

Chapter 8

The Great Lakes

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Lake Superior is greater in surface area than Lake Victoria. Lake Baikal is deeper than Lake Tanganyika. Nonetheless, the Great Lakes of East Africa are second to none, when it comes to the wealth of native fishes and the number of people dependent on these lakes. Lake Malawi is thought to host more than 500 species of fishes, nearly all endemic (27). Endemism is also >99% among the haplochromine cichlids of Lake Victoria, where more than 400 species appear to have evolved in less than 200,000 years (29) - geologically and evolutionarily little more than an instant. The most diverse faunas occur in Lake Tanganyika, the deepest and oldest lake. Fishes and snails in Lake Tanganyika are so varied in form that the occupants of this one lake might easily be mistaken for marine organisms hailing from dozens of unrelated taxa. Through the fish protein that they produce, the Great Lakes fuel a human society with currently one of the earth's highest rates of population growth.

Despite their impressive faunal diversity, large size, and fisheries production, these lakes are all threatened by changes resulting from human modification of the landscape and the effects of human activities on water quality, biological diversity, and fish stocks. In this chapter we review the distinguishing attributes of the major East African Lakes, the faunas they presently support, and current significant perturbations affecting the aquatic systems. Where possible, we identify factors underlying current patterns of change. Since Lake Victoria has experienced the most rapid and dramatic changes in the last century, we consider Lake Victoria in detail, outlining how changes in this lake may foretell the future for other lakes, unless careful management plans are constructed. We will end by briefly discussing potential conservation programs that may aid in mitigating the ecological changes that are occurring in the Lake Victoria ecosystem.

Lake Geography

East Africa is rich in aquatic resources, including nine large lakes. Lakes Albert, Kivu, Tanganyika, Malawi, and Turkana are steep-sided true Rift Valley lakes; while Lakes Edward, George, Kyoga, and Victoria are shallow-basin lakes (Fig. 8.1).

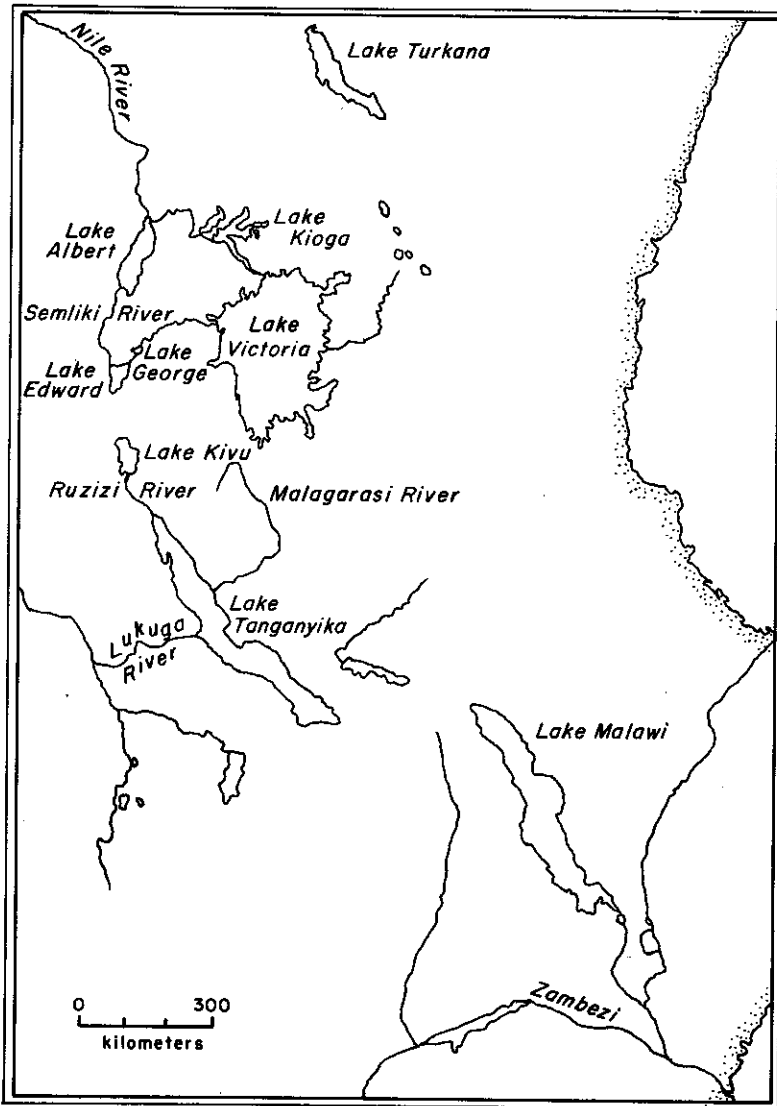


Figure 8.1. A map of the major lakes and rivers in East Africa.

Comparison of the Great Lakes of East Africa to other large lakes around the world highlights their significance from a number of perspectives (Table 8.1). Lakes Victoria (68,800 km²), Tanganyika (32,900 km²), and Malawi (22,490 km²) are among the largest lakes in the world. As such these lakes play particularly vital roles in the regulation and maintenance of tropical ecosystems on local, regional and potentially global scales.

Table 8.1. The area and maximum depth of freshwater lakes of the world (greater than 8000 km² in area).

Lake	Area, km ²	Maximum depth, m
Africa		
L. Victoria	68800	79
L. Tanganyika	32900	1435
L. Malawi	22490	706
North and Central America		
L. Superior	83270	393
L. Huron	60700	229
L. Ontario	19230	237
L. Michigan	58020	281
L. Erie	25680	64
L. Athabasca	8080	91
L. Winnipeg	24510	21
Great Bear Lake	31790	319
Great Slave Lake	8270	140
L. de Nicaragua	8270	70
South America		
L. Titicaca	8340	304
Asia		
L. Baikal	30500	1741
L. Balkhash	17400	26
Europe		
L. Ladoga	18390	230
L. Onega	9600	124

The Lakes

Lakes Victoria and Kyoga. Lake Victoria is an immense inland sea, the second largest freshwater body in the world, with a catchment area of approximately 184,00 km² (Table 8.1, Fig. 8.1). Situated across the equator at an altitude of 1134 m, the lake is set in a large shallow basin. Although Lake Victoria is enormous in area (300 km from north to south and 280 km from east to west, covering an area of 68,800 km²), it is relatively shallow with a maximum depth of only 79 m and a mean depth of only 40 m. The waters of Lake Victoria are shared by three countries: Tanzania with 51% of the lake area, Uganda with 43%, and Kenya with only 6% of the lake area within its boundaries.

Lake Victoria is fed by a number of rivers; the most significant in terms of volume is the Kagera River. The major source of water, however, is from direct rainfall on the surface (2). Lake Victoria discharges into the Nile river system, through the dam built at the Owen Falls. Subsequently, the waters flow through Lake Kyoga and then over the Murchison Falls and into Lake Albert. The Murchison Falls form a barrier to the Nile fish ascending from Lake Albert towards Lake Victoria (26). As a result of its shallow basin form, the edges of the lake are often fringed with extensive papyrus swamps (*Cyperus papyrus*). This swampy margin has potentially been very significant in the evolution of the fauna (see below) and may, in the future, play a particularly significant role in conservation of many of the fish species endemic to the lake.

The origin and past history of the lake has been an area of considerable debate (2,23). It is thought that the Lake Victoria basin started to form in the Miocene (approximately 20 million years ago) with the faulting of the Western Rift Valley and uplifting of land to the west of the basin (Table 8.2, Fig. 8.2). This process eventually resulted in the reversal of flow of major rivers such as the Katonga and Kagera. These rivers had previously drained the Lake Victoria region and flowed into Lake George. However, as a result of the uplifting, instead of flowing to the west, the water in these rivers drained to the east into the basin that was to become Lake Victoria. The uplifting process was, however, very slow and Lake Victoria may have drained into Lake George well into the late Pleistocene - possibly as late as 25,000 to 35,000 years ago (2; Table 8.2).

Sediment cores near the mouth of the Nile suggest that the level of the lake was too low to reach the outlet from about 14,500 to 12,000 years ago and again about 10,000 years ago (2). These were glacial times when the region as a whole was much cooler and drier (Chapter 1). Thus, it is likely that during one or more periods in the last 15,000 years Lake Victoria was much reduced in size, and became very shallow, and perhaps saline. It is probable that such water-level fluctuations repeatedly isolated and reconnected bays and depressions. Thus, the emerging picture is that Lake Victoria formed as a result of the uplifting and lake depression, but climatic fluctuations may have had a tremendous effect on the biological components of the lake through periods of isolation and reconnection. From a comparative perspective, climatic changes would have had an even more dramatic effect on the shallow lake basin of Victoria than on the deeper rift lakes of Tanganyika and Malawi.

Lake Kyoga lies just to the north of Lake Victoria. It receives the outflow from Lake Victoria and drains to the north, over the Murchison Falls and into Lake Albert. The lake was formed through the same tectonic changes and uplifting of the escarpment that led to the formation of Lake Victoria, but Lake Kyoga's formation may have been slightly later than that of Victoria (2).

Lake Tanganyika. Both Lakes Tanganyika and Malawi differ radically in physical or geologic structure from Lake Victoria. Unlike the shallow basin of Lake Victoria, these lakes sit in mountainous terrain with numerous precipitous drops past rocky shores and sandy beaches to the bottom of a freshwater abyss. Lake Tanganyika is 650 km long with an average width of about 50 km (2; Fig. 8.1). In general, the water depth drops off very rapidly as one moves out from the shore (maximum depth = 1470 m only 4 km from the shore, mean depth 570 m; 2). Although there is a shallow gradient in the very north and south ends of the lake (the 100 m contour is less than 10 km from shore), there are a few areas of shallow swampy water. Sections of the lake are 1470 m in depth. The majority of the deeper areas of the lake are permanently without oxygen (below 200 m) and support little life except bacteria. The lake's main inflow are the Ruzizi River from Lake Kivu (the faunas are separated by the Panzi Falls) and the Malagarasi River flowing in from a swampy region to the east. In comparison to Lake Victoria, the catchment area is very small, but again the major source of water to the lake is through direct rainfall onto the surface. The outflow is on the western side in the middle of the lake, the Lukuga River. Historical evidence suggests that this outflow was intermittent and even presently, it is not strong (2; Table 8.2). Thus, the major loss of water to the lake is through evaporation from the water surface,

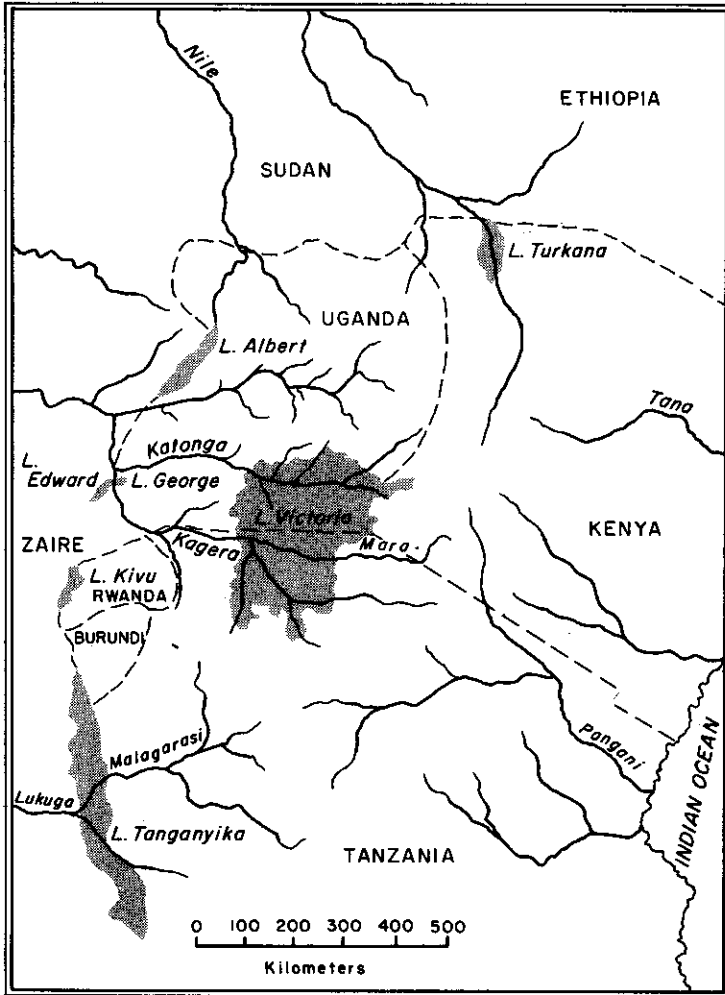


Figure 8.2. The pre-Pleistocene drainage in the East African Region, as proposed by (2).

a situation that is also true for both Lakes Victoria and Malawi, but not to the extent as observed in Lake Tanganyika (2).

Lake Malawi. Lake Malawi is physically similar to Lake Tanganyika. It is long and narrow, occupies a mountainous region (especially in the north) and drops off very rapidly as one travels out from the shore. The lake is 600 km long, up to 75 km wide, and has a maximum depth of 706 m with only one basin (Fig. 8.1). Like Lake Tanganyika, Malawi has an intermittent outlet, the Shire River (2). The catchment area of the lake is very small, and the lake is largely dependent on direct

Table 8.2. The major geological events that occurred in East Africa and the associated changes in the aquatic systems (Adapted from 3). The evidence for the approximate dating of some the events is controversial and further research is required to verify the time when each of these events occurred.

Geological Period (Years Before Present)	Event
25 Million	
Miocene	Lake Karunga covering the North East corner of the future Lake Victoria
separate Lakes Rivers	Beginning of the uplifting (by more than 1000 m) that will form the Rift Lake Basin, Edward and George from Lake Victoria and reverse the flow of the Kagara and Katonga
12 Million	
Pliocene	
7 million	
2-3 Million	Eruption of isolated volcanoes such as Kilimanjaro, Kenya, Elgon
Pleistocene	
2 million - 35,000	Rwenzori Mountains rise Further rising and formation of more rift lakes 'Kaiso' lake in Albert and Edward Basins Upwarping of the western side of the future Lake Victoria Basin Eruption of the Virunga Volcanoes
30,000 - 25,000	Uplifting on the western side of the present Lake Victoria causes the reversal of the Kagea and Katonga Rivers, and the formation of Lake Victoria, which eventually overflows into the Nile Basin to the north The water level of Lake Victoria was approximately 30 m above the present lake
25,000 - 20,000	Glacial period associated with cooler temperature and lower water levels in the lakes Major eruptions of the Virunga Volcanoes leads to the formation of Lake Kivu Lake Tanganyika drains out the Lukuga outlet

20,000 - 15,000
 14,500 -

 Maximum extension of the glaciers on the Rwenzori Mountains
 Lake Victoria falls from previous high level

Holocene

14,500 - 12,000
 12,000 - 10,000
 10,000
 10,000 - 8,000

7500
 3,700

840 - 940
 490 - 140
 30
 10

Lake Victoria is too low to reach the outlet
 Rising temperatures and higher rainfall levels
 Lake Victoria is again too low to reach the outlet
 Eruption of the Katwe and Banyuruguru craters near Lakes Edward and George occurred during this period and likely earlier and may have resulted in the extinction of a large number of fish, NileCrocodile, and mollusk species
 The period when Lake Turkana was last connected to the Nile
 The date of the last drop in Lake Victoria's water level likely associated with the cutting down of the outflow at Jinja and climatic changes
 The southern arms of Lake Malawi dried out.
 The southern arms of Lake Malawi again dried out.
 Lake Victoria rises 2 m as a result of high rainfall
 Nile crocodile again reported from Lakes Edward and George.

rainfall and small inflow streams that come directly off the mountains. The lake's level exhibits marked seasonal changes. For example, the lake fluctuates just over a meter between the wet and dry seasons (25). The area of the lake below 250 m in depth is anoxic (permanently without oxygen; 26). Rapid response to both seasonal and long-term changes in rainfall repeatedly isolate and reconnect inshore habitats. Trewavas (43) suggested that such changes facilitated the speciation of the cichlids found in the lake. One of the features that distinguishes Lake Malawi from the other Great Lakes is that it is much further from the equator than the other lakes, resulting in cooler surface water temperatures than Lake Tanganyika and Victoria (27).

The geologic history of Lake Malawi is poorly understood. The lake is younger than Lake Tanganyika, but has been isolated long enough to produce a remarkable endemic fauna (2). Geological evidence suggests that at earlier times, the lake drained to the east coast, and the fauna has ties to east coast river fishes and fishes in the Upper Zambezi. It is evident that none of the Malawi fish have come directly from the north. The lake level has fluctuated with climatic factors. For example, during drier periods of the last glacial cycle, the lake was 250 to 500 m lower than that of its present level. During a drier cycle between 1150 and 1250 A.D., and again sometime between 1500 and 1850 A.D., the southern arms of the lake dried up (2). These areas are now inhabited by many endemic rock-dwelling cichlids (26,37) that evolved since these drier periods.

Lake Albert. Lake Albert is a typical Rift Valley lake, 150 km long with an average width of about 35 km. Its maximum depth is only 56 m, which occurs 7 km from the mid-western shore. The lake has two major inflow rivers, the Semliki to the south, and the Victoria Nile, that enter the lake over Murchison Falls at the north end. Because the waters from the Victoria Nile have less effect on the lake as a whole than the waters from the Semliki, they enter immediately prior to the lake's outflow. As with the other lakes, there is evidence that its water level has changed in response to changing climatic conditions associated with glacial cycles (2; Chapter 1). For example, during the last glacial period, between 14,500 and 12,000 years ago, it seems likely that there was a stoppage of the Victoria Nile, that resulted in a drop in water level. The history of the lake corresponds to events described for Lake Victoria, involving the uplifting of the Western Rift (2).

The lake can become stratified during calm periods of the year, although dissolved oxygen in deeper waters is not greatly reduced. Consequently, a number of the species from this lake (such as *Lates niloticus*) show little tolerance to low oxygen waters (2,8).

Lake Turkana. Lake Turkana, located in the arid hot region of northern Kenya, is another large rift lake with a surface area of 4350 km². It is 265 km in length and averages approximately 30 km in width. It has a maximum depth of 120 m in a small depression in the lake's southern end, and a maximum depth excluding this depression of 80 m (2). The River Omo flowing from the Ethiopia highlands supplies 98% of the inflow to Lake Turkana. The level of the lake has fluctuated extensively, and there are fossil fish that can be found several km from the shore, indicating that it was once much larger than it is today. The geological events that lead to the formation of the lake commenced in the early Miocene (approximately 20 million years ago), and since then, the lake has had a dynamic history. Early in its

Table 8.3. Physical and biological characteristics of the major East African Lakes (biological refers to cichlid radiations only). Taken from (2,27, and the Times Atlas).

	Victoria	Tanganyika	Malawi	Albert	Turkana	Edward	George	Kivu	Kyoga
Physical									
Size	68800	32900	22490	6410	4250	2250	270
Max									
Depth(m)	100	1435	706	53	73	112	3	>500
Altitude (m)	1134	773	474	619	380	912	916	1460	1033
Mean									
Latitude	10S	70S	120S	1.50N	3.50N	0	0	20S	1.50N
Conductivity	96	610	210	735	3300	925	200	1240
Salinity									
%(g/l)	0.093	0.530	0.192	0.597	2.482	0.789	0.139	1.115
pH range	7.1-8.5	8.0-9.0	8.2-8.9	8.9-9.5	9.5-9.7	8.8-9.1	8.5-9.8	9.1-9.5
Biological									
Endemic									
Cichlids	400+	170+	500+	Few	Few	60+	60+	Few	
Trophic									
Diversity	High	Med	High	Low	Low	High	High	Low	High
Reproductive									
Diversity	Low	High	Low	Low	Low	Low	Low	Low	Low
Phyletic									
Diversity	Low	High	Med	Low	Low	Low	Low	Low	Low

history the lake exhibited rapid speciation of its molluscan fauna (2). Nonetheless, this endemic fauna did not persist, presumably the result of low water levels, high levels of salinity, or lake desiccation.

Recent history has also been dynamic. The lake experienced very high water levels about 20,000 years ago, but was again very low during the glacial dry periods around 12,000 years ago. Much of the fauna died out during this period. Subsequently, the lake rose to more than 80 m above its present level, and was connected to the Nile river system and its fauna. About 7500 years ago, the water level dropped below the outlet and the lake became isolated (2). Not surprisingly, the lake is more saline than any other of the East African Great Lakes, due to falling water levels and no outflow (Table 8.3). The lake, however, still harbors a rich fauna (2). A remarkable feature of the Lake Turkana is the absence of papyrus (*Cyperus papyrus*) which is the dominant vegetation type throughout much of the Nile basin. Beadle (2) speculates that the high salinity or alkalinity accounts for its absence.

Lakes Edward and George. Lakes Edward and George lie in a rather peculiar depression in the western rift valley, surrounded on three sides by escarpments; the Kichwamba Escarpment to the east, the Zaire Escarpment to the west, and Ruwenzori Mountains to the north (Fig. 8.1). Lake George, which is bisected by the equator in western Uganda, and lies to the west of Lake Edward, is 290 km² in size, with a maximum depth of only 3 m. The lake is fed from rivers flowing off the Ruwenzori Mountains (Nonge, Mbuku, Bumlikwesi, Dura, and Mpanga Rivers), but before they reach the lake proper, their waters filter through a large papyrus swamp at the northern edge of the lake. Lake George has higher productivity and is more saline than Lake Edward. Lake George is connected to Lake Edward by the Kazinga Channel, which is 40 km long and less than 1 km wide (2).

Lake Edward (2250 km²) is much larger than Lake George (270 km²), and has a maximum depth of 112 m. The lake's major inflows are from the Nyamugasani River, which drains off of the Ruwenzori Mountains, and the Ishasha, Rutshuru, and Rwindi Rivers, which drain the Rwandan highlands. According to Beadle (2) the annual contribution of the Kazinga Channel is probably much less than the input from these rivers. The lake has one outflow, the Semliki River, that flows to the North, eventually draining into Lake Albert. Hydrological data on Lake Edward have demonstrated prolonged stratification and water without oxygen below about 50 m (2). The faunas of the Lakes Edward and Albert are separated by a series of rapids on the Semliki. During its 250 km course from Lake Edward to Lake Albert, the river descends 300 m, the majority of this is in one section of rapids.

Like many East African lakes, geological and paleontological evidence suggest that Lakes Edward and George have had a very dynamic history. In the early Pleistocene (2 million years ago), there may have been passable connections between the Lake Edward and Lake Albert basins. The faunas of the lakes were very similar: fossil remains of *Lates*, *Hydrocynus*, and *Crocodilus niloticus* in the Edward basin, link the two faunas. Subsequently, Lakes Edward and George may have gone through a number of mass extinction and recolonization events (2). The last of these events probably occurred between 8000 and 10,000 years ago and was associated with the eruption of volcanoes that formed the Katwe and Banyuruguru craters. Beadle (2) speculates that these volcanoes may have deposited enormous amounts of toxic ash on the lake, that would have killed species such as *Lates*,

which may require well-oxygenated water. Similarly, the Nile crocodiles (*Crocodilus niloticus*) were no longer present in the areas of Lakes Edward and George after the eruption of these neighboring volcanoes. They were presumably kept from colonizing the lake by difficulties in passing the Semliki falls. However, recently with forest clearing on the sides of the falls, crocodiles have reinvaded Lake Edward.

Lake Kivu. Volcanic activity in the late Pleistocene in the Virungas created a barrier about 100 km south of Lake Edward. These eruptions completely blocked the flow of the upper Rutshuru River and the water flooded the valley forming the present day Lake Kivu. As the water levels rose, they eventually overflowed to the south, over the Panzi Falls and into Lake Tanganyika (2).

Lake Kivu is a medium-sized lake, with a maximum depth greater than 500 m. The thickness of sediments in the deep northern basin suggests that there may have been a lake in the area of the present-day Lake Kivu, prior to the volcanic activity that blocked the river (2). The surface of this lake would have been only 60 m higher than Lake Edward. This shallow grade between this older Lake Kivu and Lake Edward may have allowed exchange of species between the two lakes. This lends credence to the claim of Poll (2) who suggested in 1939 that the fauna of Lake Kivu is the remains of a richer fauna that was destroyed as a result of ash and chemical deposited on the surface of the lake during the period of volcanic activity.

The Faunas

The faunas of the Lakes Victoria, Tanganyika, and Malawi are all dominated and shaped by members of a single fish family, the Cichlidae (Table 8.3). These Great Lakes, plus Lakes Edward, George, and Kivu all have many endemic cichlids species (10,11,13,14). All are primarily evolutionary radiations of feeding-adaptation. The assemblages in the Great Lakes offer many striking examples of evolutionary convergence. Cichlids species with similar morphologies and functional characteristics have evolved independently in each of the lakes.

Lake Victoria and Kyoga. The fish fauna of Lake Victoria was dominated by a diversified, presumably monophyletic species flock of haplochromine cichlids (29). The explosive speciation and adaptive radiation displayed by these cichlids remains unrivaled among vertebrates. No other group of vertebrates is known in which such an extensive and rapid adaptive radiation was realized in so little time and with so little overall body form diversity. Lake Victoria probably had more than 400 species of endemic haplochromine cichlid fish until the early 1980s when a mass extinction occurred.

The haplochromines are a very interesting group of fish. All defend their young until self-sufficient. The large eggs and developing young are held in their mouth. They are behaviorally aggressive, physiologically adaptable, and phenotypically very plastic. Many haplochromine cichlids can individually alter tooth and skull morphology in response to diet change (11). They exhibit extraordinary evolutionary diversification that is represented to some degree by the number of feeding methods they exhibit. There are detritivores, phytoplanktivores,

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zooplanktivores, epiphytic algae grazers, fish that crush mollusks with their oral jaws, fish that crush mollusks with their pharyngeal jaws, prawn eaters, piscivores, fish scale eaters, crab eaters, and paedophages ("child eaters"; 11). Paedophages are predators with large mouths, thick rubbery lips, and outward pointed anterior teeth. They take the head end of brooding females into their mouth and suck out the eggs or young.

It is likely that the fishes of the Lake Victoria are descendants of fishes living in pre-Pleistocene rivers that flowed through the area that is now Lake Victoria, west towards Zaire (2). As in Lakes Tanganyika and Malawi, Victoria cichlid fishes are the product of rapid speciation from a few ancestors (27). However, in Lake Victoria, evolution has been more rapid than in either Lakes Malawi or Tanganyika. A variety of mechanisms may have operated to produce the difference in the rates of speciation between Lake Victoria and the deep rift lakes.

It seems likely that four different sorts of speciation mechanisms could be operating in Lake Victoria; all are associated with the relatively shallow morphometry of the lake. First, the shallow morphometry of the Lake Victoria Basin allows for speciation in satellite lakes with only modest fluctuations in lake level (11). During periods of low lake level, species can diverge from the parent stock in isolated satellite lakes. When lake level rises and satellite lakes are once again connected to the main lake, populations mix, and, if some mechanism prevents interbreeding, two distinct species may be recognized from one common ancestor. Secondly, the abundance of islands, rocky headlands, and pinnacles in Lake Victoria affords ample opportunity for speciation on these islands when lake levels are high. These offshore islands can separate populations of fish that will not cross large stretches of open water. Consequently, when water levels fall and populations come back into contact they may have diverged enough to prevent interbreeding (11). Thirdly, the shallow basin creates a situation where there are segments of vegetated swamp margins (typically papyrus) separating rocky or sandy segments of shoreline. Papyrus swamps, with their chronic low oxygen conditions, can serve as barriers to the movement of species intolerant of low oxygen conditions (5). Finally, during periods of desiccation, fish may retreat up rivers to avoid saline or hypoxic conditions. This creates the potential for a population with subpopulations now isolated in different rivers to diverge (23). Thus, speciation dynamics in Lake Victoria should be more rapid, more continuous, and more geographically diffuse than in either Lakes Malawi or Tanganyika.

The fish fauna of Lake Kyoga is extremely similar to that of Lake Victoria. Prior to the construction of the hydroelectric dam on the Victoria Nile, Owen Falls was little more than a series of rapids that was thought to be no barrier to the movement of fish from Lake Victoria and Kyoga (2). The swampy margins and lagoons of Lake Kyoga may play an important role in protecting the haplochromine fauna from Nile perch predation serving as refugia for haplochromines that are endangered or extinct in the larger lake (discussed below).

Lake Tanganyika. The cichlid fauna of Lake Tanganyika is, like the lake, very old. Several well represented lineages hail from origins that lie millions of years in the past. Unlike Lakes Malawi and Victoria, that are dominated by the mouthbrooding haplochromine and tilapiine cichlids, a large proportion of the Lake Tanganyikan cichlids are substratum-spawning "lamprologines", derived from ancestors in the Zaire River. Representative species in Lake Tanganyika of any

given feeding adaptation are more highly specialized morphologically than their look-alikes in Lakes Malawi or Victoria. Two exceptions to this pattern stand out: Lake Tanganyika is poor in species of snail-crushing cichlids, and apparently lacks true cichlids paedophages.

Lake Tanganyika has by far the richest non-cichlid lacustrine fish assemblage in East Africa (27). Included among these are the world's largest tigerfish (*Hydrocynus goliath*), four species of *Lates* (relatives of the Nile Perch, *Lates niloticus*), and two pelagic sardines, which together with the *Lates*, comprise the bulk of the fishery. The lake is also richly endowed with catfishes, carp, characoids, spiny eels, and many others (26,27).

Lake Tanganyika's long period of isolation is reflected in a high level of endemism: 220 out of the 287 species (76%) in the lake are endemic; 172 of these endemic fishes are cichlids (2,25,27). Of the 115 noncichlid species, 46% are endemic. What illustrates the greater age of Lake Tanganyika and distinguishes its fauna from that of Lake Victoria, is the wider divergence in the non-cichlids. Eight genera are endemic to Lake Tanganyika. Apart from *Xenoclaris* in Lake Victoria, none of the other lakes have endemic genera (27). Lake Tanganyika also has more fish families than the other great lakes; reflecting its ties to the species-rich Zaire River system. Of the 24 families of fishes found in the Zaire river, 18 are found in tributaries and marshes around the lake, 12 occur in the littoral and sublittoral zones, 7 families occur in the benthic zone, and 4 in the pelagic zones (27). Interestingly, there are some species presently found in Malagarasi river draining the country to the east of the lake (and south of Lake Victoria) that are evolutionarily related to species in the Zaire River system, but are no longer found in the lake itself.

The level of the Lake Tanganyika has fluctuated with changing geological and climatic patterns. Evidence suggests that 200,000 years ago, the different basins of the lake were totally separated (27). It would have required a drop in water level of 700 m to completely isolate the two basins (24). Approximately 50,000 years ago the lake was a unified body, but the north and south basins were connected only by the Kalemie Strait (27). It has been suggested that repeated separation of the two halves of the lake may have fueled a process of rapid speciation (27). There is some taxonomic evidence to support this idea. For example, there are two subspecies of the cichlid *Ophthalmochromis ventralis*, with a northern and a southern variety. However, climatic changes sufficient to cause lake-level variation of the required magnitude for basin isolation have not occurred since the last glacial period (>12,000 years ago). Thus, it seems probable that other processes are also contributing to the rapid rate of speciation.

Lowe-McConnell (27) suggests that the many rocky segments of Lake Tanganyika shoreline separated by stretches of sand or swamp have created a patchy situation that facilitates allopatric speciation particularly among mouth brooders where juvenile dispersal is minimal. Fluctuating lake levels alone do not occur at a high enough frequency to account for the present number of endemic species, but certainly may have contributed to the high endemism above the species level. These speculations are supported by the fact that the rocky habitats support the most diverse species assemblages (19,27).

Lake Malawi. Lake Malawi, like Lakes Victoria and Tanganyika, harbors an impressive endemic flock of cichlids. Like the other species flocks of cichlids, estimates of the numbers of species have changed over the years, reflecting the

difficulties of cichlid systematics and the lack of extensive collections. In 1981 Beadle (2) reported that there were 245 species known from Lake Malawi from only 7 families, which is about half the number in the other Great Lakes (25). In contrast, with further investigations and more collections, Ribbink (39) in 1988 and Lowe-McConnell (27) in 1993 report 400 and greater than 500 species, respectively, of which all but 4 are endemic.

Lake Malawi's fish fauna is most closely related to species found in the upper Zambezi, although only 9 out of the 14 families in the Zambezi are found in the lake. In addition to the species flock of cichlids found in the lake, Malawi harbors a unique flock of 12 species of clariid catfishes (25), and 4 endemic tilapias.

Lake-level events in the last 500 years have permitted us to re-evaluate the estimated speed of cichlid speciation in Lake Malawi. An early study of Lake Nabugabo (a satellite lake of Lake Victoria) by Greenwood (11) suggested that haplochromines could speciate in as little as 4000 years, since this was when Lake Nabugabo is estimated to have separated from Lake Victoria. Evidence suggests, however, that the southern end of Lake Malawi was dry 500 years ago. Presently, there are endemic species living around islands in areas that were dry only 500 years ago (27,37).

Lake Albert. Lake Albert has a diverse fish fauna but is strikingly different from other East African Great Lakes, in having very few cichlid species. Considering the present-day mass extinction of cichlids in Lake Victoria associated with the eruption of the introduced Nile perch (*Lates niloticus*), it is tempting to speculate that the scarcity of the cichlid fauna in Lake Albert might be related to the presence of predators such as *Lates* and *Hydrocynus*. However, the cichlid species flock in Lake Tanganyika where a number of species of *Lates* are abundant argues against this speculation. Fryer and Iles (10) suggest that Lakes Albert and Tanganyika received fully differentiated riverine faunas that occupied available niches after catastrophic lake-level disturbances. This may have limited opportunities for cichlid species radiation. The fauna of Lake Albert is separated from that of Lake Victoria by Murchison Falls. Commercially valuable fish are *Oreochromis niloticus*, *Lates niloticus*, *Alestes baremose*, and *Citharinus citharus* (2).

Lake Turkana. The fish fauna of Lake Turkana is derived from the Nile drainage, particularly Lake Albert and, like Lake Albert, has few cichlids. Hopson and Hopson (2) documented 48 fish species in the lake, 30 species were found throughout the Nile Drainage, 22 species also occurred in Lake Albert, and 10 species were endemic to Lake Turkana. Fish faunal diversity is relatively low, concurring with the geological evidence that the lake may have recently dried up completely, or may have become too saline to permit most fish to persist. A number of species found in Lake Albert are absent from Lake Turkana (26).

Lakes Edward and George. The fish fauna of the Lakes Edward and George is as diverse as its geological history. Some species in Lakes Edward and George are also found in Lake Albert (such as *Bagrus docmac*, *Oreochromis niloticus*), while other species (such as *Polypterus senegalus*, *Hydrocynus* spp.), and even families (such as Mastacembelidae, Characidae, Schilbeidae) that typify the Nilotic fauna from Lake Albert are absent. Many of the cichlids from Lakes Edward and George are closely related to species in Lake Victoria (2,12,13). In conjunction with geological evidence, this supports the idea that a very recent connection existed by which species moved from Lake Victoria to Lake Edward (2). As discussed previously, it is now generally agreed that Lake Victoria was formed primarily by the Kagera and Katonga Rivers when they were back-pounded 760,000 years ago (23). It is believed that the lake continued to flow westward until further uprising finally stopped and reversed the river flow (2). Connections between Lakes Victoria and Edward may have existed as recently as a few thousand years ago, but more likely during the early Pleistocene, approximately 1 million years ago (2).

It is not surprising that the fish fauna of the very productive Lake George is dominated by the herbivorous *Oreochromis niloticus* and *Enterochromis nigripinnis* (30). Commercially important fish in both lakes all originate from Lake Albert ancestors and include *Oreochromis niloticus*, *Barbus altianalis*, *Protopterus aethiopicus*, *Bagrus docmac*, and *Clarias lazera*. The number of endemic cichlids in the lakes is uncertain and requires further study. Until recently only 23 species of cichlids were reported from these lakes, five of which were considered to be common to Lake Victoria (12,13). More recently, estimates have increased to over 60 endemic cichlid species (27). Three of the five species thought to be shared with Lake Victoria have been redescribed as endemic to Lakes Edward and George (the other two are widely distributed throughout the basin - *Astatotilapia nubilis* and *Astatoreochromis alluaudi*). Occasionally massive fish kills of fish, without accessory respiratory organs, have been reported from Lake George (26) associated with the loss of water-column oxygen.

Lake Kivu. Lake Kivu has a relatively impoverished fish fauna and is considered ecologically immature due to its recent formation (2). The fish fauna is most closely aligned with Lake Edward, but a number of lineages present in Edward are lacking in Lake Kivu (families such as Lepidosirenidae, Mormyridae, Bagridae, Cyprinodontidae; 2). This is to be expected from the geological evidence that suggests that Lake Kivu was recently formed when volcanic actions damned a valley previously draining into Lake Edward (2). Families well represented in Lake Tanganyika (Characidae, Centropomidae, Mochokidae, Mastacembelidae) are absent both from Lakes Kivu and Edward. However, during the period that Lake Kivu has been isolated from Lake Edward, there has been some cichlid speciation - all six *Haplochromis* found in the lake are endemic (2). As with Lakes Edward and George, the fauna of Lake Kivu may have been reduced during periods of volcanic activity.

Freshwater herrings (*Stolothrissa tanganikae* and *Limnothrissa miodon*) were introduced to Lake Kivu from Lake Tanganyika in 1963 to fill a vacant niche for zooplanktivorous fishes. One species (*L. miodon*) became established, but was of low food value because it picked up a strong sulfur smell and taste from the volcanic waters of the lake (1).

Human Influences on African Great Lake Ecosystems

The Great Lakes do not end at the water's edge. These lakes are parts of a landscape that include terrestrial ecosystems as varied as tropical rainforest, savanna, desert, and human cities. The effects of human activities on the composition of the drainage waters hundreds of miles away directly influence the lakes' ecology. Human influences on these ecosystems have been increasing for a variety of reasons, all linked one way or the other to increasing the human population. The countries bordering these lakes have some of the highest population growth rates in the world (for example Uganda = 3.4% per annum, Kenya = 4.1%, Tanzania = 3.6%; Table 8.4).

Human activities have influenced the Great Lakes in a variety of ways. In some cases, the short term effects can, from one perspective, be viewed as very positive for the people involved. The natural resources of the basin have been used, and the capital reinvested in modernized infrastructure. Ecosystem changes and mechanization have produced vast expansions in fisheries and agricultural yields. The increase in food supplies and access to modern medicines facilitated by economic growth has allowed some people to live longer and have more productive lives.

Some would argue that some of these benefits, while desirable, have come at a high price, particularly since the development is probably unsustainable. In the Great Lakes Basins, nature is in retreat. Crocodile, whale-headed stork, python, monitor lizards, otter, hippopotamus, sitatunga, and a variety of other animal populations have been greatly reduced from precolonial levels. The forests that we see today are only remnants of much more extensive forest blocks that existed prior to clearance by man. East African forests have been affected by agriculturists for a considerable period. Evidence from pollen analyses, archeological digs, and linguistic studies suggest that widespread forest destruction occurred at least as far back as 4800 years ago (17). Little regard has been paid to the fact that resources in such forests are small, and deforestation in East Africa has been extensive (Uganda = 1.3% per annum, Kenya = 1.7%, Tanzania 0.7%; 28 and also see Chapters 1 and 2).

All of the lakes are threatened by pollution (7), increased sedimentation resulting from deforestation (6), and overfishing (7), and some lakes are threatened by potential oil exploration (Lakes Tanganyika, Malawi, and Albert). Perhaps one of the greatest threats to these ecosystems is the introduction of exotic species. The potential effect of species introductions is most dramatically illustrated in the lake that has experienced the greatest level of disturbance, the highest rate of species loss, and which is in the greatest danger of ecosystem collapse: Lake Victoria. Therefore, we focus this next section on the recent history of Lake Victoria.

Table 8.4. Vital statistics for selected African countries: their size, population characteristics, forests, and deforestation rates.

	Uganda	Kenya	Tanzania	Rwanda	Burundi	Malawi	Mozambique
Country Size (km ²) ¹	236,578	582,645	939,762	26,330	27,835	94,080	784,755
Population (1989), millions ¹	17	24.1	26.3	7.0	4.8	7.3	13.4
Annual Growth Rate ¹	3.4%	4.1%	3.6%	3.4%	3.3%	3.3%	2.6%
Doubling Time, years ¹	20	17	19	20	21	21	27
Pop. Dens. per km ²	71.9	41.4	28.0	265	196	93	19
Percent Urban	9%	19%	19%	6%	5%	13%	20%
Land Use							
Percent Cultivated ¹	28	4	5	38	47	20	4
Percent Pasture ¹	21	6	37	16	33	16	55
Original Forest (km ²) ²	103,400	81,200	176,200	9,400	10,600	10,700	246,900
Est. of Remaining Forest	7500	6900	14,400	1554	424	320	9350
Defor. Rate (%/yr) ³	1.3	1.7	0.7	2.7	2.7	1.1
Forest Rem. 1994 ³	6245	5428	13050	1057	288	8005
Prot. Areas(km ²) ⁴	6084	13,148	77,008	150	379

¹ Stuart et al. 1990; ² Groombridge 1992; ³ Based on FAO estimated Remaining Forest (1980) and on Deforestation Rates; ⁴ Tanzania and Kenya are from Groombridge 1992 and probably include many parks with little area of forest, Uganda is from the data in Howard 1991, and includes only forested areas; ⁵ McNeely et al. 1990 and FAO 1981

Lake Victoria - Brief History of Human Disturbance

In the last one hundred years Lake Victoria has experienced dramatic changes in both its limnological parameters (such as dissolved oxygen, productivity) and native fishery stock (22,23,34,44). Overfishing was the cause of the earliest recorded anthropogenic changes in the fish fauna. In the early part of the century the British introduced gill nets and other modern fishing methods to the area. This led to the rapid depletion of important anadromous fishes (*Barbus altianalis* and *Labeo victorinus*) that once made spectacular spawning runs up rivers that flow into Lake Victoria, and *Oreochromis esculentus* that was a major food fish in the lake (34). To replace these devastated fish stocks, several exotic species of tilapia were introduced into Lake Victoria in the 1950s (27,33). These introductions were slow to take hold, but eventually *Oreochromis niloticus* established itself and became an important part of the fishery. Also around this time, Nile perch, *Lates niloticus*, was introduced into Lake Victoria (33). Nile perch was slow to take hold and persisted as a minor component of the fauna for decades until the early 1980s, when their populations increased dramatically (22,34,44). The Nile perch population explosion is suggested to be the leading cause for the demise of the native fishes (1,34). The decline in native fishes, and the increase in Nile perch populations are almost perfectly reciprocal (34,44), and the replacement occurred very rapidly. In 1978, the haplochromine fauna were intact and contributed about 80% of the yield and Nile perch less than 2%, with the remainder consisting of the introduced *Oreochromis niloticus* and native non-cichlids (44). By the mid 1980s (22,34,44), the haplochromine fish community had been virtually destroyed, and the Nile perch comprised better than 80% of the catch (34). The remaining 20% consisted of *Oreochromis niloticus*, the tiny native cyprinid, *Rastrineobola argentea*, and a small remnant of other native fishes.

The Nile perch is a top predator that grows up to 2 m in length and to a weight of more than 100 kilograms and feeds on a wide range of fish and invertebrate species. It has been recorded to eat mormyrids, *Alestes*, *Barbus*, *Clarias*, *Protopterus*, *Rastineobola*, *Tilapia* sp. *Oreochromis* sp. and a variety of other fish species including its own young (33). It ingests large volumes of fish; in the stomach of a 110 cm long Nile perch, Okedi (36) recorded 57 *Haplochromis*.

The above situation is, however, not so clear cut. Coincident with the Nile perch explosion, was a dramatic change in the physical environment of the lake. In the early 1980s, the regular appearance of dense algal blooms was associated with low oxygen levels, and fish kills (31,32). Prior to 1978, the lake was well-mixed, though oxygen fell to lower levels in deeper waters (> 60 m) for brief periods during the rainy seasons (41). Now, Lake Victoria appears to be stratified for the entire year (3,18,22). Water depths between 25 and 50 m have recently experienced increases in the abundance of *Cardina niloticus* (the lake's small, native detritivorous shrimp, that appears to be highly tolerant of low oxygen conditions; 34).

Recently, water hyacinth (*Eichhornia crassipes*) was introduced into the lake. Water hyacinth occurs naturally in the floodplains of South America, where its spread is limited by naturally occurring predators, fungi, and diseases. It was introduced to Africa at the turn of the century and was first reported in Lake Victoria in 1990, where it is believed to have invaded from the Kagera River flowing into the lake from Rwanda. Unrestricted by nutrients, and natural enemies, a single plant can produce 140 million daughter plants per year, enough to cover 140 hectares with a wet weight of 28,000 tons. The plant also produces seeds that can survive in the

mud for 30 years, creating severe problems of reinfestation after elimination programs (World Bank Unpublished Report).

The water hyacinth has been established in Lake Victoria for only a few years, but it has proliferated at a great rate. It is now a common feature along shores in Uganda and Tanzania and has made its appearance in Kenya. Hyacinth floats on the water surface, often forming dense floating mats of vegetation. Hyacinth has a number of effects on the lake by reducing light penetration, limiting water-column, mixing, and increasing detrital inputs. By shading out the sun it is likely to provide concealment to ambush predators that feed on indigenous species, such as the black bass (*Micropterus salmoides*) - now established in a Kenyan river that feeds into Lake Victoria. Further it may shade out other forms of bottom-dwelling vegetation that often is located just outside of the papyrus beds (such as *Ceratophyllum*). If this is the case, it may reduce the value of the shore margins as refugia from predation. At this time the direction of these relationships is speculative; data verifying the effect of hyacinth on the ecosystem are required.

A number of other aspects of the lake's ecology also appear to have changed: productivity and turbidity have both increased, papyrus swamps are on the decline, aquatic snails are increasing in abundance, the land surrounding the lake has been extensively deforested, and human populations bordering the lake have risen dramatically.

Arguments concerning the introduction of Nile perch and Nile tilapia into Lake Victoria are in many ways moot, since their introduction is irreversible. From a fisheries perspective, the introductions may have been beneficial, at least on the short term. With the establishment of the Nile perch and Nile tilapia fisheries, the total quantity of fish landed from the waters of all three countries has increased between two and six fold (35). In Kenya the catch increased from 20,000 tons in 1977 to 123,000 tons in 1988 (35). In Uganda the catch increased from 17,000 tons in 1983 to 132,000 tons in 1988; and in Tanzania the catch increased from 64,000 tons in 1982 to 89,000 tons in 1985 (35).

Recent statistics indicate that in Lake Victoria over 100,000 artisanal fishermen using more than 20,000 small craft caught an estimated 550,000 tons of fish in 1990. The estimated market value of this catch is approximately US \$280 million (World Bank Report). This situation has led to the rapid, and virtually unchecked, development of fish processing capacity along the lake shore, including large-scale trawling, and fish freezing plants. This has occurred despite variable growth rates in the fisheries industry. There is, however, good reason to believe that the Nile perch fishery will crash in the near future. It is believed that the Nile perch stocks are being over-fished. This has been intensified by the use of small mesh sizes that capture immature fish (New Vision, Sept. 4, 1992). There is limited quantitative data since the last comprehensive assessment of fish stocks dates back to 1971, when the lake was a multispecies fishery based on indigenous fishes. Accelerated efforts in faunal survey and fisheries stock assessment are required to provide information necessary for the development of informed conservation and management plans for the lake and region as a whole.

The most likely scenario for the future of the Lake Victoria fisheries seems to be one of instability. If the Nile perch fishery crashes, there will be a period of extremely low catch. Whether fish shortage will cause the governments of these three countries or other agencies to advocate new introductions is not known. Such introductions should be discouraged, since their long-term effects on the ecosystem are unknown. Nonetheless, even if introductions are not advocated by the

appropriate governmental bodies, introductions may still be made since the control of such a large body of water will be difficult.

In any event, virtually all stakeholders would regard a stable market as better than an irruptive one. Thus, the more that is known about the present ecosystem, the better we can predict the future course of the lake, and potentially limit future instability and low catches.

Conservation of East Africa's Great Lakes

The East African Great Lakes provide many goods and services to the people who live around them including: food, water, waste dilution, transport, hydroelectric power, building materials (such as papyrus), recreation, tourism, and aquarium fishes as an export commodity. The countries in East Africa are striving for sustainable economic growth, while at the same time advocating the conservation of existing habitats. These goals are in many ways incompatible, creating tension between different factions. For example, to preserve the watershed and the quality of the water draining into the lakes, advocates for conservation of the aquatic systems favor the halt of forestry activities and the reforestation of habitats that ring the lake to prevent erosion, retard nutrient inputs, and to restore the populations of terrestrial organisms, like hippopotamus, that probably played a significant role in the ecosystems. Opposed to such plans are the powerful economic sectors in favor of agricultural and industrial development.

Opposing sectors represent differing philosophies with respect to the wise use of resources. Conservationists might argue against development schemes, on the basis that the costs in terms of ecological degradation are too high for the returns and that the development will not be sustainable. If the Nile perch fishery in Lake Victoria does crash, it could be heralded as an example of such a sequence. It seems, however, that advocating non-development is inappropriate, if not hypocritical. Thus, we must look for alternatives that are based on appropriate technologies and indigenous species. For example, there could be development of commodities based on native products like papyrus and aquaculture of indigenous food species. It is theoretically possible to draw human sustenance from intact, native ecosystems without bringing about their demise. Unfortunately, it seems probable that such an approach will not work at the present time, for two reasons; 1) the knowledge and experience to conduct projects to the economic scale that is necessary does not presently exist, and 2) the volume of goods and services derived from the lakes will, by necessity, increase as a result of human population growth.

There is, however, good reason to believe that his situation will not continue. Population growth rates are declining, and technological systems are being developed to more efficiently use existing resources. The term sustainable development is, however, an oxymoron that will remain so until demand can be brought into line with ecological production. Thus, we suggest that agencies advocating "sustainable development" must first employ "ecological first-aid" to maintain or restore ecological systems and both conserve and develop options for future economic growth. Parallel efforts are the key to success in this endeavor.

One priority is the preservation of remnant fragments of intact natural ecosystem in protected areas. This is a temporary step, since such fragments are rarely large or self-sufficient enough to remain intact for long. A second defense is the development of extractive reserves or "managed exploitation areas". These areas

should be regulated to provide materials for local use as best as the ecosystems can provide. Protected areas are often created for their long-term benefits. However, they also have the immediate value of providing a source of colonizers for managed and restored habitats. Third, the deployment of extractive reserves must be planned within the context of a desired end product, and an ecological landscape that has been recast so as to meet the needs of a large human population. Defining and managing this landscape constitutes the most challenging of all the tasks currently faced by environmental scientists and decision makers working in the Lake Victoria region.

In subsequent discussions we will attempt to illustrate ways in which such a management system could aid in long-term conservation goals, provide future options for sustainable development, and contribute to immediate needs. Let us begin by examining two examples of potential management systems that could be employed in "Managed Exploitation Areas" for Lake Victoria.

Sustainable Resources

Fish Ponds. The development of an extensive fish aquaculture industry would seem to be a prudent advancement. Conducted on a local level, this development could provide a much needed protein supply for local villagers, and potentially reduce the pressure on the existing lake fisheries. Aquaculture conducted on a larger scale has the potential of generating significant revenues. Such a development may be particularly timely, if the Nile perch fishery declines and leaves behind an extensive processing and export infrastructure. For aquaculture to be successful on the scale needed to reduce fishing pressure, wide-ranging development, education, and technological assistance are required.

Oreochromis niloticus is an ideal fish for aquaculture. An advantage of farming this species is that it is already in Lake Victoria, so there is no danger of accidental introduction. Local people are familiar with the species, and it is already in local markets. In addition *O. niloticus* breeds quickly and easily, thrives on cheap, readily available plant foods, and produces high yields. This species is both tolerant of wide temperature and salinity ranges, and low oxygen.

Aquaculture development endeavors could be situated to assist conservation efforts. It has recently been advocated (Lake Victoria Workshop, August 1992) that "Fish Parks" be established in some areas to preserve the existing haplochromines and in other areas to maintain breeding stock for commercially important species (21). If these parks were established, the economies of some villages may be negatively affected, at least on the short term until tourism or other options could be developed. Fish ponds could replace the income of villagers who relied on areas designated as fish parks.

Papyrus Swamps. Papyrus (*Cyperus papyrus*) swamps are extensively distributed around the shores of Lake Victoria and throughout wetter regions of East Africa (2,42). In Uganda alone, it is estimated that papyrus swamps occupy more than 10% of Uganda's land surface (16) with only 2.25% of this area protected in National Parks or Reserves (see Chapter 9). The swamps provide numerous benefits by maintaining microclimate, preventing flooding, purifying water, reducing sediment loading into lakes, supplying fish, and producing reeds for mats, roofing, and export. The commercial use of papyrus need not disrupt the ecosystem.

Papyrus is the fastest growing herb in the world (42), and unlike forested areas, nutrients are continuously supplied to harvested areas by flowing water.

In areas where there is high population pressure and thus high demand for agricultural land, swamps have been drained (4). However, the long-term fertility of drained swamps is questionable (42), and in many cases the reclaimed soils are not very productive in the first place (42). Drainage schemes have led to soil erosion, decreased water table levels, loss of water supplies for rural communities, and soil acidification (42). One solution to excessive swamp drainage is to increase the economic use and sustainable management of papyrus, thereby ensuring preservation of swamp ecosystems (42). Presently the technology exists to use papyrus for commercial specialty paper production and for fuel briquettes that would decrease the pressure placed on existing forests.

Interim Solutions, the Role of Scientists, and Refugia. It has been extremely difficult to develop scientifically rigorous predictions concerning ecosystem function, particularly predictions accurate over a short time and a large geographical area. However, to be able to understand and potentially manage the Great Lakes, this is exactly what must be done. We propose that the scientific community can most directly contribute to the conservation of the Great Lakes by resolving key unknowns in the ecosystem. For example, how will pollution or increased sedimentation affect limnological parameters, water quality, and species interactions. Additionally, what are the social implications of changes in the fisheries industry, and at what level of exploitation is the fisheries industry sustainable? For the remainder of the paper we focus on how scientists can contribute to the survival of endangered or threatened faunas.

The most direct means of conserving an endangered fauna is to identify and protect areas where the fauna can persist (refugia) even if perturbations to the ecosystem are not brought under control. Such an approach has been advocated for the Great Lakes a number of times. For Lake Tanganyika, rocky shores in sections of erosion-resistant watershed would be most suitable for protection. Rocky areas would have low levels of sedimentation even if deforestation was to occur (6). The extension of existing terrestrial park boundaries into the water is also feasible, since the watershed is also protected (7). In Lake Malawi, emphasis may be most appropriately placed on protecting areas harboring speciose and endemic faunas (38). Expansion of the Lake Malawi National Park boundaries to include such areas as the Chisumulu Islands and additional mainland rocky areas are good conservation possibilities (38).

In Lake Victoria, the situation becomes very complex, since Nile perch, the major threat to the fauna, is mobile and can very easily invade protected areas. As a result, identification of refugia will necessitate determining what sorts of areas Nile perch will not invade. Considering what is known about Nile perch and the changes that have occurred in the lake since their introduction, the following assumptions are tenable.

- (1) Some haplochromines can tolerate oxygen levels as low as 1 ppm for an unknown period of time (5).
- (2) Adult Nile perch require water with high dissolved oxygen since their blood has a low affinity for oxygen (8).

- (3) Nile perch of sufficient size to take large, inshore species inhabiting-shallow rocky shores or swamps cannot prey effectively because of the structural complexity of these areas.
- (4) Nile perch are less effective predators in riverine habitats due to the high ratio of marginal refugia to open water.

Based on these assumption, escape from Nile perch can be achieved by the restriction of activities to structural refugia, or (for species tolerant of low oxygen) restriction to portions of the water column where dissolved oxygen concentration is low, or by migration and colonization of riverine habitat. In consideration of these factors, we predict the existence of four refugia: 1) structural refugia, 2) low oxygen refugia, 3) peripheral refugia behind anoxic/hypoxic or geographical barriers, and 4) riverine refugia.

There is accumulating evidence that papyrus swamps can form significant barriers to the dispersal of fish species intolerant of low oxygen conditions. For example, recent collections identified remnant populations of *Oreochromis esculentus*, as well as endangered haplochromines, in Lake Kanyaboli (a small satellite lake joined to Lake Victoria by the Yala River). It is likely that these populations exist because the Nile perch has not been able to disperse through the Yala swamp. We predict that shallow-water prey species tolerant to low oxygen conditions may find refuge from predation in the enormous area of peripheral swamps. Laboratory experiments on the responses of some species Lake Victorian cichlids to progressive and acute hypoxia have demonstrated that some of these fishes can tolerate very low oxygen levels (5). We also predict that fishes tolerant of chronic and/or acute hypoxia may disperse through peripheral swamps to find refuge in hypoxic lagoon areas behind the fringing swamp. Prey species tolerant of low oxygen may also find refuge from predation by inhabiting the deeper waters of the lake.

Areas that have complex spatial elements may be serving as refugia from the Nile Perch. Previous studies have found evidence that the more tolerant haplochromines and the Nile perch are mainly rock-dwelling species and species inhabiting inshore areas close to vegetation (34,44).

Many of the non-cichlids fishes once made spawning runs up the rivers that flow into Lake Victoria (12). Recently there is evidence that some of these species may not be descending back into the lake. It seems reasonable to speculate that rivers are serving as refugia for these species from Nile perch predation, since Nile perch continue to show restricted use of riverine habitat. Examples may include *Labeo victorianus*, *Barbus* spp., *Schilbe mystus*, and various mormyrids (34). It is possible that viable populations of such species exist in the rivers. Nonetheless, they are being prevented from re-establishing in Lake Victoria by the Nile perch that prey on individuals that disperse back into the lake.

Conclusions

The Great Lakes of East Africa are windows on the relationship between biological diversity and the welfare of humans. The lakes are some of the most biologically diverse ecosystems known. For example, Lake Malawi hosts more than 500 fish species, and Lake Victoria harbors more than 400 cichlid species that have evolved

in less than 200,000 years. Similarly, the fishes and snails in Lake Tanganyika are so varied in form that the members of a single family might easily be mistaken for unrelated taxa. But this rich biological diversity is threatened by human activities. The countries in East Africa are striving for sustainable economic growth, while at the same time advocating the conservation of existing habitats. These goals are in many ways incompatible, thus creating tension between different factions. We suggest that agencies advocating sustainable development must first repair ecological damage to both conserve and develop options for future economic activity. Such a process should involve the development of 1) a series of "Protected Areas" that will serve as source of species diversity, preserving options for the future, 2) a series of "Managed Exploitation Areas" that would be regulated to provide materials for local use as best they can, and 3) a vision of the long-term goals for the ecological landscape: including patterns of land use, watershed changes, and incorporation of human needs and activities as an integral component of the landscape model. Scientists can contribute most directly to these goals by quickly and responsively resolving key unknowns in the ecosystem. In particular, the identification and protection of faunal refugia are critical to the persistence of threatened faunas.

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Edited by
T. R. McClanahan and T. P. Young

New York Oxford
Oxford University Press
1996