Catastrophic Change in Species-Rich Freshwater Ecosystems

The lessons of Lake Victoria

Les Kaufman

Living communities change frequently. Hurricanes, volcanoes, predator outbreaks, and disease destroy old patches of forest and reef, making way for new species. Shifting continents redistribute the earth's great floras and faunas. Collisions with extraterrestrial debris may bring passage from one era of life to the next. Humans, too, are a force for ecological change, perhaps now the dominant force. Conversion of tropical forest to cropland or human habitation rapidly degrades species richness.

In the marine realm, the plight of the whales, sea turtles, and seabirds is widely known. Marine fishes and invertebrates are thought to be buffered against extinction by high fecundity and widely dispersed pelagic larvae (Robins 1991), but when more is known about marine animals more may be found to be endangered (Earle 1991, Kaufman and Strysky 1991, Tudge 1990). As for freshwater fishes and invertebrates, the evidence is more telling. Freshwater communities are exposed to the full brunt of deforestation, mining, poor land-use practices, exotic species introductions, and development. Therefore, it is not surprising that more than one in five freshwater fishes may be threatened or endangered (Kaufman 1989, Williams and Nowak 1986).

Entire freshwater fish faunas are disappearing (Avise 1990, Kaufman 1989, Tudge 1990, Williams and Nowak 1986, Williams et al. 1989). The infamous snail darter is but one representative of the vanishing mollusc and stream fish fauna of the Mississippi Basin and Appalachia. The desert pupfish is one of dozens of endangered desert fishes and insects in the US southwest and Mexico (Williams et al. 1989). Aquarium fishes bred domestically and available in pet stores are almost gone from their native haunts in Madagascar, Sri Lanka, and Borneo (Andrews and Kaufman in press). The endemic species flock of Lake Lanao, in the Philippines, is virtually extinct (Kornfield and Carpenter 1984). Though usually with fewer species to lose, high-latitude freshwater ecosystems are showing similar signs of stress and disruption (Taylor et al. 1984, Wells and McLain 1972, Williams et al. 1989).

Les Kaufman is chief scientist at the New England Aquarium's Edgerton Research Lab, Central Wharf, Boston, MA 02110.

There is at least an even chance of maintaining a diverse, productive, and healthy tropical ecosystem in Lake Victoria

The recent history of the fishes of Lake Victoria, East Africa (Figure 1), exemplifies a pace and magnitude of change that is alarming. In 1988, the World Conservation Union *Red Book of Endangered Species* listed the hundreds of endemic fishes of Lake Victoria under a single heading: "Endangered." The most exuberant expression of vertebrate adaptive radiation in the world (Table 1) is now in the midst of the first mass extinction of vertebrates that scientists have ever had the opportunity to observe, an event as exciting as it is depressing.

More than 30 million people who depend on the lake are feeling the consequences of roller-coaster changes in the fauna and lake environment. The most important freshwater food fishes in East Africa have already vanished from the marketplaces and very nearly from the planet. A fishery that once drew on hundreds of species, mostly endemic, now rests on three: a native pelagic minnow called the omena (*Rastrineobola argentea*) or dagaa in Tanzania; the introduced Nile perch (*Lates niloticus*), known as mbuta; and the introduced Nile tilapia, *Orechromis niloticus* (Figure 2).

Scientists, fishermen, and environmentalists have decried the loss of Lake Victoria's native species, and others have praised the introduction of Nile perch. Some have even referred to that fish as a savior. Now the savior threatens to destroy itself, the lake ecosystem, and a major source of protein in the midst of the world's fastest-growing human population. In Lake Victoria, as elsewhere, human welfare is intimately linked to concern for species conservation and ecosystem integrity.

The African great lakes and their fishes

To understand Lake Victoria, one must see both the lake and its fauna in the context of its giant East African neighbors, Lake Malawi and Lake Tanganyika (Table 2). The faunas of all three lakes exhibit the products of rapid speciation from very few ancestors. Best known is the fish family Cichlidae, of which more than 90% of the species in each lake are endemic (Greenwood 1984). Catfishes, mormyrids (elephant-nosed electric fishes), carps, gastropod and bivalve mollusks, insects, and crustaceans also have produced clusters of endemic species, but, with the possible exception of the Lake Tanganyika gastropods, these radiations are much less diverse and morphologically varied than those of the cichlids. Closely related but less species-rich cichlid flocks also occur in the nearby, smaller lakes Edward, George, Kivu, Kyoga, and Nabugabo (Greenwood 1974, 1981).

The cichlid faunas in the three great lakes in East Africa are strikingly similar and often cited as examples of evolutionary parallelism (Eccles and Trewavas 1989, Fryer and Iles 1972, Witte 1984). Three apparent lineages are present in the lakes: haplochromines, tilapiines, and lamprologines. The haplochromines are a species-rich and geographically widespread lineage. The tilapiines are species poor but also widespread. The lamprologines are species rich, but in the great lakes occur only in Lake Tanganyika.

As a group, the cichlids stand in contrast to the Nile perch and omena, both of which invest heavily in fecundity and little in parental care. The life history profile of chiclids in general entails small broods and extended parental care. Most East African haplochromine and tilapiine cichlids brood relatively few (5 to 100) large eggs and develop their young in the mouth, but the substratum-spawning lamp-rologines and tilapiines place large clutches (hundreds to thousands) of small eggs in nests on the lake bottom. All defend their young until they are self-sufficient. They have limited dispersal (except for seasonal inshore movements to spawn or release young) and strong site attachment—characteristics that should in theory make them highly vulnerable to extinction (Jablonski 1986, Gaston and Lawton 1990).

Curiously, this view is sharply at odds with certain other of the cichlids'

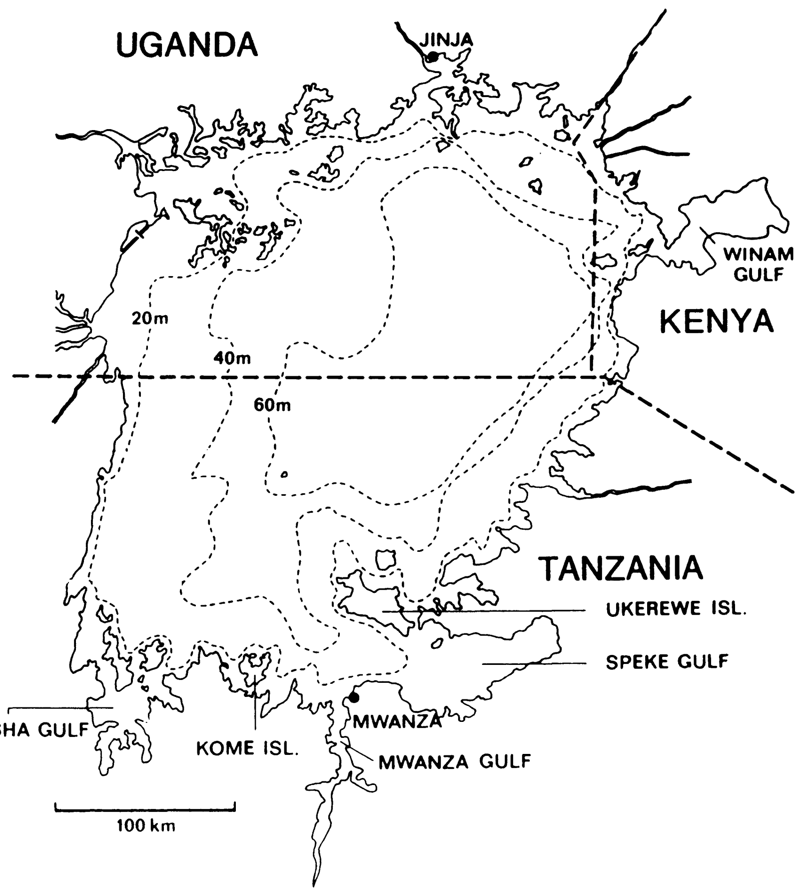

Figure 1. Lake Victoria, showing bathymetry. Note Winam Gulf in Kenya. The cluster of islands in the northwest sector is the Sesse Islands. Adapted from Witte et al. 1992.

attributes. They are aggressive, behaviorally and physiologically adaptable, phenotypically plastic, and prone to extraordinary evolutionary diversification (Avise 1990, Fryer and Iles 1972, Liem 1974). Much of this versatility has been attributed to a fundamental reorganization of the pharyngeal jaws that cichlids share with several closely allied fish families (Kaufman and Liem 1992).

Many cichlids can individually alter tooth and skull morphology in response to a change in diet (Greenwood 1965, Kaufman 1989, Meyer 1990, Sackley 1991, Witte et al. 1990). One cichlid, the Victorian snail-crusher *Astatoreochromis alluaudi,* was introduced to West Africa to help control the snail vectors for bilharzia, but these cichlids fed on insects instead of snails and stopped producing the massive dentition and musculature necessary to crush snail shells (Sloot-weg 1987).[1]

Cichlids have escaped from tropical fish hatcheries into the canals and everglades of south Florida, where they reproduce more successfully than do native sunfishes (Centrarchidae; (Courtenay and Robins 1973, Hogg 1976, Taylor et al. 1984). Introduced all over the world as a ready source of home-grown protein for developing nations, tilapiine cichlids may have affected hundreds of native fish communities.

In short, cichlids have adapted to an incredibly wide range of conditions. One might expect such adaptability and ecological versatility to offer some measure of protection against extinction. That it has not done so in Lake Victoria may be one indication of the magnitude of change that has taken place.

Recent changes in the Lake Victoria ecosystem

The recent history of Lake Victoria is one of dramatic change in limnological parameters and native fishery stocks from the late 1960s to the present (Ogutu-Ohwayo 1990). Over-

[1]Haplochromine Ecology Survey Team, 1992, University of Leiden, personal communication.

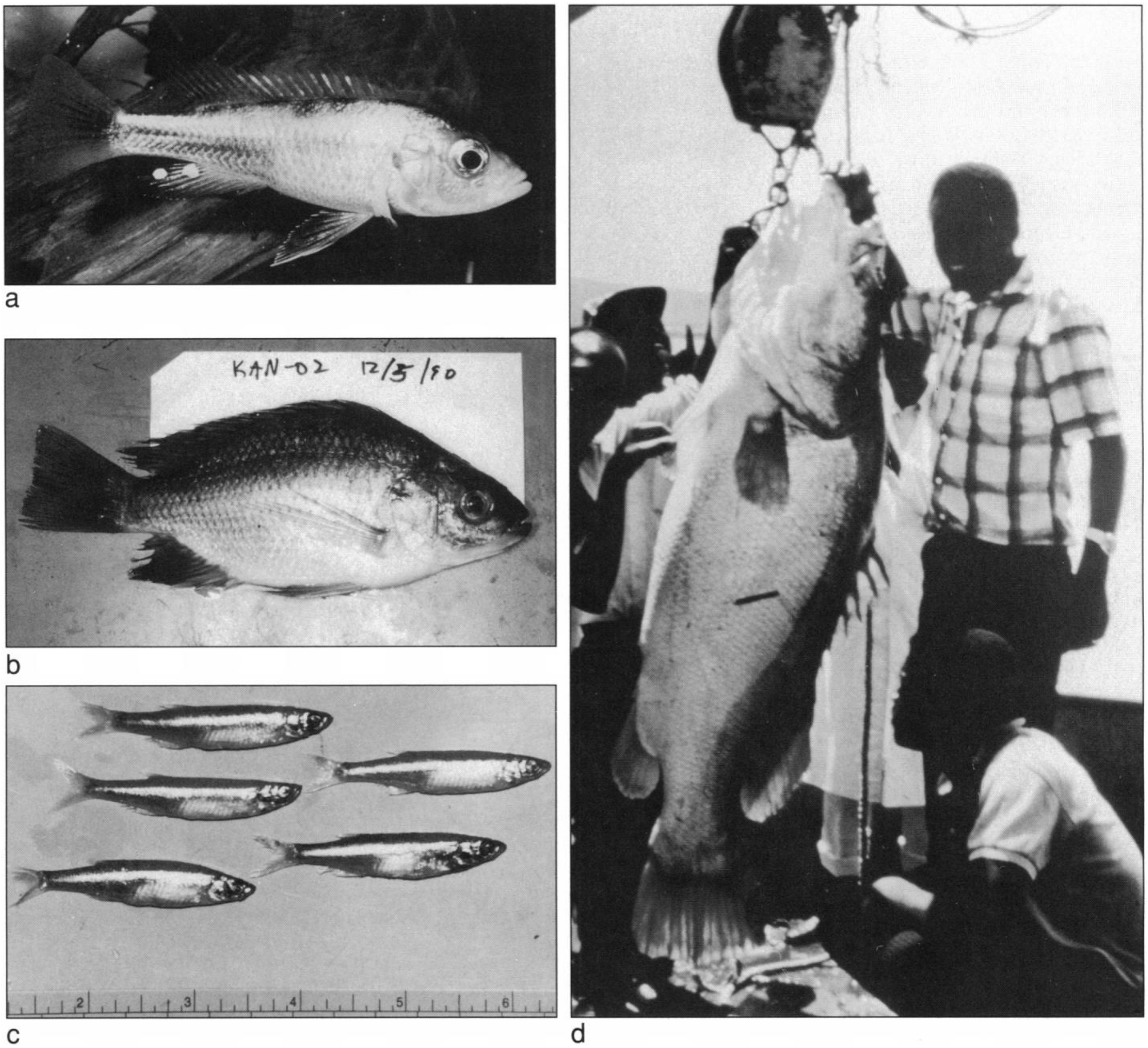

Figure 2. Some fishes of Lake Victoria. **a.** "Haplochromis" "argens," a zooplanktivorous haplochromine cichlid, is one of hundreds still undescribed (5–10 cm total length). **b.** The ngege, once the most important food fish in the region, is now near extinction (up to approximately 30 cm total length and more than 1 kg; this specimen is approximately 15 cm long). **c.** The omena, an anchovylike minnow, is the only native fish to have increased in numbers since 1978. **d.** Adult Nile perch can exceed 2 m and 200 kg in size, but most are smaller.

fishing, exotic species introductions, deleterious land-use practices, and pollution from various sources all contributed to the oxygen depletion and mass extinction of indigenous fishes now taking place.

The earliest known anthropogenic changes in the fish assemblages were the result of overfishing. Gill nets and other modern fishing methods, introduced by the British in the early part of the century, led to the rapid depletion of important anadromous fishes that once had spectacular spawning runs up the rivers that flow into Lake Victoria, and of the ngege, *Oreochromis esculentus* (Figure 2b), which originally supported the lake's most important fishery (Graham 1929, Ogutu-Ohwayo 1990).

Several exotic species of tilapia were introduced from other lakes and rivers during the late 1950s to replace the devastated stocks of native fishes. At first these introductions were not very successful, but the Nile tilapia, *O. niloticus,* eventually took hold and prospered.

High rainfall during the 1960s submerged and destroyed extensive beds of littoral vegetation, eliminating important spawning and nursery grounds for native species. This natural occurrence must have contributed to the decline of at least those native species dependent on nearshore habitats.

Beginning in 1954, Nile perch (*L. niloticus*) were introduced to the lake (Fryer 1960). Nile perch persisted as a minor component of the fauna for two decades, until the early 1980s. Then the species underwent a staggered series of population explosions in the eastern, northern, and southern waters of the lake. The trigger for the Nile perch irruptions is not known; it is interesting and mysterious that the fish should have persisted for so long and at such low densities before the explosion.

The leading hypothesis for the native fishes' demise is that they were consumed by the introduced Nile perch: the decline in native fishes and the increase in Nile perch population are almost perfectly reciprocal (Figure 3, Ogutu-Ohwayo 1990, Witte et al. 1992). Indeed, Nile perch seem to have regulated fish diversity in the past. Those East African lakes naturally inhabited by Nile perch have few haplochromine species, whereas those without the predator host species-rich communities (Greenwood 1981).

The dramatic disappearance of native fishes from Lake Victoria took place within a remarkably short time period, mostly between 1975 and 1982 (Witte et al. 1992). As recently as 1978, the haplochromine fauna was intact. Haplochromines contributed approximately 80% of the biomass and Nile perch less than 2%, with the remainder consisting of the introduced Nile tilapia and native noncichlids.

By 1983 in Kenya (Figure 4) and by 1986 in Tanzania, the native fish community had been virtually destroyed, and Nile perch comprised better than 80% of the catch. The remaining 20% consisted of Nile tilapia, the tiny native omena, and a small remnant of other native fishes. A community of more than 400 fish species collapsed to just three co-dominants: the Nile perch, the Nile tilapia, and a single indigenous species, the omena (Hughes 1986). Meanwhile, as its own supply of forage fish dwindled, the Nile perch exhibited an astonishing ecological shift. In essence, it has now become a whale, subsisting largely by scooping up great heaps of a tiny native shrimp, *Cardina nilotica*. The next most important item on the Nile perch menu is Nile perch; cannibalism is now a major link in the food chain.

At first, Lake Victoria was cited as a classic example of what can go wrong with alien fish introductions in tropical fresh waters (Barel et al. 1985, Balon and Bruton 1986). Local fisherman complained bitterly about Nile perch. The huge, clumsy fish destroyed the fishmen's nets and equipment, which had been designed for smaller quarry. Nile perch flesh is oily, and without refrigeration quickly rots. Sun-drying, a method of preservation that worked for the cichlids, does not work for large Nile perch. Nile perch could be smoked, but this method requires wood. Trees are in short supply around most of Lake Victoria, a decline that some think may have been accelerated by this new demand.

Such was the story of disaster told in the foreign press. But during the late 1980s the situation changed, as foreign aid and investors helped bring refrigerator trucks and processing plants to the lake shore. The fatty, flaky white flesh of Nile perch became popular on African hotel menus and a successful export to Europe and Israel. Scientists deplore the loss of haplochromine biodiversity (Barel et al. 1985, Witte et al. 1992), but the importance of biodiversity is readily questioned when a commodity of immediate value appears in its place.

The African view of the Lake Victoria's Nile perch is complicated, and largely misunderstood by outsiders who have caught only bits and pieces of this ecological soap opera (e.g., Avise 1990, Dawes 1986, Harrison et al. 1989, *New Scientist* 1988, Tudge 1990). The small-scale subsistence fishery that focused on the native cornucopia has taken a severe beating, with most species simply gone from the marketplace. My conversations with villagers in Kenya and Uganda revealed that, regardless of

Table 1. Examples of trophic diversification in Lake Victoria. Nomenclature follows Greenwood 1979, except for undescribed species, which are listed, by convention, as "Haplochromis" with nickname in quotes to avoid confusion with described taxa.

Trophic groups	Taxa
Plant eaters	
Pelagic phytoplanktivore	"Haplochromis" "kribensis"
Detritivore 1 (soft algae)	*Enterochromis* spp.
Detritivore 2 (diatomaceous ooze)	*Oreochromis esculentus*
Rock scraper	*Neochromis* spp.
Plant scraper	*Haplochromis lividus*
Algal browser	"Haplochromis" "kruising"
Leaf chopper	*Xystichromis phytophagus*
Algal gardener	*Neochromis nigricans* (?)
Arthropod eaters	
Crab eater	"Haplochromis" "smoke"
Prawn eater	*Psammochromis* spp.
Generalized insectivore	*Astatotilapia* spp.
Rock picker	"Haplochromis" "rockpicker"
Fat-lipped sucker	*Paralabidochromis chilotes*
Forceps-toothed picker	*Paralabidochromis victoriae*
Rock-reef, low-foraging zooplanktivore	"Haplochromis" *nyereri*
Rock-reef, high-foraging zooplanktivore	"Haplochromis" "double stripe"
Soft-bottom zooplanktivore	*Astatotilapia piceata*
Sand/rock, pit-hunting zooplanktivore	"Haplochromis" "deep black"
Pelagic zooplanktivore	"Haplochromis" "argens"
Sand sifter	*Psammochromis* spp.
Parasite picker	"Haplochromis" *teunisrasi*
Mollusc eaters	
Winkler	*Ptyochromis sauvagei*
Oral snail crusher	*Macropleurodus bicolor*
Oral clam crusher	*Hoplotilapia retrodens*
Pharyngeal crusher	*Labrochromis* spp.
Fish eaters	
Ambush piscivore	*Pyxichromis orthostoma*
Pursuit piscivore	*Prognathochromis dentex*
Snout-engulfing paedophage	*Lipochromis maxillaris*
Egg snatcher	*Astatotilapia barbarae*
Scale eater	*Allochromis welcommei*

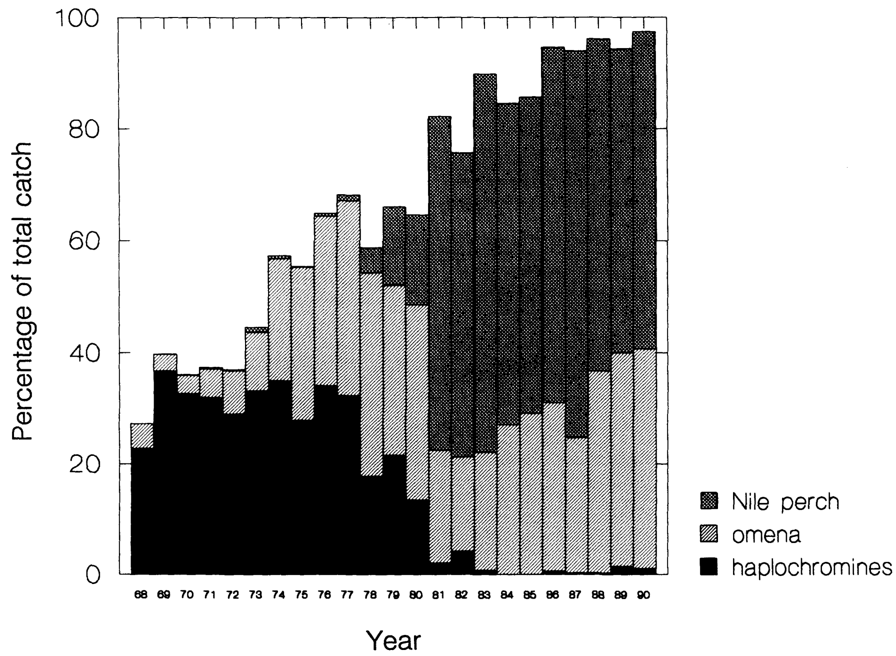

Figure 3. Percentage of the commercial catch in Kenya made up of haplochromine cichlids, omena, and Nile perch between 1968 and 1990. The remaining 40% to 70% of the catch before 1981 was dominated by native lungfish (*Protopterus*), catfishes (*Synodontis* and *Clarias*), carps (*Labeo* and *Barbus*), elephant-nose fishes (*Mormyrus*), and both native and introduced tilapiine cichlids (*Oreochromis* and *Tilapia*). (From Getabu 1987, FAO Report #388.)

how they may feel about the Nile perch, they miss the native fishery with its great variety in taste and texture.

The revenues generated by the Nile perch fishery are much greater than those ever realized from the lake's native species, but the relationship between changes in the lake's fauna and changes in revenues generated by the fishery is not a simple one. Landings data, such as those presented in Figure 5 for Kenya, suggest that the usable productivity of the lake increased by at least half an order of magnitude over 15 years. Landings data can be misleading, however. Because the traditional nearshore fishery was less mechanized, less efficient, and less wide-ranging than the new fisheries aimed at Nile perch and omena, even if productivity were unchanged, landings would be expected to soar. Some Ugandan and Tanzanian fisherman may be selling their catches in Kenya, where prices tend to be higher, thus skewing estimates of landings by country.

Experimental fishery surveys are less vulnerable to such bias and tell a strikingly different story. Experimental surveys are carried out on a routine basis by the Kenyan, Ugandan, and Tanzanian fishery research organizations; estimates of standing stocks for introduced and native fishes in Kenya's Winam Gulf region are presented in Figure 4. The sharp switchover from native to introduced species is still there, but by these data, standing stocks of introduced species were only marginally higher in 1990, if at all, than were the stocks of native species 20 years earlier.

Although more tonnage is being landed, and more valuable tonnage at that, the total amount of fish biomass produced annually by the lake may not have changed as much as first thought. From a marketing standpoint, the new product may be easier to handle because it lacks the native species' bewildering variety. This change is analogous to the common practice of clearcutting rainforest and replacing it with one or a few fast-growing, easily processed, exotic timbers.

The distribution of wealth resulting from the Nile perch fishery is also different from that of the original, artisanal fishery. Some local fisherman may actually be worse off despite the apparent plenty. Large-scale operations that exploit the introduced species for foreign currency are doing well. The small-scale fisherman and fishmongers, who never went hungry and who relied for their livelihoods on the traditional tastes and interesting diversity of the native species, are a vanishing breed. The specter of protein malnutrition in the lake basin has been raised by socioeconomists, an incredible irony in a place exporting nearly 200,000 tons of fish protein annually.

Mysterious die-offs of Nile perch, and evidence that the stocks are being overfished, have raised additional concerns. There is serious worry about the future of Nile perch, a concern much stronger than the lingering nostalgia for native food fishes and the biodiversity of haplochromines. But most people do not realize that there is now an even more serious problem: the entire lake has been placed in jeopardy by profound changes in the structure and dynamics of the ecosystem.

Along with irruptions of Nile perch, the early 1980s brought another surprise: the regular appearance of dense algal blooms and associated low oxygen levels in the lake's shallow waters (Ochumba and Kibara 1989). Anoxia brought stinking masses of dead Nile perch to the surface. Fish kills had probably occurred on Lake Victoria before,[2] but not with such frequency or intensity. In March of 1987, the US National Undersea Research Program sent a remote-operated vehicle and team of investigators to Lake Victoria to meet with local scientists as an overture to a planned Large Lakes of the World Program.

During a series of demonstration dives on the lake, the group discovered that below 30 meters there was no fish life, and the bottom was littered with dead and dying organisms. This observation was the first hint that the anoxia described by Ochumba (Ochumba and Kibara 1989, based on data collected in the early to mid-1980s) might in fact be extensive in the lake's deeper waters and thus worthy of grave concern.

The Lake Victoria Research Team was formed to spur multinational research in the northern waters of the

[2]R.L.Welcomme, 1992, personal communication. FAO, Fisheries Research and Environment Division.

lake, as part of a larger Lake Victoria Research and Conservation Program coordinated through the New England Aquarium in Boston. The National Undersea Research Program provided seed support for hydrological and remote-operated-vehicle survey work, and the National Science Foundation funded preliminary biotic survey activities. The US Agency for International Development, the Pew Foundation, the Canadian International Development Research Council, and the Conservation Food and Health Foundation also assisted.

The results of the first phase of work by Lake Victoria Research Team members are alarming. It appears that coincident with the Nile perch explosion was a violent change in the physical environment of the lake. Before 1978, aerobic life penetrated into the lake's deepest waters. The lake was well-mixed, although oxygen was lower in the deeper waters (more than 60 meters) for brief periods during the long (approximately February through April) and short (December) rainy seasons (Talling 1966). Fish biomass was high even in deep water, though the rains may have initiated inshore migration by fishes requiring higher oxygen levels (Hoogerhoud 1983).

In contrast, now Lake Victoria appears to be stratified for the entire year. Seasonality is still apparent, but mixing is restricted to periods during June and July when the oxycline (the depth at which oxygen falls precipitously), though still persistent, sinks to approximately 50 meters[3,4] (Figure 6a). The region between 50 and 25 m is subjected year-round to frequent, severe deoxygenation. We have observed local upwellings of hypoxic water, along with extensive fish kills, at the surface near rocky islets. Thus, most of the lake's volume is incapable of supporting any but the most rugged species. Adult Nile perch themselves are probably not tolerant of prolonged hypoxia.

One interesting sidelight was the discovery that in the deepest portions of Rusinga Channel at the mouth of Kenya's Winam Gulf oxygen levels are consistently higher than at equivalent depths in the main lake (Figure 6b), from which the gulf is partially isolated by a shallow sill. This protected region is inhabited by several tiny, undescribed deepwater haplochromines (e.g., Figure 2a).

Table 2. Physical characteristics and biodiversity profiles for the three largest lakes of East Africa. Lakes Victoria and Malawi excel in species and trophic diversity. Lake Tanganyikan cichlids exhibit the greatest reproductive, form, and phyletic diversity.

	Lake		
Physical characteristics	Victoria	Malawi	Tanganyika
Surface area (sq km)	62,000	28,000	32,600
Maximal depth (m)	100	700	1470
Effective depth (m) (depth at which oxygen levels fall below 1 ppm)	100 (before 1986) 40 (after 1987)	200	150
Biological characteristics			
Species diversity (Cichlidae)	Medium (350+)	High (500+)	Low (170+)
Trophic diversity	High	High	Medium
Reproductive diversity	Low	Low	High
Form diversity	Low	Medium	High
Phyletic diversity	Low	Medium	High
Age of radiation (thousands of years)	14–225	<1500	3000+

Perhaps the greatest surprise from the work using the remote-operated vehicle was the observation that the lake's small, native detritivorous shrimp, *C. nilotica*, was abundant and active in the midst of massive kills of omena at and below the point where oxygen levels declined toward zero. This observation is important because it suggests that the shrimp might have a refuge from Nile perch. The predator, which as an adult is believed to require a level of at least 5 ppm oxygen in its water, would probably be unable to destroy this food base the same way that it wiped out the old one.

Myriad other aspects of the lake's ecology also appear to have changed: productivity and turbidity have both increased, papyrus swamps seem to be on the decline, snails seem greatly increased in abundance, locals say lake fly (mostly *Chaeoborus* swarms) are larger and more prevalent than before, and water hyacinth, a noxious floating plant introduced from South America, has invaded Lake Victoria from Rwanda via the Kagera River; now it is spreading and increasing in the lake. It will take a while to assess the validity, the timing, and the relative importance of such changes.

The collapse of the species-rich Lake Victoria ecosystem and its replacement by a highly simplified, largely exotic community raises of plethora of varied and important questions. The answers must address the dynamics of speciation and extinction, the wisdom of alien introductions, and the practices of fisheries management in the tropics.

What happened to Lake Victoria?

The recent changes in Lake Victoria are astonishing, but they are not without precedent: this lake has a tumultuous past. The Victorian Basin as a whole was formed approximately 750,000 years ago when crustal uplifting and doming reversed the westward flow of the Kagera and Katonga rivers into the new lake basin (Kendall 1969). The basin's lakes have varied in depth, shape, and number several times since its formation (Greenwood 1974, 1981, Scholz et al. 1990). On reflection, there must already have been several cycles of explosive speciation and mass extinction, with the recent faunas of lakes Victoria, Kyoga, Edward, George, Nabugabo, Kanyaboli, and Kivu being only the latest bursts in a series of massive speciation events (Greenwood 1981). Lake Victoria itself may have completely dried up only 14,000 years ago (Scholz et al. 1990). The speciation rate that this history would imply (more than 350 species arising in 14,000 years) is overwhelming.

The current crisis probably began with the eutrophication of the lake basin. Algal productivity in Lake

[3]L. Kaufman, 1992, manuscript in preparation.
[4]R. Hecky, 1992, manuscript in preparation. Freshwater Institute, Canada.

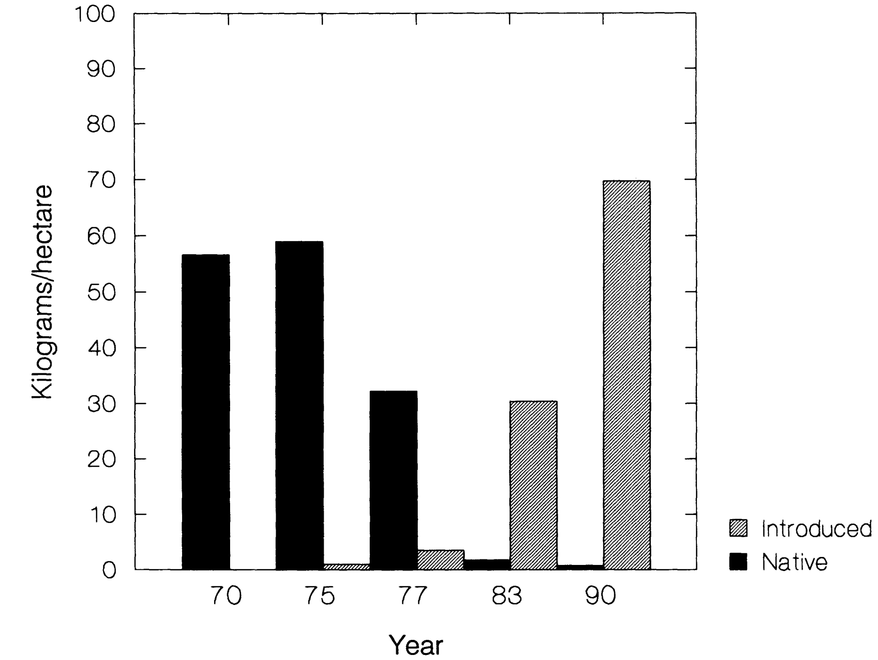

Figure 4. Demise of the native fishes of Lake Victoria, as illustrated by fisheries surveys in Kenyan water by the Kenyan Marine and Fisheries Research Institute. Standing stock estimates derived from the following numbers of hauls: 1969–1970 = 19; 1975 = 69; 1977 = 167; 1982–1983 = 54; 1989–1990 = 41. (Data courtesy P. Ochumba, A. Asila, and J. Ogari of KMFRI.)

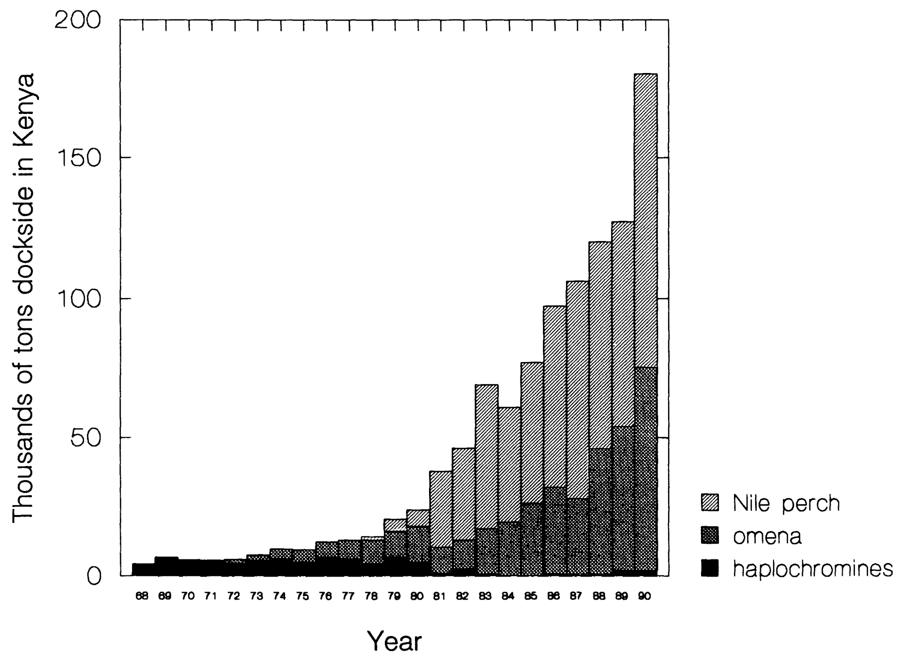

Figure 5. Total landings for haplochromines, omena, and Nile perch in the Kenyan waters of Lake Victoria, 1968–1990. (From Getabu 1987, FAO Report #388.)

Victoria has increased fourfold over several decades, with a concomitant drop in water transparency (Ogutu-Ohwayo 1990). This change could be due to an increase in anthropogenic nutrient loads and/or changes in nutrient dynamics within the lake. Even before the Nile perch irruptions, the Lake Victoria ecosystem probably had already been altered by eutrophication. The huge stocks of detritivorous haplochromines observed before the collapse of the 1980s might have been at least partly a reflection of the increase in primary productivity.

It is remarkable that the Lake Victoria ecosystem was able to cope with increased productivity over several decades without an earlier collapse. This resilience may have been related to the high proportion of haplochromine cichlids, which eat virtually everything—especially each other, with more than half the haplochromine species once preying on other haplochromines (Greenwood 1981, Witte et al. 1992). In addition to the tight internal recycling that they provided, the haplochromines helped to move biomass and nutrients in the course of their vertical and horizontal migrations (e.g., Goldschmidt 1989).

This biological mixing could have been as important in lake dynamics as is the physical mixing of the water column. First, it could have retarded the accumulation of rotting biomass in the deeper portions of the lake. The importance of this effect should not be underestimated: 80% of the haplochromine biomass, or approximately 60% of the lake's total biomass, consisted of cichlids that fed in the lake's thick layer of detritus. The second effect of biological mixing was to expose much of the lake's biomass to potential export through predation on fishes by birds (Wannink 1990), snakes, crocodiles, otters, and other amphibious organisms, including, of course, the human population.

In sum, Nile perch may have decoupled the recycling capacity in Lake Victoria by converting the recycling machinery itself, (i.e., the haplochromines) into Nile perch flesh. A primary question is whether the present, still-presumptive links from detritus to shrimp to Nile perch are indeed less efficient than those of the original food web. If so, then the impact of this cessation of recycling and biological mixing, combined with a long-term increase in anthropogenic nutrient loading on the lake and resulting increase in algal growth, could have caused a build-up of biomass in the lake's deeper waters. Biological oxygen demand would surge, and the deeper water column would be rapidly depleted of oxygen during periods of thermal stratification.

Native fishes, seeking reliable refugia in their seasonal moves between shallow and deep water habitats, may have faced a choice of death by asphyxiation in deeper water or death by Nile perch predation in the more

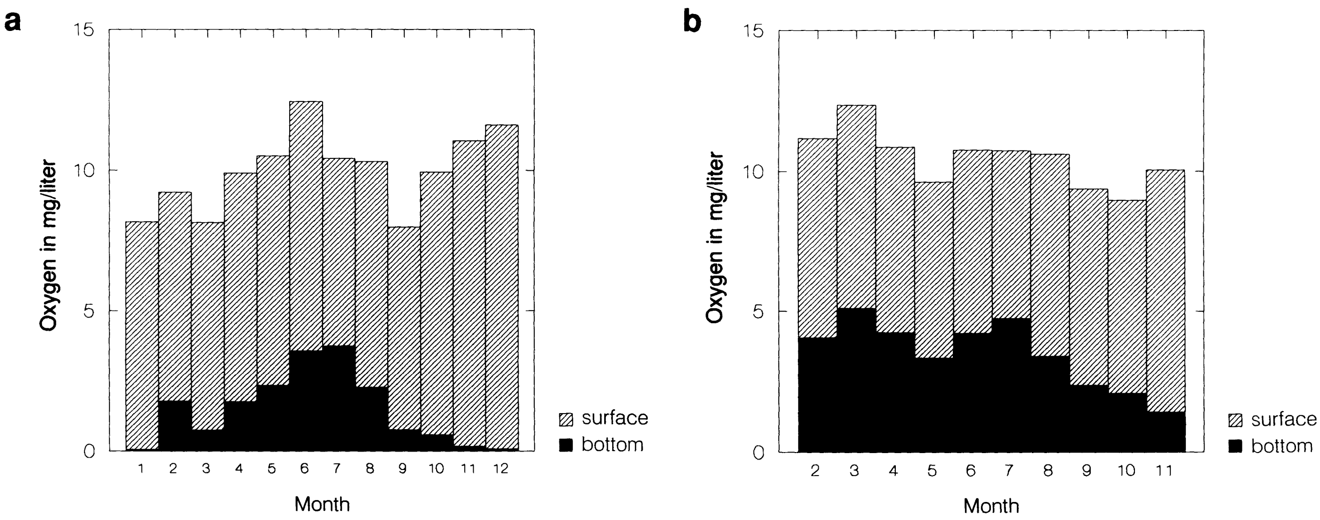

Figure 6. Mean monthly oxygen concentrations at the surface and bottom (depth 40–60 m) of Lake Victoria (measurements were made with a Hydrolab multiprobe). **a.** Open lake, based on six stations in the open waters of northeastern Lake Victoria (Kenya and Uganda). **b.** Rusinga Channel, Kenya, based on two stations located near the mouth of Winam Gulf. Note higher oxygen levels in Winam Gulf during those months for which comparative data are available. (From Lake Victoria Research Team; 22 missions conducted during 1989–1991.)

oxygen-rich shallows. Each force—deoxygenation and predation—selected for a mutually exclusive refugium. It is most likely this combination of complementary impacts, rather than any one factor by itself, that brought about the rapid disintegration of the hap-lochromine assemblage.

Alternative hypotheses can be constructed, but their assessment is hindered by a lack of comprehensive data. For example, little is known about the potential for the new food web to functionally replace the old one. The shrimp *Caridina* is both a detritivore and, and as seen from the remote operated vehicle, a facultative anaerobe, so it could transport organic material from the benthos into the lake's upper waters. We do not know, however, if the shrimps actually extend over much of the lake bottom, or if a significant portion of the population is available for consumption by Nile perch.

It is clear from temperate lakes, however, that changes in shrimp abundance can have profound impacts on aquatic food webs (Spencer et al. 1991). Lake fly larvae (*Chaeoborus*) such as those in Lake Victoria are well-known for their vertical migrations and tolerance of low oxygen levels, and when they metamorphose into winged adults, they could export benthic nutrients to the birds that feed on them. We do not know, however, if there are trophic links that could funnel benthic-derived nutrients into the fly larvae. One of the most interesting questions concerns the extent to which Nile perch juveniles can replace haplochromines as a manifold for nutrients to higher trophic levels (mostly adult Nile perch). Small Nile perch differ from large ones only in scaling, whereas 60% of the haplochromine species were piscivores that varied considerably in form and behavior as well as size.

Could it happen again?

The story of Lake Victoria, told and retold at scientific meetings, has become a kind of ballad, warning of the dangers of meddling with nature. Are other tropical lakes equally vulnerable to this kind of disturbance? Strong superficial similarities among the cichlid faunas of Lake Victoria, Tanganyika, and Malawi suggests that they are (Witte 1984). On the other hand, comparison of different facets of biodiversity in the East African lakes reveal properties unique to each fauna (Table 2). These differences are worth exploring in terms of their implications for conservation biology.

Lake Malawi has the highest species diversity of the three great lakes. Lake Tanganyika's cichlids exhibit the greatest variation in body form, as well as the greatest diversity in reproductive behavior. Lake Tanganyika also has the highest phyletic diversity—the greatest number of distinct, ancient lineages, each of which gave rise to independent radiations within the lake basin (Nishida 1991). Lake Tanganyika's great age and complex history probably explain the high phyletic diversity, which in turn provided the broad morphological substratum from which the lake's high form and reproductive diversity are derived. In contrast, the haplochromine flock in Lake Victoria exhibits four characteristics that clearly set it apart from the cichlid faunas of Lake Malawi and Lake Tanganyika:

- Species diversity out of proportion to age. The cichlid fauna of Lake Tanganyika could be anywhere from 3 to 100 times older than that of the Lake Victoria, yet Lake Victoria has (or had) two to five times as many haplochromine species as Lake Tanganyika. The implied rates of speciation in Lake Victoria are phenomenal regardless of whether one estimates age on the basis of tectonic, sedimentary, or molecular clues.
- High functional diversity. The Victorian haplochromines exhibit behavioral and dietary specializations comparable to those of the Malawian and Tanganyikan cichlids. In fact, Lake Victoria shares guilds with Lake Malawi that are absent in Lake Tanganyika. The best example is the functional group of piscivores known

Resolutions of the Workshop on People, Fisheries, Biodiversity, and the Future of Lake Victoria

After careful consideration of available evidence, based on research results, we conclude that the environment of Lake Victoria is changing rapidly and the fishery is unsustainable at its present composition and yield. Due to overfishing and the development of an export market, the amount of fish protein now available for local consumption is inadequate. The changing condition of the fishery will affect the social and economic welfare of millions of people in the Lake Victoria basin. Prospects for the future are cause for grave concern and reason for immediate action designed to resolve key unknowns and establish research and management policies that can be developed and applied expeditiously. The resolutions presented below outline the urgent need to understand current changes in limnology and the environment, to understand how fish biology affects the sustainability and management of the fishery, and to understand and mitigate the social and economic impacts of anticipated changes and varied management options.

General recommendation

It is necessary to form a Lake Victoria Fisheries Commission to harmonize research and management strategies for the Lake Victoria Basin. An important scientific function of the commission should be to foster close international cooperation, standardization of research and management methods, cross-calibration of scientific instruments, and continuity of monitoring.

Limnology and environment

- There is need to develop a general ecosystems model of Lake Victoria that includes the physical, chemical, biological, and human factors required to understand and predict lake productivity.
- Due to increased oxygen depletion, loss of fish habitat and fish kills are extensive. There is urgent need to understand the controls on oxygen distribution and levels in Lake Victoria, including the influence of low levels on fish stocks.
- Tremendous alterations in the food web have occurred in the last 30 years. Understanding the effects of these changes on water quality and lake productivity requires determination of the flows of nitrogen, phosphorus, sulfur, silicon, oxygen, and carbon into the lake ecosystem.
- There is need to determine the energy flow through the two major trophic pathways (grazing and detritus) that couple fish productivity with primary production.
- A research and management program for the wetland and forest habitat in the riparian zone of the lake and its waterways should be undertaken, with special attention to the water hyacinth.

Fish biology

- We must quantify interactions among food-web structures, water quality, and life-history characteristics of fishes in order to understand the relationship between fish production and the causes of eutrophication and anoxia in Lake Victoria.

as baby suckers, or paedophages (Wilhelm 1980). Paedophages are predators with large mouths, thick rubbery lips, and odd, stout, outward-pointed anterior teeth. Paeodophages take the head end of brooding females into the mouth, suck out the eggs or young, and then eject the spent female to eventually produce another meal.

- Low phyletic diversity. The entire Victorian haplochromine flock is descended from a single ancestral stock, no more than 225,000 years ago (Meyer et al. 1990). Lake Malawi may be monophyletic, but it has had time to produce several distinct descendent lineages. Lake Tanganyika's cichlids are definitely derived from a diverse ancestry (Nishida 1991).
- Low form diversity. The high species and functional diversity of Victorian haplochromines is out of proportion to their limited variation in body form. The low form diversity greatly complicates taxonomic work with these organisms, though data on both behavior and morphology support their validity as biological species (Hoogerhoud et al. 1983).

These attributes make the Victorian radiation especially important to evolutionary biologists, but they also raise a red flag. Species that share so much in genetics and outward appearance may also share vulnerabilities.

No matter how adaptable they may be individually, all of the Victorian haplochromines are likely to share many of the same weaknesses. Just as genetic diversity among individuals may be critical to the long-term survival of a species, the genotypic and phenotypic diversity among species could provide a community with some hedge against mass extinction and ecological collapse. If so, Lake Victoria may have been unusually vulnerable to the dramatic events that have overtaken it.

- There is continuing need for stock assessment such as that now underway with support from the European Community. Such assessments are necessary to guide ecosystems modelers, policy makers, fisheries investors, and fisheries managers.
- Refuge areas (fish parks) should be established to protect the diversity of the native fish species and maintain spawning stocks of commercially important species.
- The possible contribution of aquaculture and management of alternative fisheries to the fishery industry should be fully explored, including their potential for restoring and rehabilitating indigenous stocks.
- Proposals for the introduction of exotic flora and fauna to the Lake Victoria ecosystem should be submitted to the Lake Victoria Commission for evaluation. Such proposals must be treated with great caution and rigorously evaluated with respect to biological, economic, and social impacts. Introductions must meet with the approval of all three riparian nations. Management of species already introduced is essential to the welfare of existing fisheries.

Policy, management, and socioeconomics

- The quality of runoff water from the land is deteriorating and may affect fish habitat. Fishery scientists should define water quality requirements of the fishery and work closely with limnologists in drafting overall guidelines for the water quality of Lake Victoria.
- Proposals for fisheries planning and development should be submitted to the Lake Victoria Commission for detailed social and environmental impact assessment before implementation. All proposals must be cognizant of the changing patterns of ownership and the control of harvesting and processing facilities. They should also analyze the differential incomes received by the various participants in the fishery industry.
- The fisheries planning process needs to be integrated with the development of information systems encompassing regional, social, economic, and biological data. Programs should be developed to assist those groups most likely to suffer the effects of predicted declines in the current fishery.
- Research should identify the factors that facilitate or impede local participation in fisheries management, and fisheries officials should be familiarized with programs in other countries that involve local fishers and fisheries management.
- The supply of fish within the lake basin available to local populations is insufficient to meet their needs. Studies should be conducted to determine if the expansion of the Nile Perch fishery and export marketing have contributed to reduced dietary protein and malnutrition in local people.
- An economic assessment of the value of the native fauna is needed, taking into account their value for food, aquarium trade, medicine, and tourism.
- The feasibility of levying a tax on fish exported from the basin to support the research, management, and monitoring of the fisheries should be determined. Proceeds should be directed initially toward the effective implementation of regulations on fishing gear, methods, and allowable catch.

Workshop was held in Jinja, Uganda, 17–20 August 1992. It included scientists from Uganda, Tanzania, Europe, and North America. The meeting was sponsored by the US National Science Foundation.

What can be done?

Talk of large-scale manipulation to improve or "rescue" Lake Victoria never fails to fuel heated debate, because not everyone regards management of severely damaged ecosystems as a practical enterprise. At the rate that tropical ecosystems are deteriorating, however, it would behoove us to begin to think seriously about management.

There is some room for optimism. Huge Lake Erie, declared "dead" only 30 years ago, is once again an important recreational and fishery resource. The success in Lake Erie is empowering, so long as it is understood that Lake Erie was rehabilitated, not restored; the present biotic assemblage is dominated by introduced species. In addition, the story of Lake Erie is not finished. The introduction and spread of the exotic zebra mussel (Roberts 1990) is a new challenge.

To do nothing at all in Lake Victoria would clearly be foolish, because there are genuine threats facing the people of the lake basin. Most immediate is the threat to the fishery posed by the lake's hypoxic bottom waters and physical instability. There have been many local fish kills caused by mixing events that have trapped fish populations in oxygen-depleted water. Exploration with remote-operated vehicles has shown that the fish kills seen on the surface are even more extensive on the lake bottom at 30 m and deeper. Thus, a large-scale fishery collapse from a major mixing event is a real possibility. Another threat may come from sharp reductions in the abundance of snail-eating fishes, which will probably affect the prevalence of bilharzia. This effect can be complex, either raising or lowering the incidence of disease according to the age distribution of the snails.

Wholesale species extinctions have made it impossible to restore Lake Victoria, but that observation does not rule out an attempt to rehabilitate it. Cautious management of the watershed, the lake ecosystem, and the fishery could have positive effects. Much more must be known about the lake ecosystem before any sophisticated manipulations can be attempted, but meanwhile there are numerous actions that can bring definite benefits to the people of the region.

The identification and reduction of anthropogenic nutrient inputs is one potential action. This challenge could be combined with afforestation projects with indigenous species to rebuild some of the native forests and their biodiversity, reduce materials and contaminants in runoff, and help restore the dwindling supply of firewood. Careful management of the Nile perch population could aid both the Nile perch fishery and the survival of native species. The establishment of separate management areas for native and introduced species could be a useful approach, because there do appear to be distinct refugia, or at least geographically circumscribed remnants of the native fauna. Native food fishes, if kept from extinction, can certainly be restored to the marketplace through aquaculture.

Many of the native species are of great value, and their remnant populations are potentially significant economic assets. For example, the anadromous ningu (*Labeo victorianus*) lends itself well to hatchery-style aquaculture and in situ restoration efforts, much like those employed for North American trout and salmon species. The ngege, though smaller and slower growing than the introduced Nile tilapia, is reputedly the most delicious tilapia species in the world. Its genome is a prize for the tilapia aquaculture industry, whose products are derived from selective breeding and hybridization of wild gene pools. The ngege is also one of the most specialized phytoplanktivores among the East African lake fishes; it could someday assist in cropping algal blooms in Lake Victoria.

Similar arguments can be made for the lake's haplochromines. They can be eaten (though never among the most desirable speciest, they were locally important both for food and medicinal use), help control disease-carrying snails and insects, serve as forage for larger edible fishes, and offer intriguing possibilities for polyculture because of their functional diversity.

Perhaps the greatest opportunities for positive change come from development projects now slated for the lake basin. Though traditionally thought of as harbingers of further devastation, plans to expand industry or tourism can, if properly planned and executed, bring great benefit to the local people, to the investors, and to the long-term security of biodiversity and the environment.

An excellent example of this potential, as well as the potential for disaster, is a project planned for Uganda's Sesse Islands. More than 80 small islands and islets located in the lake's northwest corner (Figure 1), the Sesse Islands, are still largely forested and are an important conservation area for flora and fauna, both terrestrial and aquatic. They would be an ideal location for experiments in sustainable development, habitat conservation, and species restoration. Whether the investors can muster the wisdom, the foresight, and the morals to conduct this project in an exemplary manner remains to be seen. If they fail, Uganda will lose one of the last shreds of the Lake Victoria Basin still in a reasonably intact state.

There is at least an even chance of maintaining a diverse, productive, and healthy tropical ecosystem in Lake Victoria, drawing on both native and introduced species as building blocks. The details of the new system depend on the ingenuity of restoration biologists, multinational cooperation, and socioeconomic vision. Most important, those involved must be prepared to accept the fact that some aspects of the system will be highly nonlinear or totally unpredictable and therefore beyond control.

There is no lack of dissenting views. Colleagues and proposal reviewers have stated that Lake Victoria should be written off so that scarce resources can be focused on conservation in Lakes Malawi and Tanganyika. This idea is not popular around Lake Victoria. It is considered in the same vein as the view that AIDS is beneficial because it will solve the problem of overpopulation in the region. The continued presence of Nile perch in the lake raises obvious doubts about reintroduction, but data from Tanzania, Kenya, and Uganda indicate that at least 10% of the original fauna in the well-sampled nearshore region is persistent and sympatric with high Nile perch densities. It would pay to learn which taxa are resistant to extinction in the lake as it is today, why they are resistant, and what other native species might with some assistance also have a chance to survive.

To the scientist, the haplochromines of Lake Victoria have a great deal to teach about both speciation and extinction. To the conservationist, the remnants of the native fauna are the building blocks for attempting to reconstruct the Lake Victoria ecosystem. We echo Aldo Leopold's advice to intelligent tinkerers: do not throw away the pieces. These pieces are the most critical of all resources for the future, provided that a safe, productive context for them can be created in a future ecosystem.

In 1987, the New England Aquarium proposed programs to save the pieces of three disintegrating fish faunas through captive breeding: Lake Victoria, North American desert fishes, and Appalachian stream fishes (Kaufman 1987). Lake Victoria was chosen as the first trial project, and today the program engages the efforts of more than 30 institutions, led by the New England Aquarium and the Columbus Zoo aquarium.

Captive breeding programs only make sense as part of in situ conservation efforts (Kaufman 1987, 1989, Reid 1990). Ironically, their greatest contribution may be in acting as a wedge to build awareness and garner institutional and grant support for programmatic work, such as that of the Lake Victoria Research and Conservation Program. Certainly the fauna rescue and captive breeding program for Lake Victoria has had this effect, even though it had its humble beginnings in an attempt to maintain an array of Victorian haplochromines as a living archive for research purposes, an effort initiated in the mid-1980s by researchers at the University of Leiden and the British Museum. The Lake Victoria Research and Conservation program picked up where the earlier research left off.

Now it is possible to contemplate using rescued haplochromines in polyculture and reintroduction. Furthermore, the experiences with the Lake Victoria breeding program can inform efforts to conserve freshwater fish species around the world, the focus of a workshop held in Columbus, Ohio, in October 1992. Hopes, are running high for coordinated ecosystems, fisheries, and resource management planning for Lake Victoria as a whole.

The Lake Victoria Research and Conservation Program has focused on three objectives: to understand biological processes in the lake and its watershed well enough to offer management alternatives to decision makers in the three countries; to track and where possible prevent the extinction of native species; and to restore endangered food fishes to the marketplace through aquaculture. In August 1992, scientists, policy makers, and government administrators met on the Ugandan shoreline of Lake Victoria to discuss the condition of the lake and the further steps that might be taken (see box page 854).

Preservation of virgin natural ecosystems, the world's "last great places" in the words of The Nature Conservancy's celebrated program, is a major preoccupation of conservationists, and deservedly so. But perhaps this approach is too limited to the situation of the moment. Lake Victoria may inspire some attention to salvaging orphaned pieces of ecosystems that can never again be precisely as they were.

Conservationists scan the scars of civilization for those places where the odds and the payoff for biological salvage and reconstruction are the greatest. On land, such a place may be Madagascar, Hawaii, or the dry forest of Costa Rica (Janzen 1986). On water, it is without question Lake Victoria. The value of conservation efforts, even in badly damaged ecosystems, should not be doubted. Anything is better than waiting 20 millennia for a new fauna, or a new source of food, to evolve.

Acknowledgments

Seed funds for the Lake Victoria Research and Conservation Program were provided by the New England Aquarium for coordination and public education, the National Undersea Research Program for hydrology and visual exploration by remote vehicles, the National Science Foundation for preliminary faunal survey and research planning, the Environmental Protection Agency for rescue and propagation of endangered native food fishes, the Institute for Museum Services for the haplochromine captive breeding program, US-AID and IDRC of Canada for limnological studies, and the Conservation Food and Health Foundation for work by African colleagues. The author is grateful to the Pew Scholars Program for Conservation and the Environment for core support. The data and insights presented are the result of a team effort, led in particular by P. Ochumba, J. Ogari, and E. Okemwa (Kenya) and F. Bugenyi, R. Ogutu-Ohwayo, P. Basasibwaki, and B. Kudhongonia (Uganda), with major contributions by W. Cooper, M. Gophen and R. Hecky, P. Kilham, and R. Robinson. The author thanks P. H. Greenwood, F. Witte, R. Lowe-McConnell, R. Welcomme, and five reviewers for their stimulating comments. We applaud the efforts of our other colleagues and friends of the fisheries research institutes of Kenya, Uganda, and Tanzania, who have worked for so long, with so little, to understand Lake Victoria and brings its benefits to their people and the world. This article is dedicated to the memory of Peter Kilham.

References cited

Andrews, C., and L. S. Kaufman. In press. The role of captive breeding in the conservation of endangered freshwater fishes. *6th Conference on Breeding Endangered Species.*

Avise, J. C. 1990. Flocks of African fishes. *Nature* 347: 512–513.

Balon, E. K., and M. N. Burton. 1986. Introduction of alien species or why scientific advice is not heeded. *Environ. Biol. Fish.* 16: 225–230.

Barel, C. D. N., R. Dorit, P. H. Greenwood, G. Fryer, N. Hughes, P. B. N. Jackson, H. Kanawabe, R. H. Low-McConnell, F. Witte, and K. Yamaoka. 1985. Destruction of fisheries in Africa's lakes. *Nature* 315: 19–20.

Courtenay, W. R. Jr., and C. R. Robins. 1973. Exotic aquatic organisms in Florida with emphasis on fishes: a review and recommendations. *Trans. Am. Fisheries Soc.* 102: 1–12.

Dawes, J. 1986. Lake Victoria cichlids face extinction. *Aquarist and Pondkeeper* July: 22.

Earle, S. 1991. Sharks, squids, and horseshoe crabs—the significance of marine biodiversity. *BioScience* 41: 506–509.

Eccles, D. H., and E. Trewavas. 1989. "Malawian Cichlid Fishes: The Classification of Some Haplochromine Genera." Lake Fish Movies, Herten, Germany.

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

Fryer, G. and T. D. Iles. 1972. *The Cichlid Fishes of the Great Lakes of Africa: Their Biology and Evolution.* Oliver and Boyd, London.

Gaston, K. J. and J. H. Lawton. 1990. The population ecology of rare species. *J. Fish Biol.* 37(Suppl. A): 97–104.

Getabu, A. 1987. Aspects of the Lake Victoria fisheries with emphasis on *Oreochromis niloticus* and *Alestes sadleri* from the Nyanza Gulf. Kenya Marine and Fisheries Research Institute, Kisumu, Kenya.

Goldschmidt, T. 1989. An ecological and morphological field study on the haplochromine cichlid fishes (Pisces: Cichlidae) of Lake Victoria. Ph.D. dissertation, University of Leiden, Leiden, Netherlands.

Graham, M. 1929. The Victoria Nyanza and its fisheries: a report on the fish survey of Lake Victoria 1927–1928 and appendices. Crown Agents for the Colonies, London.

Greenwood, P. H. 1965. Environmental effects on the pharyngeal mill of the cichlid fish *Astatoreochromis alluaudi. Proc. Lin. Soc. Lond.* 176: 1–10.

______. 1974. Cichlid fishes of Lake Victoria, East Africa: the biology and evolution of a species flock. *Bull. British Museum (Natural History) Zoology Suppl.* 6: 1–134.

______. 1981. Species flocks and explosive evolution. Pages 61–74 in P. H. Greenwood and P. L. Forey, eds. *Chance, Change and Challenge: The Evolving Biosphere.* Cambridge University Press and British Museum (Natural History), London.

______. 1984. African cichlids and evolutionary theories. Pages 141–154 in A. A. Echelle and I. Kornfield, eds. *Evolution of Fish Species Flocks.* University of Maine Press, Orono.

Harrison, K., O. Crimmen, R. Travers, J. Maikweki, and D. Mutoro. 1989. Balancing the scales in Lake Victoria.

Hogg, R. G. 1976. Ecology of fishes of the family Cichlidae introduced into the fresh waters of Dade County, Florida. Ph.D. dissertation, University of Miami, Coral Gables, FL.

Hoogerhaud, R. S. C. F. Witte, and C. D. N. Barel. 1983. The ecological differentiation of two closely resembling *Haplochromis* species from Lake Victoria, *H. iris* and *h. hiatus* (Pisces: Cichliadae). *Neth. J. Zool.* 33: 283–305.

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

Jablonski, D. 1986. Mass extinctions: new answers, new questions. Pages 43–61 in L. S. Kaufman, and K. G. Mallory, eds. *The Last Extinction.* MIT Press, Cambridge, MA.

Kaufman, L. S. 1987. Caught between a reef and a hard place: why aquariums must invest in the propagation of endangered species. Pages 362–385 in *Proc. Amer. Assoc. Zool. Parks and Aquaria.* Front Royal, VA.

Kaufman, L. S. 1989. Challenges to fish faunal conservation programs as illustrated by the captive biology of Lake Victoria cichlids. Pages 105–120 in B. L. Dresser, R. W. Reece, and E. J. Maruska, eds. *Fifth World*

Congress on Breeding Endangered Species in Captivity.

Kaufman, L. S., and K. F. Liem. 1982. Fishes of the suborder Labroidei (Pisces: Perciformes): phylogeny, ecology, and evolutionary significance. *Breviora* 472: 1–19.

Kaufman, L. S., and A. Strysky. 1991. Designation of marine species for protection under US Endangered Species Act. Report to the Office of Protected Resources, New England Aquarium, Boston.

Kendall, R. L. 1969. An ecological history of the Lake Victoria Basin. *Ecol. Monogr.* 39: 121–176.

Kornfield, I., and K. E. Carpenter. 1984. Cyprinids of Lake Lanao, Philippines: taxonomic validity, evolutionary rates and speciation scenarios. Pages 69–84 in A. A. Echelle and I. Kornfield, eds. *Evolution of Fish Species Flocks.* University of Maine Press, Orono.

Liem, K. 1974. Evolutionary strategies and morphological innovations: cichlid pharyngeal jaws. *Syst. Zool.* 22: 425–441.

Meyer, A. 1990. Morphometrics and allometry in the trophically polymorphic cichlid fish, *Cichlasoma citrinellum*: alternative adaptations and ontogenetic changes in shape.

Meyer, A. T. D. Kocher, P. Basasibwaki, and A. C. Wilson. 1990. Monophyletic origin of Lake Victoria cichlid fishes suggested by mitochondrial DNA sequences. *Nature* 347: 550–553.

New Scientist. 1988. Monster fish may be innocent of ecological crimes. *New Scientist* 1622: 34.

Nishida, M. 1991. Lake Tanganyika as an evolutionary reservoir of old lineages of East African cichlid fishes: inferences from allozyme data. *Experentia* 47: 974–979.

Ochumba, P. B. O., and D. I. Kibara. 1989. Observations on blue-green algal blooms in the open waters of Lake Victoria, Kenya. *African J. Ecol.* 27: 23–34.

Ogutu-Ohwayo, R. 1990. The decline of the native fishes of Lakes Victoria and Kyoga (East Africa) and the impact of introduced species, especially the Nile perch, *Lates niloticus* and the Nile tilapia, *Oreochromis niloticus*. *Environ. Biol. Fish.* 27: 81–90.

Owen, R. B., R. Crossley, T. C. Johnson, D. Tweddle, I. Kornfield, S. Davison, D. H. Eccles, and D. E. Engstrom. Major low levels of Lake Malawi and their implications for speciation rates in cichlid fishes. *Proc. R. Soc. Lond. B* 240: 519–553.

Reid, G. M. 1990. Captive breeding for the conservation of cichlid fishes. *J. Fish Biol.* 37 (Suppl. A): 157–166.

Robbins, C. R. 1991. Regional diversity among Caribbean fish species. *BioScience* 41: 458–459.

Roberts, L. 1990. Zebra mussel invasion threatens U.S. waters. *Science* 249: 1370–1372.

Sackey, P. 1991. Morphological and behavioral plasticity in fishes. Master's dissertation, University of Massachusetts at Boston.

Scholz, C. A., and B. R. Rosendahl. 1988. Low lake stands in Lakes Malawi and Tanganyika, East Africa, delineated with multifold seismic data. *Science* 240: 1645–1648.

Slootweg, R. 1987. Prey selection by molluscivorous cichlids, foraging on schistosomiasis vector snail, *Biomphalaria glabrata*. *Oecologia* 74: 193–202.

Spencer, C. N., B. R. McClelland, and J. A. Stanford. 1991. Shrimp stocking, salmon collapse, and eagle displacement. *BioScience* 41: 14–21.

Talling, J. 1966. The annual cycle of stratification and phytoplanktion growth in Lake Victoria (East Africa). *Int. Rev. Ges. Hydrobiol.* 51: 545–621.

Taylor, J. F., W. R. Courtenay Jr., and J. A. McCann. 1984. Known impacts of exotic fishes in the continental United States. Pages 322–373 in W. R. Courtenay, Jr. and J. R. Stauffer, eds. *Distribution, Biology, and Management of Exotic Fishes.* John Hopkins University Press, Baltimore.

Tudge, C. 1990. Underwater, out of mind. *New Scientist* 3 November: 40–45.

Wannink, J. H. 1990. The pied kingfisher (*Ceryle rudis*) and dagaa (*Rastineobola argentea*): estimating the food intake of a prudent predator. In *Proceedings of the Seventh Pan-African Ornithological Congress.* Nairobi, Kenya.

Wells, L., and A. McLain. 1972. Lake Michigan: effects of exploitation, introductions, and eutrophication of the salmonid community. *J. Fish. Res. Bd. Can.* 29: 889–898.

Wilhelm, W. 1980. The disputed feeding behavior of a paedophagous haplochromine cichlid (Pisces) observed and discussed. *Behavior* 74: 310–323.

Williams, J. E., J. E. Johnson, D. A. Hendrickson, S. Contreras-Balderas, J. D. Williams, M. Navarro-Mendoza, D. E. McAllister, and J. E. Deacon 1989. Fishes of North America endangered, threatened, or of special concern: 1989. *Fisheries* 14(6): 2–20.

Williams, J. E., and R. M. Nowak. 1986. Vanishing species in our own backyard: extinct fish and wildlife of the United States and Canada. Pages 107–139 in L. S. Kaufman and K. G. Mallory, eds. *The Last Extinction.* MIT Press, Cambridge, MA.

Witte, F. 1984. Ecological differentiation in Lake Victoria haplochromines: comparison of cichlid species flocks in African lakes. Pages 155–167 in A. A. Echelle and I. Kornfield, eds. *Evolution of Fish Species Flocks.* University of Maine Press, Orono.

Witte, F., T. Goldschmidt, J. H. Wanink, M. J. P. van Oijen, P. C. Goudswaard, E. L. M. Witte-Maas, and N. Bouton. 1992. The destruction of an endemic species flock: quantitative data on the decline of the haplochromine species from the Mwanza Gulf of Lake Victoria. *Environ. Biol. Fishes* 34: 1–28.