Biodiversity and Fishery Sustainability in the Lake Victoria Basin: An Unexpected Marriage?

JOHN S. BALIRWA, COLIN A. CHAPMAN, LAUREN J. CHAPMAN, IAN G. COWX, KIM GEHEB, LES KAUFMAN, ROSEMARY H. LOWE-McCONNELL, OLE SEEHAUSEN, JAN H. WANINK, ROBIN L. WELCOMME, AND FRANS WITTE

Lake Victoria is Africa's single most important source of inland fishery production. After it was initially fished down in the first half of the 20th century, Lake Victoria became home to a series of introduced food fishes, culminating in the eventual demographic dominance of the Nile perch, Lates niloticus. *Simultaneously with the changes in fish stocks, Lake Victoria experienced dramatic changes in its ecology. The lake fishery during most of the 20th century was a multispecies fishery resting on a diverse lake ecosystem, in which native food fishes were targeted. The lake ended the century with a much more productive fishery, but one in which three species—two of them introduced—made up the majority of the catch. Although many fish stocks in Lake Victoria had declined before the expansion of the Nile perch population, a dramatic increase in the population size of Nile perch in the 1980s roughly coincided with the drastic decline or disappearance of many indigenous species. Now, two decades after the rise of Nile perch in Lake Victoria, this species has shown signs of being overfished, and some of the native species that were in retreat—or even thought extinct—are now reemerging. Data on the resurgence of the indigenous species suggest that heavy fishing of Nile perch may enhance biodiversity; this has spawned renewed interest in management options that promote both fishery sustainability and biodiversity conservation.*

Keywords: aquatic conservation, East Africa, Nile perch, haplochromine cichlids, tropical fisheries

Overfishing, environmental degradation, and re-distribution of surface water have placed great stress on inland fisheries throughout the world. Human activities usually shift the balance among fish species, causing the extirpation of many indigenous species and the dominance of a reduced set of often introduced fish species. The result has been a massive reshaping of fish communities in the world's fresh waters over the past few centuries, with the pace of change quickening of late in the tropics.

It has been known for some time that fishes react to environmental degradation and fishing pressures with a characteristic series of changes. If too much of the brood stock is caught, fewer and fewer recruits appear in the population in succeeding years. This is called *recruitment overfishing*. The impact is somewhat different if the large fish in a population are taken first, then smaller ones, and so on. The mean size of individuals drops, and there is selection for individuals that mature at a smaller and less fecund size. This is *growth overfishing*. Each of these phenomena has a counterpart corresponding to effects that become apparent when more than one species or stock is taken into consideration.

Three decades ago, Regier and Loftus (1972) observed a multispecies analog to growth overfishing while they were researching the anthropogenic transformation of fish communities in the Great Lakes of North America. What they described—the successive removal of the largest-bodied species—was later generalized (Regier and Henderson 1973, Welcomme 1995) and has been called the "fishing-down

John S. Balirwa is acting director of the Fisheries Resources Research Institute of Uganda, Box 343, Jinja, Uganda. Colin A. Chapman and Lauren J. Chapman (e-mail: lchapman@zoo.ufl.edu) are associate professors in the Department of Zoology, University of Florida, Gainesville, FL 32611, and associate scientists at the Wildlife Conservation Society, 185th Street and Southern Boulevard, Bronx, NY 10460. Ian G. Cowx is director of the University of Hull International Fisheries Institute, Hull, HU6 7RX, United Kingdom. Kim Geheb was a member of the Lake Victoria Fisheries Research Project and is currently a natural resources management consultant, PO Box 581, Nairobi 00502, Kenya. Les Kaufman is a professor in the Department of Biology at Boston University, 5 Cummington Street, Boston, MA 02215. Rosemary H. Lowe-McConnell was a research associate of the British Museum of Natural History when this article was prepared; her current address is Streatwick, Streat near Hassocks, Sussex, BN6 8RT, United Kingdom. Ole Seehausen is a lecturer in the Department of Biological Sciences, University of Hull, Hull, HU6 7RX, United Kingdom. Jan H. Wanink is a member of the Haplochromis Ecology Survey Team (HEST), a guest researcher at the Institute of Biology, University of Leiden, and an ecology project leader at Koeman en Bijkerk BV, Ecological Research and Consultancy, PO Box 14, 9750 AA Haren, The Netherlands. Robin L. Welcomme was formerly chief of FAO's (Food and Agriculture Organization of the United Nations) Inland Water Resources Assessment and Aquaculture Service and is now a principal research fellow in the Department of Environmental Science and Technology, Imperial College, 8 Princess Gate, London, SW7 2Q2, United Kingdom. Frans Witte is coordinator of HEST and a lecturer at the Institute of Biology, University of Leiden, PO Box 9516 , 2300 RA Leiden, The Netherlands.

process." Greater fishing pressure can initially bring about a higher catch, followed by a plateau over a range of increasing exploitation as component fish stocks are serially depleted. First large, and then successively smaller, species are removed and their places taken by even smaller and faster-growing ones, producing an illusion of sustained productivity that conceals deep changes in community and food web structure. Eventually there are no more economically exploitable stocks, and both the fishery and the fish community collapse or are changed beyond recognition (Welcomme 1995, 2003).

In Africa, overfishing is a recurrent problem closely tied to environmental conditions. Africa has suffered food crises for decades, exacerbated in the Sahelian zones by prolonged drought through the late 1970s and the 1980s. When severe drought compromises production of livestock, rural communities turn to hunting and fishing to satisfy their protein needs. What worked for a long time when people were relatively few can have quite different impacts on wildlife at the currently very high human population densities. Thus, food crises, together with a political orientation of open access to wild resources such as fish, have led to a rapid increase in fishing pressure. This effect is further compounded by the rapid improvement and dissemination of fishing technologies. For example, in the central delta of the Niger the number of fishers increased from 43,000 in 1966 to 63,000 in 1989; over a similar period (1968 to 1989), the fish landings declined from 90,000 to 45,000 metric tons (Lae 1995). The number of fishers in the Oueme Delta fishery in Benin rose from about 29,000 in 1958 to 34,500 in 1969 (Welcomme 2003). In these systems, a decline in fish yields was accompanied by a marked shift in catch composition toward individuals and species that mature at a very small size or age (Welcomme 2003).

In fresh waters, where community overfishing often sets in very quickly, ecologists and land managers have long known that things are going from bad to worse, and practical strategies for making fisheries sustainable have been considered of paramount importance for some time. Some freshwater systems have already been through one or more cycles of overfishing, extirpations, introductions, and explosive production of introduced species, leading into a new round of overfishing. Careful study of such examples may lead to useful and generalizable inferences.

Lake Victoria, a lake the size of Ireland, is the African continent's single most important source of inland fishery production. After it was initially fished down in the early part of the 20th century, Lake Victoria became home to a number of introduced food fishes, culminating in the eventual dominance of the Nile perch, *Lates niloticus* (Ogutu-Ohwayo 1990). The rise of Nile perch was associated with dramatic changes in Lake Victoria's ecology. The lake fishery during most of the 20th century was a multispecies fishery resting on a diverse lake ecosystem, in which native food fishes were eagerly sought. The lake ended the century with a much more productive fishery, but one in which three species, two of them introduced, made up most of the catch. The recent history of Lake Victoria was considered to represent one of the most extreme cases of mass extinction documented this century (Kaufman 1992, Witte et al. 1992a, 1992b). Now, two decades after the rise of Nile perch to ecological dominance in Lake Victoria, the invading species is showing signs of being overfished (LVFRP 2001, Cowx et al. 2003), and some of the native species that were in retreat—or even thought extinct—are now reemerging (Seehausen et al. 1997a, Witte et al. 2000). In this article, we provide a description of the changes to the Lake Victoria system, consider agents responsible for driving the changes, and summarize management options that may favor both the maintenance of biodiversity and a sustainable fishery in Lake Victoria.

History of biodiversity loss and change in functional relationships in Lake Victoria

Lake Victoria is the largest tropical lake in the world (68,000 square kilometers), with its waters shared by three countries (Tanzania, 51%; Uganda, 43%; Kenya, 6%). However, the lake is best known to scientists for its more than 600 endemic species of haplochromine cichlids (figure 1a, 1b), representing one of the most rapid, extensive, and recent radiations of vertebrates known (Greenwood 1974, Kaufman 1992, Seehausen 1996, Kaufman et al. 1997). In addition, a rich assemblage of noncichlids inhabits the basin. At the beginning of the 20th century, the lake was sparsely fished with a variety of simple traditional methods (Graham 1929). Human occupancy was relatively low, much of the shoreline was covered in riparian forest (though there was apparently an earlier epoch of deforestation), and there were extensive riparian wetlands.Toward the close of the century, the lake supported an intensive fishery, human occupancy of the basin greatly accelerated, the shoreline was denuded of trees, and many of the wetlands were converted for agriculture (Balirwa 1998). The fish stocks of the lake were subjected to three major series of events: (1) Fishing intensified over the century, associated with new technologies (e.g., commercially produced, artificial-fiber nets; outboard motors; increasingly destructive fishing gear), diversification of markets (especially the export of Nile perch), and increased numbers of fishers. (2) The introduction of nonindigenous fishes influenced community composition and functional relationships in the lake. (3) Increased human population density and its consequences—agricultural and industrial activity, change in fish composition, and shoreline deforestation—all contributed to a change in lake trophic state from mesotrophic to eutrophic (Hecky 1993).

As a consequence of these events, a diverse fishery that exploited several native species changed to one in which three species—two of them introduced—make up almost the whole catch (Ogutu-Ohwayo 1990, Kaufman 1992). This extremely dynamic situation has developed further: The introduced Nile perch is showing signs of overexploitation, and a subset of the basin fauna is reemerging. We consider each of these interacting events in turn and explore management

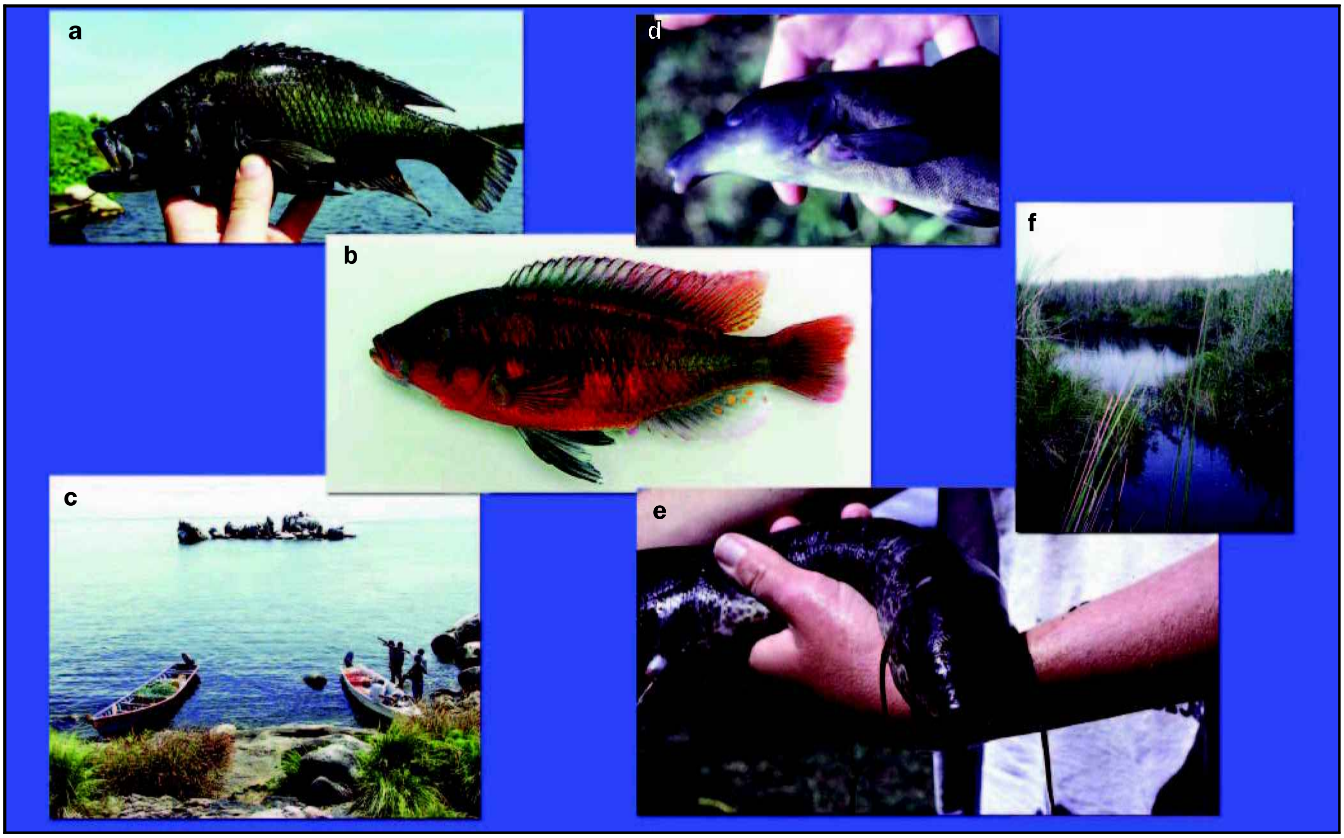

Figure 1. (a) More than 100 endemic species of large piscivorous haplochromine cichlids are known from Lake Victoria. Most of them vanished at about the time Nile perch increased. Today rocky reefs and islands serve as refugia for a few of these magnificent species. (b) This undescribed **Paralabidochromis** *species is one of more than 100 stenotopic cichlid species that are specialized for living over rocky bottoms. (c) Where the water is still clear, rocky habitats in Lake Victoria still harbor a large diversity of endemic cichlids, consisting of habitat specialists and of generalists that survive only in rocky refugia. However, species diversity is strongly correlated with water clarity and is poor where water is murky. (d) The elephant-nose fish* **Mormyrus kannume** *is one of over 200 species of mormyrids, a family well known for their remarkable electrogenic and electoreceptive capabilities. This species suffered a dramatic decline in Lake Victoria but has been recently showing signs of resurgence, particularly in the Napoleon Gulf area of Uganda. (e) The African lungfish,* **Protopterus aethiopicus,** *known for its primitive lungs and reliance on atmospheric air, was an important component of the pre–Nile perch fishery, particularly after the collapse of the* **Oreochromis esculentus** *stock in the early 1970s. The dramatic decline of lungfish in the 1970s and 1980s may reflect the interaction of fishery overexploitation; Nile perch predation (albeit at a low level) that restricts lungfish to wetland refugia; large-scale conversion of wetlands to agricultural land; and harvesting of nest-guarding male lungfish, which leads to decreased recruitment of young. (f) Wetlands serve as refugia from Nile perch predation for a number of species.*

options that reconcile sustainability of fisheries with conservation of biodiversity.

Fishing

Fishing accelerated over the 20th century; by the 1950s and 1960s, there was alarming evidence that most large species were overexploited (Graham 1929, Ogutu-Ohwayo 1990). In 1957, *Oreochromis esculentus* dominated the fish catch at the Lake Victoria Fisheries Service recording stations in Kenya (46.7% of the catch by number) and in Uganda (52.5% of the catch; table 1); it is a highly palatable suspension and suspension-deposit feeder that masses in open waters just offshore. *Oreochromis variabilis,* a more littoral species that is also endemic to the region, was abundant at the stations in Kenya (14.9%) and Uganda (20.2%) as well. In Tanzania, the anadromous carp-like fish *Labeo victorianus,* the large catfish *Bagrus docmak,* and *O. esculentus* dominated the catch (table 1). However, by the 1970s, catches by mass of several species, including *O. esculentus, O. variabilis, Labeo victorianus, B. docmak,* and *Mormyrus kannume* (a large elephant-nose fish that feeds on insect larvae on muddy bottoms; figure 1d), had fallen dramatically (figure 2, table 2; Kudhongania and Cordone 1974, Goudswaard et al. 2002a). Catches of the African lungfish *Protopterus aethiopicus* (figure 1e) also showed local declines (figure 2; Kudhongania and Cordone 1974, Goudswaard et al. 2002b). By the late 1960s,

Table 1. Annual summary of fish species found in landings (gill net data) for Lake Victoria at recording stations in Kenya, Uganda, and Tanzania in 1957.

	Percentage of total catch (by number)		
Species	**Kenya (7 stations)**	**Uganda (10 stations)**	**Tanzania (16 stations)**
Oreochromis esculentus	46.7	52.5	18.0
Oreochromis variabilis	14.9	20.2	3.9
Haplochromines	2.6	1.9	12.7
Labeo victorianus	14.7	2.4	31.9
Bagrus docmak	8.0	9.0	15.9
Barbus altianalis radcliffi	1.5	1.3	0.5
Mormyrus spp.	6.0	3.7	3.3
Clarias gariepinus	1.5	1.8	0.9
Schilbe intermedius	2.4	0.2	4.7
Brycinus jacksonii	1.1	5.8	2.6
Synodontis spp.	0.1	0.2	4.8
Protopterus aethiopicus	0.5	1.0	0.5
Other species	0.0	0.0	0.2

Source: LVFS 1958.

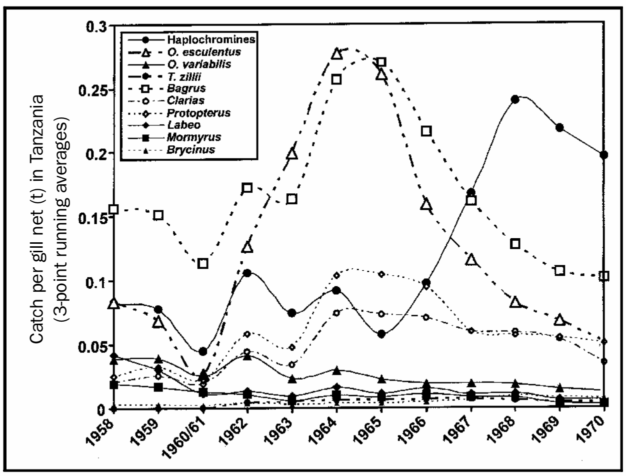

Figure 2. Fish catch per gill net (metric tons) in the Tanzanian waters of Lake Victoria (1958 to 1970). Data are expressed as three-point running averages and were derived from a compilation of annual commercial landings in Kudhongania and Cordone (1974).

haplochromines constituted an important component of the Tanzanian fishery (figures 2, 3); however, even there, intensive trawl fishing reduced local stocks (Witte et al. 1992b). In Kenya, haplochromines were also an important component of the fishery in the mid- to late 1970s (figure 3), while in Uganda *B. docmak* was the most heavily harvested species during this period (figure 4). In addition to fisheries within the main lake, fisheries in the rivers for high-value species, such as *Labeo victorianus,* resulted in the fishes' near-disappearance in the 1960s (Cadwalladr 1965).

We argue that the changes in the Lake Victoria fish stocks between 1950 and 1980 conform to the "fishing-down" model. In Kenya and Tanzania, the fishery was characterized by a drift to what were then the smallest species: the haplochromine cichlids and *Rastrineobola argentea* (figures 2, 3). In Uganda, the fishing-down process was also evident; the sequence of change for key taxa is illustrated in figure 4. The decline in the landings of tilapiines (representing primarily native *O. esculentus* and *O. variabilis* stock) in the late 1960s coincided with increased fishing pressure and catch of newly preferred taxa, including the two large catfishes *B. docmak* and *Clarias gariepinus,* the African lungfish *P. aethiopicus,* and haplochromine cichlids (table 2, figure 4). This was followed by a major fishing-down sequence in late 1960s (Tanzania) and 1970s (Uganda) that was characterized by a dramatic decline in tilapia, sharply followed by a decline in the large catfishes *(Bagrus, Clarias)* and lungfish and an increase in smaller taxa, including haplochromines, characids, and synodontid catfishes (table 2, figures 2, 4).

The fishing-down sequence in Tanzanian and Ugandan waters was initially not based on size; rather, it represented a shift to other preferred large species (e.g., the large catfishes and lungfish). Nonetheless, it demonstrates a general shift in fishing pressure to sequentially less-preferred stocks. The fishing-down sequence also correlates in a general way with characteristics of the species' life history. For example, the larger catfishes, *Bagrus* and *Clarias,* have a lower reproductive load (length at first maturity divided by asymptotic [maximum] length; 0.52 and 0.51, respectively), a lower growth coefficient (0.22), and a higher age at maturity (3.6 and 6.5 years, respectively) than the synodontid catfishes (reproductive load 0.58) and haplochromine cichlids (reproductive load about 0.62, growth coefficient about 1, age at maturity 0.5 to 1 year; Froese and Pauly 2000, Wanink and Witte 2000a). The close resemblance of the sequence of events resulting from fishing down in Tanzania and in Uganda, despite a 10-year difference between them, is remarkable. It should be noted that this analysis of fishery shifts is based on landing statistics that are likely to reflect not only changes in absolute abundance of taxa but also changes in gears, fishing effort (corrected for in the Tanzanian data set), and target species.

Introduction of nonindigenous fishes

The Nile perch, a large centropomid piscivore that can reach over 2 meters (m) in length, was introduced into Lake Victoria from Lakes Albert and Turkana during the 1950s and 1960s to compensate for depleting commercial fisheries by converting low-value haplochromines into higher-value and more easily captured fish (Fryer 1960, Ogutu-Ohwayo 1990, 1993, Witte et al. 1999). Although many fish stocks in Lake Victoria had declined before the expansion of the Nile perch population (figures 2, 3, 4), a dramatic increase in the stock size of Nile perch in the 1980s roughly coincided with a drastic decline in populations of many indigenous species (table 2, figure 3; Ogutu-Ohwayo 1990, Kaufman 1992, Witte et al. 1992a, 1992b, Kaufman et al. 1997). Particularly devastating was the disappearance of more than 50% of the nonlittoral haplochromine cichlids (figure 1a, 1b), or about 40% of the endemic haplochromine community (Kaufman 1992, Witte et al. 1992b, Kaufman and Ochumba 1993, Seehausen et al. 1997a). Several noncichlids, some of which were important in the pre–Nile perch fishery, also declined or disappeared (table 2). The Nile perch seems to have been a key contributor to the apparent mass extinction (table 2; Ogutu-Ohwayo 1990, Witte et al. 1992a, 1992b), although other perturbations to the system must also have significantly contributed to the decline (see "Environmental change," below). In the 1969–1970 trawl survey of Kudhongania and Cordone (1974), haplochromine cichlids contributed an estimated 83% of the biomass and Nile perch less than 0.5%. By 1983 in Kenya and by 1987 in Tanzania, the situation had reversed: Nile perch constituted more than 80% of the catch (Kaufman 1992, Witte et al. 1999). Changes in assemblage structure have produced major changes in the food web and functional roles of particular species. For example, before the increase in Nile perch, zooplanktivorous haplochromines represented more than 25% of the catch of commercial bottom trawlers in sublittoral areas of Mwanza Gulf (Goldschmidt et al. 1993). By the late 1980s, *R. argentea* was the only indigenous zooplanktivore still abundant and had shown a surprising sixfold increase in biomass (Wanink 1999), coupled with an explosion in landings (figure 3). Other introduced species, including the tilapiines *Oreochromis leucostictus, Tilapia zillii,* and *Tilapia rendalli,* have remained at low levels and do not appear to have had major impacts on the lake. The flourishing *Oreochromis niloticus,* however, is thought to have outcompeted or genetically subsumed the already overfished native *O. esculentus* and *O. variabilis* (Lowe-McConnell 2000, Goudswaard et al. 2002a) and is now a major component of the Lake Victoria fishery.

The introduced Nile perch and Nile tilapia, which grow to a large size, temporarily reversed the fishing-down trend that was evident in Lake Victoria up to the 1980s (table 2, figures 3, 4). In particular, the dramatic increase in Nile perch landings in the late 1980s and early 1990s represented a shift back to a large target species with a relatively low reproductive load (0.49), a low growth coefficient (0.17), and a relatively high age at maturity (3.4 years; Froese and Pauly 2000).

This dynamic situation in Lake Victoria has received much attention, both regionally and internationally, because of its economic importance and the extraordinary loss of biodiversity in the system. Similar changes have coincided with Nile perch introductions into other lakes in the region, including Lake Kyoga (Ogutu-Ohwayo 1990) and Lake Nabugabo

Table 2. Catch (in metric tons) for the Ugandan waters of Lake Victoria for four time periods.

Taxa	1966–1967	1976–1977	1986–1987	2000
Lates	4	500	58,809	72,632
Tilapiines	17,747	2480	5772	30,530
Bagrus	6646	4645	8173	152
Mormyrus	486	130	156	443
Clarias	2237	1620	655	69
Protopterus	2627	2035	309	469
Barbus	813	330	85	0
Synodontis	122	305	28	127
Haplochromines	1955	1280	3	4
Brycinus	223	0	0	0
Labeo	204	20	0	0
Rastrineobola	0	5	1001	70,333
Others	41	0	7	17

Note: For 1966–1967, 1976–1977, and 1986–1987, the values represent the average of the 2 years. Tilapiines were mainly *Oreochromis esculentus* and *Oreochromis variabilis* in 1966–1967, mainly *Oreochromis niloticus* in 1976–1977, and exclusively *O. niloticus* thereafter.

Source: Data for 1966–1987 were compiled for the Lake Victoria Fisheries Research Project; data for 2000 are from Muhoozi 2003.

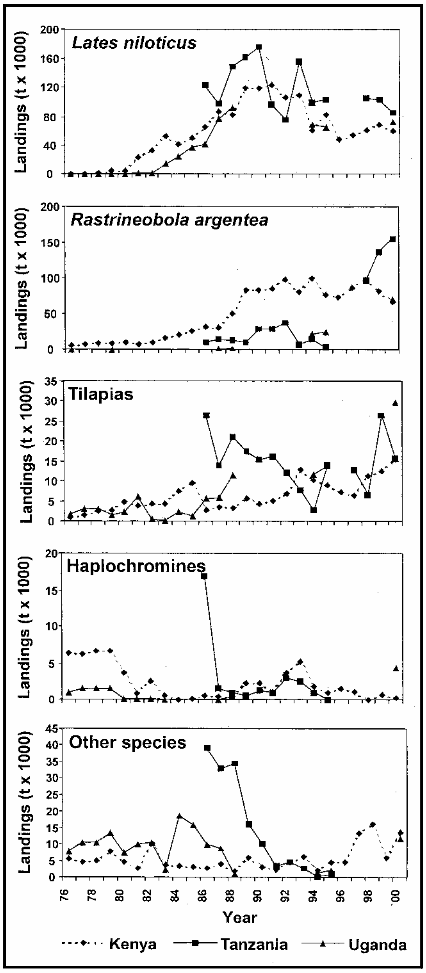

Figure 3. Fish catch of selected species in Lake Victoria (in metric tons) for Tanzania, Uganda, and Kenya between 1976 and 2000. For years with no lines and symbols, data were not available. Source: Cowx et al. 2003.

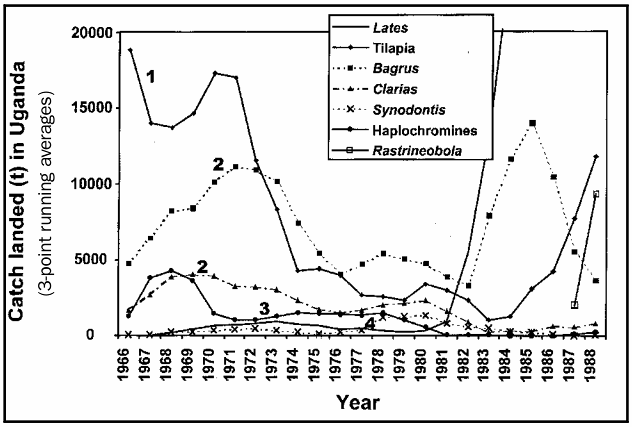

Figure 4. Fish catch, in metric tons, for key taxa in the Ugandan waters of Lake Victoria, 1966 to 1988. Data are expressed as three-point running averages. This figure demonstrates the sequence of fishing-down events in Uganda and the temporary nature of the reversal. Numbers represent the sequence of fishing down for key taxa (tilapia, **Bagrus docmak, Clarias gariepinus,** *haplochromines,* **Synodontis** *spp.). Tilapiines were mainly* **Oreochromis esculentus** *and* **Oreochromis variabilis** *in the 1960s but mainly* **Oreochromis niloticus** *by the mid-1970s. Source: Data were compiled for the Lake Victoria Fisheries Research Project.*

(Ogutu-Ohwayo 1993, Chapman et al. 1996a, 1996b) (see box).

Environmental change

As a result of anthropogenic change in the watershed, the lake changed from a mesotrophic system in the 1920s, dominated by diatoms, to a eutrophic system dominated by blue-green algae (Hecky 1993). Primary productivity doubled, and algal biomass increased 8- to 10-fold (Mugidde 1993), accompanied by a shift in algal species composition (Hecky 1993). Although some specialized haplochromine phytoplankton feeders fed predominantly on blue-green algae (Goldschmidt et al. 1993), not all phytoplanktivores may have been supported by the takeover of blue-green algae.

The change in trophic status was accompanied by a decrease in water transparency. Water clarity is by far the strongest environmental predictor of species diversity among haplochromine cichlids (Seehausen et al. 1997b). Loss of water clarity causes loss of genetic and ecological differentiation among haplochromine species, and the decrease in water transparency associated with eutrophication probably contributed to the loss of species diversity among cichlids (Seehausen et al. 1997b).

Another dramatic change to the Lake Victoria system has been the development of hypolimnetic anoxia. The deeper part of the lake (> 40 m) became stratified throughout much of the year (Hecky 1993, Hecky et al. 1994), and the duration and severity of hypoxia also increased in shallower areas (10 to 40 m deep; Wanink et al. 2001), although there is some evidence to suggest that this process is breaking down (Mkumbo 2002). The increased hypoxia may reflect a combination of increased nutrient levels and loss of detritivorous haplochromine cichlids. Although it is difficult to assess the impacts of increasing hypoxia on the fish community, fish kills associated with upwellings of anoxic water, along with the possible effects of phytotoxins, point to a high risk for some species (Ochumba 1990, Kaufman and Ochumba 1993). In addition, many of the deep-water haplochromines did not visibly shift into shallower waters in response to the lake's changing status. Instead, most of them simply disappeared.

Increasing hypolimnetic anoxia in Lake Victoria has coincided with changes in the macroinvertebrate community. There has been a notable increase of the detritivorous shrimp *Caridina nilotica* (Witte et al. 1992a, Goldschmidt et al. 1993), which may relate to *Ca. nilotica's* use of low-oxygen refugia from Nile perch predation, to the increased availability of algal and detrital foods, and to reduced predation pressure on juvenile shrimps caused by the disappearance of the haplochromines (Kaufman 1992, Goldschmidt et al. 1993, Branstrator and Mwebaza-Ndawula 1998).

Ecological changes in the lake, including oxygen availability, also reflect the invasion of the nonindigenous water hyacinth, *Eichhornia crassipes.* Water hyacinth (native to South America) appeared in Lake Kyoga, Uganda, in 1988 and in Lake Victoria in 1989 (Twongo et al. 1995). The weed became firmly established along the Nile, and in Lakes Victoria, Naivasha, Kyoga, and Albert, in two distinct forms: as stationary fringes along shorelines and as mobile mats. In the Ugandan waters of Lake Victoria, stationary fringes were estimated to cover 2200 hectares along 80% of the shoreline by 1995 (NARO 2002). Water hyacinth invasion had significant socioeconomic and environmental impacts, including disruption of transport, fishing, and fish marketing activities; disruption of lakeside recreational business; reduction of water supply; negative impacts on water quality for humans and livestock; and spread of waterborne diseases (Twongo 1996, NARO 2002, Njiru et al. 2002).

Water hyacinth disappeared almost completely over most of its previous range by the late 1990s. Its disappearance was not universally welcomed by fishers, because the area under the water hyacinth acted as a refuge for valuable fishes such as *C. gariepinus* and *P. aethiopicus,* and catches of these species declined after the disappearance of the weed (Njiru et al. 2002). A number of interactive factors apparently account for water hyacinth remission, including the introduction of the weevils *Neochetina eichhorniae* and *Neochetina bruchi* for biological control, the changes in hydrological conditions during the El Niño of 1997–1998, ecological succession, mechanical removal at strategic locations, and manual removal programs (NARO 2002).

Despite the success of efforts to control the water hyacinth, scientists have been concerned about the weed's possible return. Clearly, the nutrient enrichment of Lake Victoria and related water bodies, in addition to the high growth and reproductive potential of the weed, could promote its resurgence (NARO 2002). After a few years of water hyacinth recession, evidence of resurgence was observed in 2000 in Lakes Victoria and Kyoga, with the most prolific regrowth in Murchison Bay, an area of very high nutrient concentration (NARO 2002). The expectation is periodic outbreaks of water hyacinth that will demand continued vigilance and control efforts (NARO 2002).

A fourth, poorly studied contributor to biodiversity decline is the loss of riverine migratory routes to important potamodromous fishes. A number of indigenous noncichlids (e.g., several catfishes, cyprinids, and mormyrids) periodically migrated upriver to spawn during the rainy seasons (Whitehead 1959), but many of their migratory routes are now unavailable. For example, in the Napoleon Gulf of Uganda, the Nile River is blocked by the Owen Falls Dam; many small streams are choked with dense papyrus; and the River Katonga, also blocked by papyrus, is unavailable in most years except during major floods. The surviving species that have persisted in the Napoleon Gulf are presumably spawning within the gulf, and the inability of some of the potamodromous species to adapt to spawning within the lake may have contributed to their demise. Degradation of floodplains, caused by agriculture and deforestation in riparian zones, may also have contributed to the decrease of preferred migratory and spawning grounds in other areas of the basin.

Faunal refugia

The tremendous loss of biodiversity in the Lake Victoria basin has sparked several studies directed toward identification of faunal refugia—habitats where native fishes might be protected from Nile perch predation. Currently two major types of faunal refugia are recognized: (1) structural refugia within the lake (wetlands [figure 1f] and rocky habitats [figure 1c]) and (2) refugia outside the lake (satellite water bodies). Wetlands serve as structural and low-oxygen refugia for fishes that can tolerate wetland conditions; they also function as barriers to dispersal of Nile perch (figure 1f; Chapman et al. 1996a, 1996b, Kaufman et al. 1997, Balirwa 1998, Schofield and Chapman 1999, Chapman et al. 2002). Some haplochromines and some indigenous noncichlids are relatively tolerant of hypoxia, while Nile perch is not (Chapman et al. 2002), thus permitting some indigenous species to persist in wetlands under reduced predator pressure. Ecotonal wetlands are particularly important refugia because interaction with the main lake waters elevates dissolved oxygen, making these habitats more accessible than the dense swamp interior. Nile perch are rare in these ecotonal habitats, and species richness is higher than in the interior swamp (Chapman et al. 1996a, 1996b, 2002, Balirwa 1998, Schofield and Chapman 1999). However, even areas deep within the fringing swamp are important in the maintenance of a subset of the basin fauna (Chapman et al. 1996a, 2002).

Rocky shores and offshore rocky islands (figure 1c) and reefs are the other major refugia within Lake Victoria. High structural complexity and relatively clear waters in offshore regions facilitate coexistence of many species; in fact, these habitats are characterized by the highest fish species richness of all lake habitats (Seehausen 1996, 1999, Seehausen et al. 1997b). Rocky refugia harbor a large number of rock-dwelling specialists (> 150 species of diverse cichlid lineages and at least one native cyprinid). They also serve as refugia for a number of species that were not specialized rock-dwellers in the pre–Nile perch era; these species either actively shifted to rocky habitats or represent remnants of species with a broader pre–Nile perch distribution (Witte et al. 1992b, Seehausen 1996, Seehausen et al. 1997a). It should be noted that several other high-diversity refugia within Lake Victoria have been identified, but these refugia are less readily defined topographically (Kaufman and Ochumba 1993, Seehausen et al. 1997a). Examples include the benthos near the oxycline and the structured benthic microbial mats in the deep waters and water column (Kaufman and Ochumba 1993).

A small portion of the fauna considered extirpated from Lakes Kyoga, Victoria, and Nabugabo can still be found in satellite water bodies around the main lakes (Ogutu-Ohwayo 1993, Kaufman et al. 1997). For example, Lake Nawampasa is a small (1 x 5 kilometers) refugium of the former Lake Victoria–Lake Kyoga fauna; it harbors more than three dozen haplochromine taxa representing most of the described Lake Victoria region's genera (Kaufman et al. 1997). In many cases, dense hypoxic swamps separate these satellite lakes from the main lake and act as a biological filter preventing Nile perch colonization and, probably, nutrient influx.

Renewed overfishing and resurgence of indigenous species

The remnant populations of species that have persisted represent seeds for resurgence of these species if predator pressure is reduced and if environmental conditions allow for ecological diversity. In most sections of Lake Victoria and some lakes of the basin, intense fishing has reduced the numbers of large Nile perch; this reduction has coincided with a resurgence of some indigenous species (Seehausen et al. 1997a, Witte et al. 2000, Cowx et al. 2003). Evidence for a decline in Nile perch biomass derives from bottom trawling and acoustic surveys conducted by the Lake Victoria Fisheries Research Project (LVFRP 2001, Cowx et al. 2003), from catch landings (figure 3), and from data on catch per unit effort for commercial fisheries (LVFRP 2001, Cowx et al. 2003). The acoustic surveys indicated that the Nile perch stock declined between September 1999 and September 2001; their biomass index decreased from 1.59 to 0.89 million metric tons (LVFRP 2001, Cowx et al. 2003). More recent surveys suggest the standing stock is now less than 50% of that found in 2001. The bottom trawls produced a catch rate of 195 kilograms (kg) per hour of fish (mostly Nile perch), substantially less than the 514 kg per hour of mostly cichlids (83%) recorded during the last comparable survey in 1969–1970 (Kudhongania and Cordone 1974). In the recent trawl surveys, Nile perch made up the largest component of the catch; however, approximately 70% (by mass) of the perch catch were immature fish, suggesting that the current exploitation rate may be excessive

(LVFRP 2001, Cowx et al. 2003). Similarly, commercial gill net catches include a high proportion of immature fish (LVFRP 2001, Cowx et al. 2003). This suggests that there is still good recruitment into the Nile perch population, but the relatively small proportion of large, mature fish is a concern for the fishery (LVFRP 2001, Cowx et al. 2003). Over the same period, acoustic surveys indicated that the biomass of small pelagic fishes (*R. argentea* and pelagic haplochromine cichlids) increased to compensate for the fall in the Nile perch stocks (LVFRP 2001, Getabu et al. 2003). On a research transect in the Mwanza Gulf, Nile perch made up 97% of bottom trawl catches in 1987, with a catch size of 208 kg per hour. However, in a bottom trawl in 1997, they made up only 76% of the catch, with a catch size of 152 kg per hour, while haplochromines increased from 0.2% of the catch in 1987 to 21.3% of the catch in 1997 (Witte et al. 2000).

Data on landings of Nile perch indicate a decline in total catch (figure 3), although levels of fishing effort have grown from an estimated 12,041 boats in 1983 to 22,700 in 1990 and 42,548 in 2000, and the number of gill nets has grown more than eightfold over the same time period (LVFRP 2001, Muhoozi 2003). Estimates of average catch per unit effort for Nile perch in gill net commercial fisheries declined from 145.2 kg per boat per day in 1989 to 50.2 kg per boat per day between 1994 and 1998 (LVFRP 2001). Catch per unit effort for Nile perch in beach seines (an illegal gear) also declined between 1989 (387.8 kg per boat per day) and 1994 (52.3 kg per boat per day) but then increased again, reaching 164.7 kg per boat per day in 1998 (LVFRP 2001). The decline in catch per unit effort coincided with an increase in the use of small mesh-sized nets and illegal gear (LVFRP 2001). For example, 20% of the gill nets used in the lake are below the legal mesh size of 5 inches (12.7 centimeters [cm]), and the use of 5- to 6-inch (15.24 cm) mesh gill nets increased from 22% to 55% while mesh sizes greater than 6 inches decreased from 75% to 27% in Ugandan waters between 1990 and 2000 (Cowx et al. 2003).

Intense fishing pressure has coincided with reduced size at maturity of Nile perch. The average length at maturity (the length at which 50% of fish are mature) in 1988 was 60 to 70 cm total length (TL) in males and 95 to 100 cm TL in females. In 1999–2000, it was only 54 to 64 cm TL in males and 73 to 78 cm TL in females (LVFRP 2001). Similar trends have been evident in *O. niloticus* and *R. argentea.* In 1970–1974, the lower limit of size at maturity for *R. argentea* was 52 millimeters (mm) standard length (SL) for males and 44 mm SL for females; by 1987–1988, it had dropped to 46 and 33 mm, respectively (Wanink and Witte 2000a). This appeared to have stabilized around 39 mm for both sexes between 1990 and 2000 (Marshall and Cowx 2003); however, preliminary analysis of data collected for 2001–2002 showed values as low as 34 mm for females (Jan H. Wanink, Koeman en Bijkerk BV, Haren, The Netherlands, personal communication, 2003).

The community- and ecosystem-level effects of intense fishing pressure on the Nile perch are largely unknown. It is clear, though, that some indigenous species are resurging. They comprise a biologically filtered fauna, representing species that persisted in the face of eutrophication, deoxygenation of deep water, and invasion of Nile perch; these species have demonstrated the flexibility to respond quickly to changing environments. The resurgence of haplochromine cichlids in the sublittoral zone of the Mwanza Gulf and elsewhere involves only a few species that occur in large quantities. Only a few trophic groups are represented, mainly zooplanktivores and detritivores (Seehausen et al. 1997a, Witte et al. 2000). In Lake Nabugabo, intense fishing of large Nile perch has similarly coincided with a resurgence of some endemic haplochromine species and several noncichlids (see box). Lake Bisina, a Kyoga satellite, reputedly once supported a Nile perch fishery, but today it hosts a diverse haplochromine assemblage, with Nile perch extremely rare or absent (Schwartz 2002).

The overfishing of Nile perch, with the associated resurgence of indigenous species, represents a second fishing-down episode in Lake Victoria. The introduction of Nile perch and Nile tilapia temporarily reversed an initial fishing-down process that had occurred in the indigenous community on the advent of modern fishing methods (figures 3, 4). The sudden appearance of a new preferred stock (Nile perch) may have released the previously overfished stocks (e.g., *B. docmak, O. niloticus)* from fishing pressure, facilitating some degree of stock recovery, as shown for the Ugandan waters in figure 4. For *B. docmak,* however, this recovery was short-lived (figure 4). Similar effects on *O. niloticus* were reported by Goudswaard and colleagues (2002a) for Tanzanian and Kenyan waters of Lake Victoria, where a dramatic increase in the stock of *O. niloticus* and an increase in that species' average size coincided with a shift in the local fishery toward the Nile perch (and presumably an associated reduction of fishing pressure on *O. niloticus).* Many years of intense fishing of large Nile perch are now leading to exploitation of smaller Nile perch and smaller species.

Resurging populations of indigenous species in Lake Victoria, Lake Nabugabo, and other bodies of water in the Lake Victoria region will encounter an environment much changed from 20 years ago. Only a subset of the basin fauna now exists, and limnological conditions are still being strongly influenced by a lake basin seriously affected by intense human land use. Thus, it is reasonable to expect that the resurgent fauna will differ in richness, composition, and ecosystem function from the original fauna. The recovered food web may be very different from the original food web. For example, resurging species may experience reduced prey encounter rates in turbid water, affecting levels of specialization, niche partitioning, and species coexistence (Seehausen et al. 2003). A broadening of the diet spectrum has been observed recently in the cyprinid *Rastrineobola* in the Mwanza Gulf (Wanink and Witte 2000a). Some of the resurging haplochromines have survived during periods of strongly reduced population abundance or in refugia with turbid water (or both). Given that haplochromines tend to hybridize under such conditions, we anticipate that some of the resurging populations represent genetically mosaic stock derived from two or more prerefugial species (Seehausen et al. 1997b, Witte et al. 2000). Other resurging species have survived in wetland refugia, where they have experienced strong selection pressure for tolerance of low-oxygen conditions over several generations. For such species, we anticipate differences between the characteristics of the original populations and those of the resurging populations with respect to traits such as gill morphology and respiratory physiology. Preliminary observations revealed an increase in gill size in two zooplanktivores, *R. argentea* (Wanink and Witte 2000b) and *Yssichromis pyrrhocephalus* (Witte et al. 2000), but it is unknown whether this is caused by heritable response to selection or by environmentally induced phenotypic plasticity.

Food web structure in water bodies in the Lake Victoria basin appears to be very dynamic. An understanding of these dynamics is essential if the management of the lakes is to move from one that responds to unforeseen change to one that can both predict and respond to anticipated change. With the introduction of Nile perch, the importance of predation has become apparent, and the degree of faunal recovery will clearly depend to some extent on the direction and intensity of fishing efforts. It is possible that heavy fishing pressure on Nile perch may keep the numbers of perch low enough to permit maintenance of the resurging assemblage. However, the level of ecological, genetic, and species diversity attained by this fauna will depend heavily on water quality management and on close attention to a broad range of ecological indicators in the system.

Conservation of biodiversity in the Lake Victoria region

The use of natural resources involves dual imperatives that are often in conflict: the need to meet the increasing requirements of an exponentially growing human population and the need to maintain existing genetic, ecological, and ecosystem biodiversity. Conflict arises because fulfillment of human needs for food, goods, and services involves the disruption and often degradation of natural habitats. Efforts to resolve such discord have been encouraged in a number of international forums, including the Convention on Biological Diversity. Resolution of these conflicts for inland tropical waters is a particularly tough challenge. Lakes, rivers, and wetlands are economically important and rich in readily costed values, whereas coming up with a comparative costing for intact ecosystems and species survival requires insights and assumptions that are unfamiliar to classical economists. For example, it is fairly easy to determine that the 122,000 metric tons of fish processed in the Lake Victoria region in 2000 (total landing 220,000 metric tons) is valued at US$220 million (LVFRP 2001). These numbers are easy to believe because invoices track the resultant exchange of goods and funds. Real values can also be attached to the ecosystem services provided by a healthy environment, or values can be assumed on the basis of the opportunity cost of benefits forgone in the conservation process. The question is whether anybody will accept these sums in equal measure against the profits of extraction. While there is considerable external pressure to preserve the biodiversity of the Lake Victoria region, it is difficult to convince local stakeholders, or the foreign interests funding them, that exploitation should be guided by an interest of maintaining biological diversity. The value of natural services, however significant, is often ignored.

The resurgence of some indigenous fishes in the Lake Victoria region appears to be the direct result of fishing pressure on Nile perch. A steady-state trophic balance model based on the Ecopath/Ecosim program (Christensen and Pauly 1992), which predicted that the changes observed would occur, suggests that doubling of the fishing effort over the next few years will result in a collapse of the Nile perch stocks and resurgence of haplochromine biomass (figure 5; Takashi Matsuishi, Department of Fisheries, University of Hakkaido, Sapporo, Japan, personal communication, 2003). The resurgence that we are now seeing in the biomass of haplochromines (predicted by the Ecopath model) does not reflect a careful tweaking of the management system. What it does suggest, however, is that conservation goals in the Lake Victoria region need not be in total conflict with establishment of a sustainable fishery. Management strategies in the future that facilitate a heavy, but sustainable, Nile perch fishery may allow the coexistence of Nile perch with a number of indigenous species, although it has to be clearly stated that the predicted and observed increase in haplochromine biomass is attributed to only a few species.

Kitchell and colleagues (1997) used a bioenergetic model of Nile perch predation rates to evaluate the effects of fishery exploitation patterns on fisheries and on the ecology in Lake Victoria. They concluded that the development of fisheries based on large-mesh gill nets could reduce predation by Nile perch to about 40% of predation estimates in the late

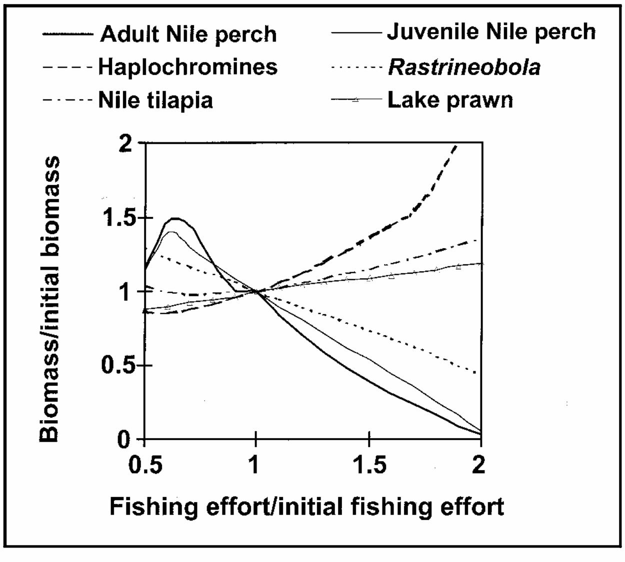

Figure 5. Predicted long-term change in average biomass of selected species as a result of changing fishing effort in Lake Victoria. Catch and effort are standardized as unity based on statistics for the year 2000 (Cowx et al. 2003).

Faunal collapse and resurgence in Lake Nabugabo

Lake Nabugabo is a small satellite lake (24 square kilometers), isolated from Lake Victoria approximately 4000 years ago (Greenwood 1965). Like Lake Victoria, Lake Nabugabo has a recent history of dramatic change in fish faunal structure and diversity, although unlike Lake Victoria it has been a eutrophic lake for at least several decades. Twenty species of noncichlids, eight species of haplochrome cichlids (five endemic and three widely distributed), and two species of tilapiine cichlids were recorded by the Cambridge expedition to Lake Nabugabo in 1962 (CNBS 1962, Greenwood 1965). At that time, the fishery was dominated (in terms of mass) by lungfish *(Protopterus aethiopicus),* followed by *Bagrus docmak, Schilbe intermedius, Clarias gariepinus, Oreochromis esculentus, Oreochromis variabilis,* and several species of haplochromine cichlids. A survey conducted in 1991 and 1992 in the open lake, 30 years after the introduction of Nile perch, showed a dramatic change in the fish community. Of the species that formed the pre–Nile perch fishery, *O. esculentus, O. variabilis,* and *B. docmak* were extirpated, and *S. intermedius, C. gariepinus, P. aethiopicus,* and haplochromines were very rare. *Lates niloticus, Oreochromis niloticus, S. intermedius, Brycinus sadleri,* and *Rastrineobola argentea* dominated the open waters of the lake (Ogutu-Ohwayo 1993). However, an intensive survey of wetland areas surrounding Lake Nabugabo in 1993–1994 revealed that several species no longer present in the main lake could be found in the wetland ecotones or beyond the margins of the lake in lagoons and tributaries deep in the swamp. Haplochromines were primarily confined to wetland ecotones, whereas some other species were recovered in deep swamp refugia (Chapman et al. 1996a, 1996b).

As in Lake Victoria, intense fishing of Nile perch in Lake Nabugabo has coincided with a resurgence of some indigenous species in the open waters, particularly some haplochromine cichlids. In 1995, haplochromine cichlids were largely confined to inshore areas and were very rare in Nile perch stomachs (Chapman et al. 2003). By 2000, haplochromine cichlids had increased dramatically in abundance both in the lake and in Nile perch stomachs (figure 6). However, one piscivore, *Prognathochromis venator,* has never been recovered. Several noncichlids also reappeared or increased in abundance in main Lake Nabugabo (Chapman et al. 2003). With respect to species numbers, the Nabugabo cichlid fauna was poor even before Nile perch was introduced; the species richness of the lake and its pattern of faunal recovery are comparable to some turbid inshore areas of Lake Victoria. In previously high-diversity areas of Lake Victoria, we are not likely to see this level of recovery, in terms of original diversity, unless the eutrophic status of the lake can be reversed. Nonetheless, the pattern of faunal loss and recovery in Lake Nabugabo demonstrates the importance of faunal refugia in providing the seeds of resurgence under reduced predator pressure and provides a model to understand some of the changes in Lake Victoria.

1970s. Their model also suggested that increased pressure on Nile perch juveniles (through beach seining and small-mesh gill net fisheries) could reduce Nile perch predation to about 25% (Kitchell et al. 1997). However, such practices may have a direct negative impact on the small resurgent species. In a similar bioenergetics modeling analysis, Schindler and colleagues (1998) found that enforcement of a 5-inch minimum mesh size in Lake Victoria would reduce both Nile perch cannibalism and predation on other indigenous fishes by as much as 44%, with only a small decrease (10%) in the yield of Nile perch. Building on the work of these earlier models, Kaufman and Schwartz (2002) noted that Nile perch seemed to prefer, and grow fastest on, a haplochromine prey base. A dynamic, mass-balance fishery model incorporating these data demonstrated that haplochromine conservation could actually help to maximize Nile perch production rates. According to the model, a key to sustainability in the Nile perch fishery is to maintain sufficient fishing pressure to ensure an abundance of haplochromine prey but not so much pressure as to threaten the Nile perch stock itself. The specific rate of Nile perch biomass accumulation (grams accumulated per gram total biomass per day) should be highest when haplochromines are most abundant. However, the absolute rate (grams accumulated per day) is at a maximum level at intermediate haplochromine density and intermediate fishing pressures on Nile perch—a situation in which the mass of sexually mature Nile perch of marketable size is optimized. Allowing too many big fish in the system encourages cannibalism and the loss of other desirable fisheries, as concluded earlier by Kitchell and colleagues (1997) and Schindler and colleagues (1998). But too high a fishing effort shifts fishery dependence onto small, barely mature individuals.

Modeling efforts like those described above suggest that fishing is an extremely potent ecological force in aquatic systems. Careful management of fishing pressure can potentially regulate the Nile perch population and food web dynamics and contribute to patterns of faunal resurgence. Faunal resurgence can in turn feed back to produce tangible fishery benefits. Faunal resurgence resulting from exploitation of Nile perch, as far as haplochromine cichlids are concerned, is primarily resurgence in biomass of a few indigenous species, but it could lead to a real resurgence of biodiversity if accompanied by a reversal of the eutrophication of the lakes. Careful consideration of these effects would suggest that Lake Victoria fisheries, and the ecosystem as a whole, might be managed to promote both protein production and biological diversity. Clearly, the two goals may not be mutually exclusive. However, the degree to which a measure like mesh size limits can, by itself, have practical regulatory value is questionable. Both export and domestic markets seem open for undersized Nile perch, which leads to overexploitation of immature fish, major challenges to mesh size enforcement, and a serious threat to sustainability of the fishery (Geheb 1997, LVFRP 2001). This has in part been resolved by imposing a slot size of 55 to 85 cm total length of Nile perch that can be processed for the export market (Cowx et al. 2003). By restricting the size of fish that the processing factories—the major driver of the fishery—can accept, perhaps exploitation patterns can be altered away from immature fish.

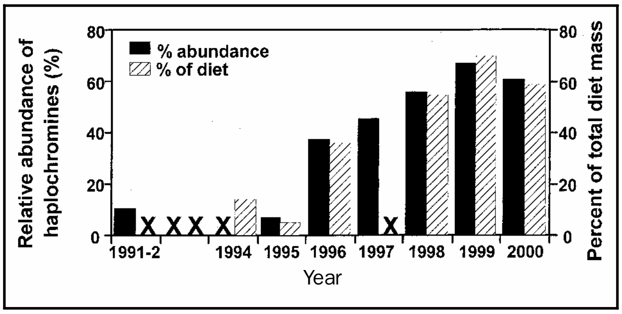

Figure 6. Relative abundance of haplochromine cichlids (1991/1992–2000) and percentage of the total diet mass of Nile perch that was composed of haplochromine cichlids (1994–2000) in Lake Nabugabo, Uganda. The relative abundance of haplochromine cichlids is expressed as a percentage of all fishes captured in experimental gill nets. An X *indicates that data were not available. Data for 1991/1992 were derived from Ogutu-Ohwayo (1993); other data were adapted from Chapman and colleagues (2003).*

Specific recommended avenues for biodiversity conservation

The array of approaches needed to maintain a significant proportion of the original biodiversity in the Lake Victoria basin may ultimately prove as diverse as the community whose welfare is at stake. Here we present four issues that we view as particularly vital.

1. Protection and restoration of biodiversity in the Lake Victoria basin should become part of an integral lake basin plan. This is necessary so that national priorities can be developed at a high political level, leading to relevant legislation and allocation of funds to fulfill the newly legislated mandates. It is only by having priorities set at a high political level that the influence of upstream activities on Lake Victoria can be regulated and that guidelines for controlling nutrient influx and fishing pressure can be established and implemented through education and enforcement.

2. Any attempt to conserve habitats and biodiversity in the lake will succeed only if the general environmental quality permits. Efforts to ensure this should include maintenance and restoration of water quality in the lake, its tributaries, and its associated wetlands. Most important, nutrient levels (mainly phosphorus) should be reduced to pre-1990 levels to halt and at least partly reverse eutrophication, and toxic contamination should be kept within acceptable limits. To achieve this, we suggest that the lacustrine wetland fringe near densely populated areas and areas of intensive agriculture be restored and that there be adequate investment in modern sewage treatment plants in anticipation of future population levels. We also suggest that a biological monitoring system be established, based on elements of the indigenous flora and fauna (Kaufman 1992, Seehausen 1999). Such biological monitoring systems are necessary complements to conventional physical and chemical tests. The latter are snapshots in time, whereas biological monitoring systems average environmental effects over longer time spans and thus have greater power as indicators of environmental change.

3. Fishing has exerted a major effect on the composition of Lake Victoria fisheries. Stock management strategies linked to rational regulation of fishing efforts are needed to prevent another serial collapse of stocks. Appropriate levels of fishing efforts on selected size classes, such as the slot size described above, and target species will contribute to maintenance and, potentially, enhancement of biodiversity. Since the historical precedent for the practical implementation of mesh size limits is a bit shaky, funding initiatives should concentrate on collaborative development of managerial strategies that befit the financial and administrative constraints of the riparian countries. One such strategy is the imposition of slot size regulation, which has been proven to be the economically and sustainably best scenario for exploitation of Nile perch (Asila 2001).

4. Representative habitats in the lake should be reserved for strict conservation, with special emphasis on high-diversity zones such as rocky areas, sandy shores, wetlands, and parts of mud-bottomed gulfs within the main lake. The small satellite lakes are also valuable conservation units, because they have only a small number of stakeholders, which facilitates integrated conservation and development. The maintenance of wetlands in the basin is critical both to ecosystem function and to the conservation of indigenous species. Current strategies for sustainable wetland management include co-management systems for shoreline wetland resources, protection mediated by economic valuation (e.g., Yala Swamp), and Ramsar protected status (e.g., Lake George, Lake Nabugabo). To date, no management strategies exist for other habitats. Cichlid populations at rocky islands are currently heavily fished (estimated at about 5000 metric tons per year; Cowx et al. 2003) by hook and line to be used as longline bait for Nile perch. The same applies to other cichlid species that swim near exposed sandy shores fished with small meshed seines. Collection of data and development of management options are pivotal to prevent further loss of diversity.

Conclusions

The resurgence of some indigenous species evident in areas of Lake Victoria and Lake Nabugabo has given new hope for the maintenance of biodiversity in the Lake Victoria region. It has also spawned a renewed interest in careful management options that promote both the sustainability of the fishery and biodiversity conservation. Resurgence data suggest that heavy fishing on Nile perch may contribute to enhanced biodiversity, although the eutrophic state of much of the lake basin is currently a heavy constraint to resurgence of haplochromine diversity. There is clearly a need to work out the fishing pressures that can optimize both biodiversity and sustainability of catch through time.

A coherent plan for conservation and rehabilitation of the fish fauna in the Lake Victoria basin should be developed without delay. Central tenets of such a plan should include provisions for halting and reversing eutrophication and for setting up reserves that typify the various habitats of the lake and its tributary rivers, associated wetlands, and satellite lakes. It must also consider the human aspects of such reserves through consultation with local groups. The plan should be incorporated into more general policies for the management of the fishery and for the range of other human activities in the lake basin. This will involve negotiation with all interested stakeholders. To aid in this process and in the formulation of strategies to reinforce conservation, efforts should be made to quantify the financial and social value of the resources to be protected. The plan should be supported by education programs, addressed to all levels of society, that clarify the benefits of conservation and define the processes needed to achieve it.

Acknowledgments

The authors have a long history of research in the Lake Victoria region—for some, dating back to the 1950s. Thus, we would like to thank the many scientists who have participated in documenting the patterns of change in Lake Victoria and surrounding systems; the fishers who have worked with all of us over the years; and the Fisheries Resources Research Institute of Uganda, the Tanzania Fisheries Research Institute, and the Kenyan Marine and Freshwater Fisheries Research Institute. We also acknowledge funding from the following sources: the Wildlife Conservation Society; the National Science Foundation (INT 93-08276, DEB-9622218, IBN-0094393); the National Oceanic and Atmospheric Administration's National Undersea Research Program; the Netherlands Organization for the Advancement of Tropical Research; the Dutch Science Foundation; the Wageningen Agricultural University; the Netherlands Ministry for Development Cooperation, Section for Research and Technology; the Schure-Beijerinck-Popping Foundation; the Leiden University Fund (Stichting Leids Universiteits-Fonds); the National Geographic Society; the Pew Charitable Trusts; the US Environmental Protection Agency; the American Association of Zoological Parks and Aquaria; the US Agency for International Development; the US National Institutes of Health; the World Bank; the European Union (Lake Victoria Fisheries Research Project, project no. EDF 7ACP-RPR-372); and many smaller but critical sources who have kept us in the field and lab through difficult times.

References cited

Asila A. 2001. Selectivity of gillnets on Nile perch populations in Lake Victoria. Master's thesis. University of Moi, Eldoret, Kenya.

Balirwa JS. 1998. Lake Victoria wetlands and the ecology of the Nile tilapia, *Oreochromis niloticus* Linne. PhD dissertation. Wageningen Agricultural University, Wageningen, The Netherlands.

Branstrator DK, Mwebaza-Ndawula L. 1998. Low-oxygen tolerance of the atyid prawn, *Caridina nilotica,* in Lake Victoria (East Africa): Implications for refuge from Nile perch predation. Pages 125–134 in Lehman JT, ed. Environmental Change and Response in East African Lakes. Dordrecht (The Netherlands): Kluwer.

Cadwalladr DA. 1965. The decline in the *Labeo victorianus* Boulenger (Pisces: Cyprinidae) of Lake Victoria and an associated deterioration in some indigenous fishing methods in the Nzoia River, Kenya. East African Agriculture and Forestry Journal 30: 249–256.

Chapman LJ, Chapman CA, Chandler M. 1996a. Wetland ecotones and refugia for endangered fishes. Biological Conservation 78: 263–270.

Chapman LJ, Chapman CA, Ogutu-Ohwayo R, Chandler M, Kaufman L, Keiter AE. 1996b. Refugia for endangered fishes from an introduced predator in Lake Nabugabo, Uganda. Conservation Biology 10: 554–561.

Chapman LJ, Chapman CA, Nordlie FG, Rosenberger AE. 2002. Physiological refugia: Swamps, hypoxia tolerance, and maintenance of fish biodiversity in the Lake Victoria region. Comparative Biochemistry and Physiology 133 (A): 421–437.

Chapman LJ, Chapman CA, Schofield PS, Olowo JP, Kaufman LS, Seehausen O, Ogutu-Ohwayo R. 2003. Fish faunal resurgence in Lake Nabugabo, East Africa. Conservation Biology 17: 500–511.

Christensen V, Pauly D. 1992. ECOPATH II—a software for balancing steady-state ecosystem models and calculating network characteristics. Ecological Modelling 62: 169–185.

[CNBS] Cambridge Nabugabo Biological Survey. 1962. Preliminary Report of the Cambridge Nabugabo Biological Survey. Nabugabo (Uganda): CNBS.

Cowx IG, Muhoozi L, Mkumbo O, Getabu A, Okaranon J. 2003. Evidence of overexploitation of the fisheries resources of Lake Victoria, with special reference to Ugandan waters. Fisheries Management and Ecology. Forthcoming.

Froese R, Pauly D, eds. 2000. Fishbase 2000. Makati City (Philippines): International Center for Living Aquatic Resources Management.

Fryer G. 1960. Concerning the proposed introduction of Nile perch into Lake Victoria. East African Agricultural Journal 25: 267–270.

Geheb K. 1997. The regulators and the regulated: Fisheries management, dynamics and options in Kenya's Lake Victoria fishery. PhD dissertation. University of Sussex, United Kingdom.

Getabu A, Tumwebaze R, MacLennan DN. 2003. Spatial distribution and temporal changes in the fish populations of Lake Victoria. Aquatic Living Resources. Forthcoming.

Goldschmidt T, Witte F, Wanink JH. 1993. Cascading effects of the introduced Nile perch on the detritivorous/phytoplanktivorous species in the sublittoral areas of Lake Victoria. Conservation Biology 7: 686–700.

Goudswaard K, Witte F, Katunzi EFB. 2002a. The tilapiine fish stock of Lake Victoria before and after the Nile perch upsurge. Journal of Fish Biology 60: 838–856.

Goudswaard K, Witte F, Chapman LJ. 2002b. Decline of the African lungfish *(Protopterus aethiopicus)* in Lake Victoria (East Africa). Journal of African Ecology 40: 42–52.

Graham M. 1929. The Victoria Nyanza and Its Fisheries: A Report on the Fish Survey of Lake Victoria 1927–1928 and Appendices. London: Crown Agents for the Colonies.

Greenwood PH. 1965. The cichlid fishes of Lake Nabugabo, Uganda. Bulletin of the British Museum of Natural History (Zoology) 12: 313–357.

———. 1974. The cichlid fishes of Lake Victoria, East Africa: The biology and evolution of a species flock. Bulletin of the British Museum of Natural History (Zoology) 6 (suppl.): 1–134.

Hecky RE. 1993. The eutrophication of Lake Victoria. Verhandlungen der Internationale Vereinigung für Theoretische und Angewandte Limnologie 25: 39–48.

Hecky RE, Bugenyi FWB, Ochumba P, Talling JF, Mugidde R, Gophen M, Kaufman L. 1994. Deoxygenation of the deep water of Lake Victoria, East Africa. Limnology and Oceanography 39: 1476–1481.

Kaufman L. 1992. Catastrophic change in species-rich freshwater ecosystems: The lessons of Lake Victoria. BioScience 42: 846–858.

Kaufman L, Ochumba P. 1993. Evolutionary and conservation biology of cichlid fishes as revealed by faunal remnants in northern Lake Victoria. Conservation Biology 7: 719–730.

Kaufman L, Schwartz J. 2002. Nile perch population dynamics in Lake Victoria: Implications for management and conservation. Pages 257–313 in Ruth M, Lindholm J, eds. Dynamic Modeling for Marine Conservation. New York: Springer-Verlag.

Kaufman LS, Chapman LJ, Chapman CA. 1997. Evolution in fast forward: Haplochromine fishes of the Lake Victoria region. Endeavour 21: 23–30.

Kitchell JF, Schindler DE, Reinthal PN, Ogutu-Ohwayo R. 1997. The Nile perch in Lake Victoria: Strong interactions between fishes and fisheries. Ecological Applications 7: 653–664,

Kudhongania AW, Cordone AJ. 1974. Batho-spatial distribution patterns and biomass estimates of the major demersal fishes in Lake Victoria. African Journal of Tropical Hydrobiology and Fisheries 3: 15–31.

Lae R. 1995. Climatic and anthropogenic effects on fish diversity and fish yields in the central delta of the Niger River. Aquatic Living Resources 8: 43–58.

Lowe-McConnell RH. 2000. The roles of tilapias in ecosystems. Pages 129–162 in Beveridge MCM, Andrews BJ, eds. Tilapias: Biology and Exploitation. Dordrecht (The Netherlands): Kluwer.

[LVFRP] Lake Victoria Fisheries Research Project. 2001. Lake Victoria Fisheries Research Project Phase II, 1997–2001: Final Report of UNECIA Ltd. Compiled by Cowx IG, Crean K, Geheb K, MacLennan D. Sheffield (United Kingdom): Universities of the North of England Consortium for International Activities.

[LVFS] Lake Victoria Fisheries Service. 1958. Annual Report 1957/1958. Jinja (Uganda): LVFS.

Marshall J, Cowx IG. 2003. Will the explosion of *Ligula intestinalis* in *Rastrineobola argentea* lead to another shift in the fisheries of Lake Victoria? Pages 244–256 in Cowx IG, ed. Interactions between Fish and Birds: Implications for Management. Oxford (United Kingdom): Blackwell Science.

Mkumbo O. 2002. Population dynamics of the three important commercial fish species in Lake Victoria: *Lates niloticus, Oreochromis niloticus* and *Rastrineobola argentea.* PhD dissertation. University of Hull, United Kingdom.

Mugidde R. 1993. The increase in phytoplankton primary productivity and biomass in Lake Victoria (Uganda). Verhandlungen der Internationale Vereinigung für Theoretische und Angewandte Limnologie 25: 846–849.

Muhoozi l. 2003. Aspects of the commercial exploitation of fish stocks in Lake Victoria. PhD dissertation. University of Hull, United Kingdom.

[NARO] National Agricultural Research Organization. 2002. Experiences with Managing Water Hyacinth Infestation in Uganda. Jinja (Uganda): Fisheries Resources Research Institute, NARO.

Njiru M, Othina A, Cowx IG. 2002. Lake Victoria invasion by water hyacinth a blessing for Lake Victoria fisheries. Pages 255–264 in Cowx IG, ed. Management and Ecology of Lake and Reservoir Fisheries. Oxford (United Kingdom): Blackwell Science.

Ochumba PBO. 1990. Massive fish kills within the Nyanza Gulf of Lake Victoria, Kenya. Hydrobiologia 208: 93–99.

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

———. 1993. The impact of predation by Nile perch, *Lates niloticus* L., on the fishes of Lake Nabugabo, with suggestions for conservation of endangered endemic cichlids. Conservation Biology 7: 701–711.

Regier HA, Henderson HF. 1973. Towards a broad ecological model of fish communities and fisheries. Transactions of the American Fisheries Society 1: 56–72.

Regier HA, Loftus KH. 1972. Effects of fisheries exploitation on salmonid communities in oligotrophic lakes. Journal of the Fisheries Research Board of Canada 29: 959–968.

Schindler DE, Kitchell JF, Ogutu-Ohwayo R. 1998. Ecological consequences of alternative gill net fisheries for Nile perch in Lake Victoria. Conservation Biology 12: 56–64.

Schofield PJ, Chapman LJ. 1999. Interactions between Nile perch, *Lates niloticus,* and other fishes in Lake Nabugabo, Uganda. Environmental Biology of Fishes 55: 343–358.

Schwartz JDM. 2002. The functional role of fish diversity in Lake Victoria, East Africa. PhD dissertation. Boston University, Boston.

Seehausen O. 1996. Lake Victoria Rock Cichlids: Taxonomy, Ecology, and Distribution. Zevenhuizen (The Netherlands): Verduyn Cichlids.

———. 1999. A reconsideration of the ecological composition of the Lake Victoria cichlid species flock before and after the Nile perch upsurge. Pages 281–293 in van Densen WLT, Morris MG, eds. Fish and Fisheries of Lakes and Reservoirs in Southeast Asia and Africa. Otley (United Kingdom): Westbury Publishing.

Seehausen O, Witte F, Katunzi EF, Smits J, Bouton N. 1997a. Patterns of the remnant cichlid fauna in southern Lake Victoria. Conservation Biology 11: 890–904.

Seehausen O, van Alphen JJM, Witte F. 1997b. Cichlid fish diversity threatened by eutrophication that curbs sexual selection. Science 277: 1808–1811.

———. 2003. Implications of eutrophication for fish vision, behavioral ecology, and species coexistence: A theoretical framework. Pages 268–287 in Crisman TL, Chapman LJ, Chapman CA, Kaufman LS, eds. Conservation, Ecology, and Management of African Fresh Waters. Gainesville: University Press of Florida.

Twongo T. 1996. Growing impact of water hyacinth on nearshore environments of Lakes Victoria and Kyoga (East Africa). Pages 633–642 in Johnson TC, Odada EO, eds. The Limnology, Climatology and Paleoclimatology of the East African Great Lakes. Amsterdam: Gordon and Breach.

Twongo T, Bugenyi FWB, Wanda F. 1995. The potential for further proliferation of water hyacinth in Lakes Victoria, Kyoga and Kwania and some urgent aspects of research. African Journal of Tropical Hydrobiology and Fisheries 6: 1–10.

Wanink JH. 1999. Prospects for the fishery on the small pelagic *Rastrineobola argentea* in Lake Victoria. Hydrobiologia 407: 183–189.

Wanink JH, Witte F. 2000a. The use of perturbation as a natural experiment: Effects of predator introduction on the community structure of zooplanktivorous fish in Lake Victoria. Advances in Ecological Research 31: 553–570.

———. 2000b. Rapid morphological changes following niche shift in the zooplanktivorous cyprinid *Rastrineobola argentea* from Lake Victoria. Netherlands Journal of Zoology 50: 365–372.

Wanink JH, Kashindye JJ, Goudswaard PC, Witte F. 2001. Dwelling at the oxycline: Does increased stratification provide a predation refugium for the Lake Victoria sardine *Rastrineobola argentea?* Freshwater Biology 46: 75–86.

Welcomme RL. 1995. Relationships between fisheries and the integrity of river systems. Regulated Rivers: Research and Management 11: 121–136.

———. 2003. River fisheries in Africa: Their past, present, and future. Pages 145–175 in Crisman TL, Chapman LJ, Chapman CA, Kaufman L, eds. Conservation, Ecology, and Management of African Fresh Waters. Gainesville: University Press of Florida.

Whitehead PJP. 1959. The anadromous fishes of Lake Victoria. Revue de Zoologie et de Botanique Africaines 59: 329–363.

Witte F, Goldschmidt T, Goudswaard PC, Ligtvoet W, van Oijen MJP, Wanink JH. 1992a. Species extinction and the concomitant ecological changes in Lake Victoria. Netherlands Journal of Zoology 42: 214–232.

Witte F, Goldschmidt T, Wanink JH, van Oijen MJP, Goudswaard PC, Witte-Maas ELM, Bouton N. 1992b. The destruction of an endemic species flock: Quantitative data on the decline of the haplochromine cichlids of Lake Victoria. Environmental Biology of Fishes 34: 1–28.

Witte F, Goudswaard PC, Katunzi EFB, Mkumbo OC, Seehausen O, Wanink JH. 1999. Lake Victoria's ecological changes and their relationships with the riparian societies. Pages 189–202 in Kawanabe H, Coulter G, Roosevelt A, eds. Ancient Lakes: Their Cultural and Biological Diversities. Ghent (Belgium): Kenobi Productions.

Witte F, Msuku BS, Wanink JH, Seehausen O, Katunzi EFB, Goudswaard PC, Goldschmidt T. 2000. Recovery of cichlid species in Lake Victoria: An examination of factors leading to differential extinction. Reviews in Fish Biology and Fisheries 10: 233–241.