakes, London.
Reference: Pitcher & Hart (1995).
- 1992 Biodiversity, Fisheries and the Future of Lake Victoria, Jinja, Uganda.
Reference: Kaufman (1992).
- 1993 International Decade of East African Lakes (IDEAL).
Limnology, Climatology and Paleoclimatology of the East African Lakes, Jinja, Uganda.
Reference: Johnson & Odada (1996).
- 1993 Speciation in Ancient Lakes (SIAL), Belgium.
Reference: *Archiv für Hydrobiologie* 44, 1994, eds K. Martens, B. Goddeeris & G. Coulter, 508 pp.
- 1993 PARADI. Biological Diversity of African Fresh- and Brackish Water Fishes, Senegal.
Reference: Teugals et al. (1994).
- 1995 Lake Tanganyika Research, Kuopio, Finland.
Reference: Molsa (1995), Abstracts.
- 1997 International Conference on Ancient Lakes (ICAL), Lake Biwa, Japan.
References: 'Ancient lakes their cultural and biological diversity' (Kawanabe et al. 1999); 'Ancient lakes: biodiversity, ecology & evolution' (*Advances in Ecological Research* 31, 2000, eds A. Rossiter & H. Kawanabe, Academic Press, London, 624 pp.).
- 1998 PARADI/FISA African Fish and Fisheries-Diversity and Utilization, Grahamstown, South Africa.
Reference: Skelton & Teugels (2001).
- 2000 GLOW II Great Lakes of the World, Sustainability: Research, Monitoring and Management, Sligo, Ireland.
Reference: Papers in *Aquatic Ecosystem Health & Management* 5 (3), 2002, by Allison; Buat et al.; Darwell & Allison; Langenberg et al.; Molsa et al.; Sarvala et al.; van der Knapp et al.

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Lake Victoria

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Symposia which included African Great Lakes

- 1989 SIL Symposium on Resource Use and Conservation of the African Great Lakes, Bujumbura.
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