A Comparative Introduction to the Biology and Limnology of the African Great Lakes

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ABSTRACT. *The East African rift valley region contains the earth's largest aggregation of tropical lakes. Three of these lakes—Victoria, Tanganyika, and Malawi—hold one quarter of the earth's total surface freshwater supply, and are home to a myriad of fish species. Apart from the diversity and endemicity of their biota, properties that distinguish the African Great Lakes from their North American counterparts include their great age, long sedimentary records, long residence times, persistent stratification, continuously warm temperatures at all depths, major ion composition, and a propensity for nitrogen limitation. Current management problems include over-fishing, increased input of sediment and nutrients, and in the case of Lake Victoria, loss of endemic fish species and the proliferation of the introduced water hyacinth. As in the Laurentian Great Lakes basin, the harmonization of research programs and management strategies among the various riparian countries is a challenge. While research activities on all three lakes have increased in the last decade, there remains a need for integrated, multidisciplinary research in order to develop conceptual and numerical models that provide insight into the functioning of large, tropical, freshwater aquatic ecosystems. Particular issues that may be pursued most profitably in the African Great Lakes include the links between climate and biogeochemical cycles, the role of biodiversity in ecosystem functioning, and paleoclimate reconstruction over millions of years.*

INDEX WORDS: *Africa, tropical, Lake Malawi, Lake Tanganyika, Lake Victoria.*

"It is hoped that from time to time there may be other contributions to the meetings, and the Proceedings, concerning distant waters whose qualities either by comparison or contrast will enlighten the Great Lakes scene." (Editorial preface to proceedings of 11th Conference on Great Lakes Research (1968), in which D.V. Anderson commented on the Lake Tanganyika paper presented by G.W. Coulter.)

The earliest maps of Africa are notable for their nearly complete lack of lakes. In several maps produced in the early 1800s, the only body of water south of the equator is Lake Maravi (Malawi), a long, narrow water body whose dashed boundary indicates it was probably mapped on the basis of hearsay rather than direct knowledge of the cartographer. The lower reaches of the Nile and Congo (Zaire) rivers were mapped, but Lakes Victoria and Tanganyika, along with the other lakes in the East African Rift Valley (Fig. 1), were completely absent. Until further exploration in the latter half of the 19th century, the presence of these tropical inland seas was known only to those who lived in their near vicinity. Although early explorers heard rumors of inland water bodies, they probably never expected that within the continent there were three lakes so large that they hold a quarter of the earth's total supply of surface fresh water (Table 1).

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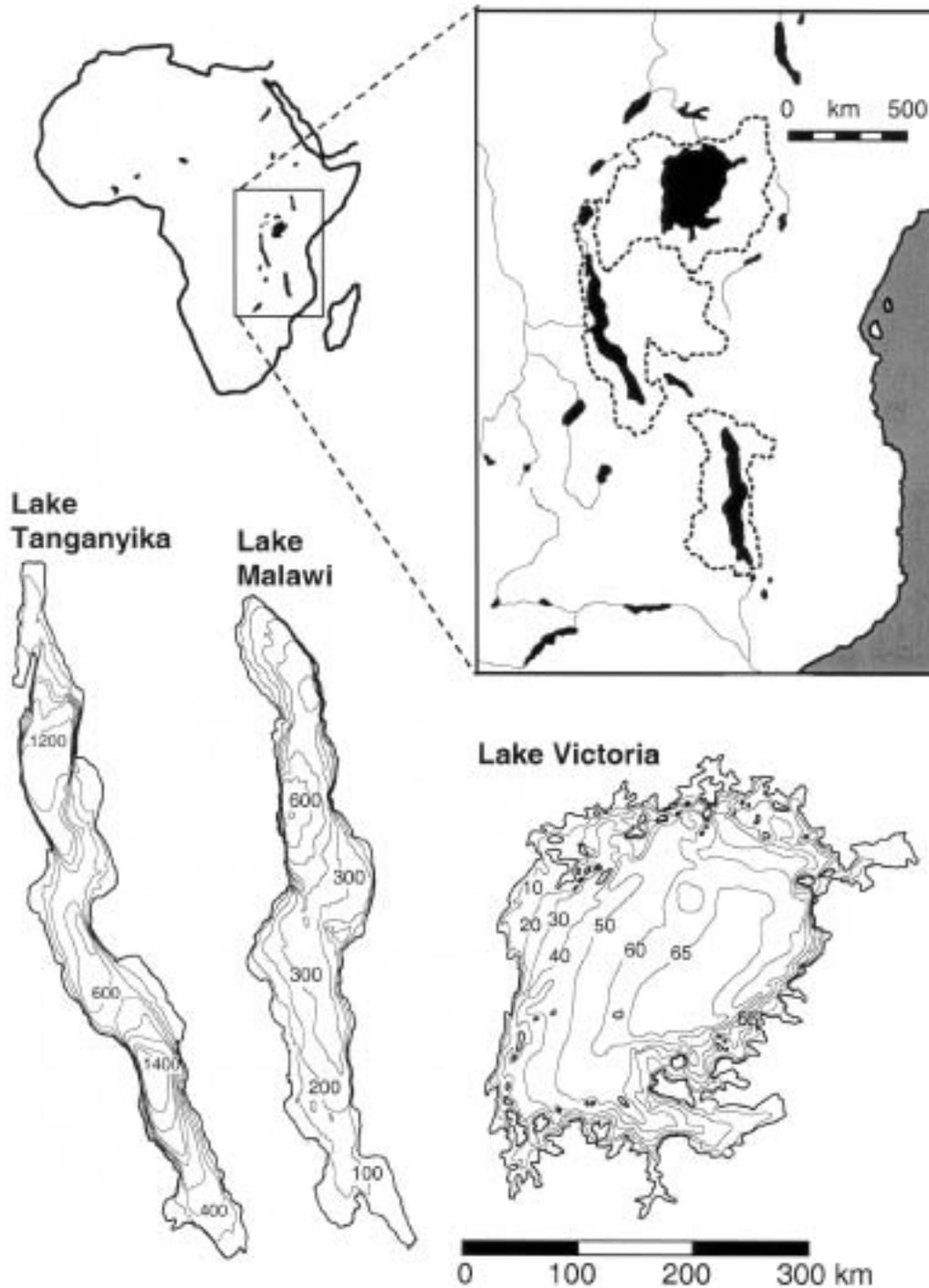
FIG. 1.   The East African Great Lakes. Dashed lines represent drainage basin boundaries. Bathymetric contour depths are given in meters, and are based on Tiercelin and Mondeguer (1991; Tanganyika), T.C. Johnson and B.M. Halfman (unpublished data for Malawi), and Lake Victoria bathymetry data collected during the IDEAL project, as given in Talbot and Lærdal (2000).

TABLE 1.   *Physical characteristics of the African and Laurentian Great Lakes. Morphometric data for the Laurentian Great Lakes are from Herdendorf (1982). Laurentian hydrology data are based on monthly data reported by Croley and Hunter (1994) and recent data provided by T.E. Croley II, GLERL, NOAA. Morphometric data for the African lakes are from Rzoska (1976), Gonfiantini* et al. *(1979), Bootsma and Hecky (1993), and a bathymetric map for Lake Malawi (T.C. Johnson and B.M. Halfman, unpubl.).*

	Victoria	Tanganyika	Malawi	Superior	Michigan	Huron	Erie	Ontario
Surface Area (km^2)	68,800	32,600	29,500	82,100	57,750	59,800	25,800	19,000
Maximum Depth (m)	79	1,470	700	407	282	229	64	245
Mean Depth (m)	40	580	264	149	85	59	19	86
Volume (km^3)	2,760	18,900	7,775	12,230	4,920	3,537	483	1,637
Drainage Area (km^2)	195,000	220,000	100,500	128,000	118,100	134,000	61,000	64,000
Altitude (m amsl)	1,134	774	474	183	177	177	174	75
River Inflow (km^3/yr)[*]	20[a]	14[b]	29[c]	50	36	165	196	229
River Outflow (km^3/yr)	20[a]	2.7[b]	12[c]	71	47	170	196	230
Rainfall (km^3/yr)	100[a]	29[b]	39[c]	65	47	51	24	17
Evaporation (km^3/yr)	100[a]	50[d]	57[e]	48	42	40	24	13
Residence Time (years)	23	440	114	107	59	16.4	2.2	6.7
Flushing Time (years)	138	7,000	648	172	105	21	2.5	7.1

[*] For the Laurentian Great Lakes, inflow includes both runoff and inflow from channels connecting upriver lakes.
[a] Rzoska (1976)
[b] Coulter and Spigel (1991)
[c] Kidd 1983
[d] Spigel and Coulter (1996)
[e] based on estimates of Eccles (1974), Spigel and Coulter (1996), and Hamblin *et al.* (2002)

East Africa contains the tropics' densest aggregation of lakes. Although many of these lakes can be considered large (*sensu* Herdendorf 1982), Lakes Victoria, Tanganyika, and Malawi stand out, with surface areas and volumes comparable to those of the Laurentian Great Lakes. Within this paper these three lakes are referred to as the African Great Lakes. With a surface area of nearly 69,000 km^2, Lake Victoria is the second largest freshwater lake on earth. Lake Tanganyika is second only to Lake Baikal with regard to depth, followed by Lake Malawi (Table 1. Lake Malawi is referred to as Lake Nyasa in Tanzania, and Lake Niassa in Mozambique). The lakes were formed by tectonic activity associated with the formation of the East African rift valley, a slowly widening divide that extends from the Red Sea in the north to Botswana in the south. Lakes Malawi and Tanganyika are located within the rift valley; hence their long, narrow, deep morphometry and mountainous shorelines. The shallower Lake Victoria basin occupies an uplifted region between the western and eastern arms of the rift valley. In addition to these three large lakes, the East African rift resulted in the formation of a number of other water bodies, including Lakes Edward and Albert in the western rift branch along the border between Uganda and the Democratic Republic of the Congo, Lake Turkana (formerly Lake Rudolf) which straddles the Kenya—Ethiopia border, and smaller Ethiopian, Kenyan, and Tanzanian lakes in the eastern rift branch.

In contrast to the relatively young Laurentian Great Lakes, the African Great Lakes are extremely old. Lakes Tanganyika and Malawi date back to the Miocene, with age estimates ranging from 10 to 20 million years (Haberyan and Hecky 1987, Tiercelin and Mondeguer 1991, Cohen *et al.* 1993). As a result of their great age, each of these two lakes is underlain by more than 4 kilometers of sediment (Rosendahl 1987, Tiercelin and Mondeguer 1991). The long time span covered by these records, combined with the short temporal scales at which they can be resolved, make them ideal for the reconstruction of paleolimnological and paleoclimatic conditions (Johnson 1996). To date, cores of varying completeness have been collected dating back to > 23,000 BP for Lake Victoria (Talbot and Livingstone 1989, Talbot and Lærdal 2000), > 25,000 BP for Lake Tanganyika (Gasse *et al.* 1989), and > 46,000 BP for Lake Malawi (Finney *et al.* 1996). These have provided a wealth of information about

the environmental conditions under which the diverse fish communities of these lakes evolved, and about short- and long-term climatic change in this part of the world. Currently there are plans for a deep drilling project on Lake Malawi, which will result in the collection of sediment records extending back as far as several hundred thousand years (Cohen *et al.* 2000).

LAKE FAUNA

The African Great Lakes are distinguished not only by their age, but also by their extremely diverse assemblages of fish. The precise number of fish species is not known for any of the lakes, since many remain undescribed. Lake Malawi is the most species-rich lake in the world, with an estimated 500 to 1,000 species of fish (Fryer and Iles 1972, Konings 1995). Eleven families of fishes exist in the lake, but one family—the Cichlidae—is by far the most speciose, making up over 90% of all fish species in the lake, almost all of which are endemic. Lake Tanganyika's fauna is similarly rich, with a total of 16 families and more than 200 cichlid species. Lake Victoria is also species-rich, and may have held more than 500 species, but many have either declined in number or become completely extinct over the past several decades, due to predation by the introduced Nile perch (*Lates niloticus*) (Ogutu-Ohwayo 1990, Goldschmidt *et al.* 1993) compounded by changes in water quality (Bootsma and Hecky 1993, Hecky 1993, Seehausen *et al.* 1997).

Diversity of the pelagic cichlids is high by any standards, but it is in the nearshore communities that diversity is the greatest. In the rocky nearshore waters of Lake Malawi, more than 500 individuals and 22 species can be found in a 50 m^2 area (Ribbink *et al.* 1983). Not only are the cichlid species endemic to each lake, but within each lake local endemicity is common among the nearshore fishes, so that certain species or color forms are confined to specific islands or isolated rocky segments of the shoreline (Fryer and Iles 1972, Ribbink *et al.* 1983, Konings 1995). While lake age may be an important factor promoting high diversity, the presence of endemic cichlid species in areas of Lakes Malawi and Victoria that were apparently completely dry within the Holocene (Owen *et al.* 1990, Johnson *et al.* 1996, Beuning *et al.* 1997) suggests that this diversity is largely a result of the genotypic plasticity of cichlids, which is given opportunity for expression as a result of the stenotopic behavior and

strong sexual selection exhibited within this family (Seehausen 2000).

Diversity of invertebrates within the African Great Lakes is variable. Benthic invertebrate diversity in Lake Malawi appears to be comparable to that in the Laurentian Great Lakes, with diversity being greatest among the ostracods, insects, and gastropods (Abdallah and Barton 2003). While Lake Tanganyika is home to fewer fish species than Lake Malawi, it boasts a much larger number of invertebrate species, particularly gastropods and ostracods (Coulter 1991a, Michel *et al.* 1992), many of which are endemic. The marine-like appearance of many of the gastropods, along with the presence of cnidarian medusae (*Limnocnida tanganyicae*), prompted speculation by earlier researchers that some of Lake Tanganyika's fauna is of marine origin, and that the lake at one time was directly connected to a marine basin (Brooks 1950). Although some of the lake's fauna, including its pelagic clupeid fish species, may have marine origins, more recent zoogeographical and geological studies suggest that the connection was indirect, through the Zaire basin (Coulter 1991a).

FISHERIES

The fishes of the African Great Lakes represent one of Earth's highest concentrations of vertebrate species. These species-rich communities present exciting opportunities to study rates and modes of speciation, and the interplay between biodiversity and ecosystem functions such as energy flow and nutrient cycling. However, to the riparian countries surrounding these lakes, their greatest assets are their fisheries. These fisheries account for a significant proportion of the economies of East African countries, and they represent a major source of food. For example, within Malawi, approximately 70% of dietary animal protein is in the form of fish (Bland and Donda 1995). Total catch for each of the lakes is difficult to estimate, due to the large number of small-scale fishers and the limited capacity of national governments to collect sufficient catch data. Estimates of annual catch are approximately 30,000 metric tons for Lake Malawi (Thompson 1995) and 80,000 to 100,000 metric tons for Lake Tanganyika (based on data summarized by Coulter 1991b). In both of these lakes, many species have been overfished in nearshore waters (Roest 1992, Alimoso *et al.* 1990), but there appear to be opportunities for further exploitation of pelagic stocks. Relative to Lake Malawi, the offshore commercial fishery in

Lake Tanganyika is well developed, but poor transportation and communication hamper further growth. Menz and Thompson (1995) have determined that exploitation of Lake Malawi's pelagic stocks would be economically viable, but because of the large investment in larger vessels and gear that would be required, and because the response of multi-species pelagic fish stocks to fishing pressure is uncertain, a cautious approach has been recommended.

The fishery of Lake Victoria has experienced dramatic changes over the past century. Initially dominated by tilapiine cichlids, increasing fishing pressure and steadily decreasing net mesh size between the 1930s and the 1970s resulted in declining catches and a shift toward dominance by smaller haplochromine cichlids and the small cyprinid, *Rastrineobola argentea* (Ogutu-Ohwayo 1990). In the late 1950s and early 1960s, the Nile perch (*Lates niloticus*) and several tilapiine species were introduced to the lake. Various rationales have been suggested for these introductions, but in fact it appears that they were not preceded by much forethought or consensus. The Nile perch population remained small for two decades after its introduction, but exploded in the early 1980s, when it made up well over half of the total fish catch (Ogutu-Ohwayo 1990). The haplochromine cichlid stocks that were already suffering from excessive fishing pressure were decimated as a result of predation by the Nile perch, and as many as 200 species are believed to have become extinct or are on the verge of disappearing (Goldschmidt et al. 1993, Witte *et al.* 1992). This is undoubtedly an ecological disaster, but not all would agree that introduction of the Nile perch was undesirable. Since the 1980s, the Lake Victoria fishery catch has more than quadrupled, with the catch consisting of three species—*L. niloticus*, the introduced tilapiine *Oreochromis niloticus*, and the indigenous cyprinid *R. argentea* (Ogutu-Ohwayo 1990). Currently, nearly one quarter of all freshwater fish caught in Africa come out of Lake Victoria (FAO 1999). The degree to which the local human population benefits from this fishery remains uncertain. The Nile perch was supposedly introduced to help convert small, bony cichlids into a more edible fish. However, the perch appear to be more valuable as a source of foreign exchange than as a local food source, as most of the catch is exported.

MANAGEMENT

Each of Africa's three largest lakes is shared among several countries. Lake Malawi is bordered by Malawi, Mozambique, and Tanzania; Lake Tanganyika by Zambia, Tanzania, Burundi, and the Democratic Republic of the Congo; and Lake Victoria by Tanzania, Kenya, and Uganda. As a result, water quality and fisheries management face challenges similar to those in the Laurentian Great Lakes, such as the coordination of research activities, the dissemination of data, and the harmonization of management strategies. There is a long history of collaboration on Lake Victoria, where the British colonial government established the East African Freshwater Fisheries Research Organization (EAFFRO) in 1947. In addition to promoting collaborative research and management efforts, EAFFRO established the African Journal of Tropical Hydrobiology and Fisheries, which is published intermittently. EAFFRO collapsed in 1977, when the treaty that had established the East African Community was officially dissolved. In 1971, the UN Food and Agriculture Organization (FAO) established the Committee for Inland Fisheries of Africa (CIFA), with the stated purpose of promoting research, education, training, and management of inland waters throughout Africa. With the recognition of emerging problems and the increasing value of the fisheries in the Lake Victoria region, the Lake Victoria Fisheries Organization was formed by the three riparian countries in 1994, and its head office in Jinja, Uganda became operational in 1997.

Unlike the countries around Lake Victoria, those around Lakes Tanganyika and Malawi were not previously linked by a common colonial government, and therefore international collaboration on these two lakes does not have as long a history. Some coordination is provided by the Southern African Development Community (SADC), established in 1979, of which Malawi, Mozambique, Zambia, Tanzania, and the DRC are members. However, although SADC includes a fisheries sector, the SADC mandate is very broad, and communication between researchers and managers in the various riparian countries has been limited.

While a common past facilitated international collaboration on Lake Victoria, exchange between the lake's bordering countries has also been fostered out of necessity in the past two decades as a result of the dramatic ecosystem-scale changes that have occurred in the lake. Although different views are held on the desirability of Nile perch in the lake, the invasion of the water hyacinth (*Eichhornia crassipes*) was an undisputed disaster. The plant entered the lake in the early 1980s, and by the early 1990s its numbers had increased to the point of cov-

ering much of the lake's shoreline, affecting water supply, fish distribution, transportation, and public health (Twongo 1996, Willoughby *et al.* 1996). In the last 2 years, there has been a dramatic decline in the abundance of the hyacinth, which is attributed at least in part to a weevil (*Neochetina eichorniae*) that was introduced in 1995. However, meteorological conditions and nutrient supply may have also played a role, and there is continued concern that the weed could make a comeback.

Recent changes in Lakes Tanganyika and Malawi have been less dramatic, but the combined effects of overfishing and deteriorating water quality in the lakes and their tributaries have raised concerns about the future of these species-rich systems (Bootsma and Hecky 1993, Cohen *et al.* 1996). As a result, there has been closer collaboration among the riparian countries, with support from international organizations such as the FAO, UNEP, and various European, North American, and Asian development organizations. In particular, collaborative projects to foster research, management, and training have been facilitated by the Global Environmental Facility (GEF), a facility that was born out of the 1992 UN Conference on Environment and Development (Earth Summit) in Rio de Janeiro. GEF programs have been in operation on all three of the African Great Lakes for the past several years, and much of the research published in this special issue was conducted as part of these programs.

A LIMNOLOGICAL COMPARISON WITH THE LAURENTIAN GREAT LAKES

Like their North American counterparts, the African Great Lakes are huge reservoirs of water—an invaluable resource in a region that is otherwise relatively dry. Annual rainfall in much of East Africa is generally between 800 and 1,200 mm per year (Nicholson 1996), similar to that around the Laurentian Great Lakes. But rapid evaporation leaves only a small proportion of this rain for human uses such as agriculture, industry, hydroelectric generation, and direct consumption (Table 1). Terrestrial evapotranspiration also leaves little water to flow into the lakes. River discharge to the African Great Lakes is much lower than that to the Laurentian Great Lakes, even though the drainage: lake surface area ratios for the African lakes (2.8 to 6.7) are similar to or larger than those for the North American lakes (1.6 to 3.7). As a result, most of the water input to the African Great Lakes is in the

form of rainfall directly on the lakes' surfaces (Table 1).

Due to high evaporation rates, the lake surface is also the path by which most water leaves the African Great Lakes (Table 1). The difference in evaporation rates between the African and North American lakes can be attributed to high year-round air temperatures over the African lakes, relatively low humidity, and the absence of ice cover. These high evaporation rates leave little water to flow out of the lakes. As a result the lake levels are very sensitive to small changes in climate. Lake Malawi was completely closed between 1915 and 1935, when it was 6 m lower than its peak height in 1980, and Lakes Tanganyika and Victoria may have also been closed basins within the past few centuries (Haberyan and Hecky 1987, Grove 1996). Between the 1960s and early 1980s, all three lakes were at their highest levels in the past century. Since then, Lake Victoria levels have dropped slightly, but Lakes Tanganyika and Malawi have dropped by about 4 m, and in 1997 low flows out of Lake Malawi through the Shire River resulted in the rationing of electrical power in Malawi. Ironically, this crisis might have been even worse if deforestation had been less extensive in Malawi over the past several decades, since the loss of forest has likely resulted in increased runoff to the lake (Calder *et al.* 1995).

Not only does evaporation represent a major water loss process in the African Great Lakes, it is also a large heat budget component, and therefore plays an important role in the annual mixing regime of these and other tropical lakes (Eccles 1974, Lewis 1983, Talling 1990, Spigel and Coulter 1996). While seasonal variation of solar radiation may be partly responsible for the annual stratification cycle, especially at the latitude of Lake Malawi, its role is minor compared to that in the Laurentian Great Lakes. Rather, wind and air temperature appear to be the main variables controlling the seasonality of mixing and thermal structure in large tropical lakes, by means of evaporative cooling and turbulence. This generality does not necessarily apply to smaller tropical lakes, where temporal changes in thermal structure, nutrient availability, and plankton production may be controlled to a large degree by hydrologic inputs (e.g., Coche 1974, Talling and Lemoalle 1998).

A number of authors have discussed the factors that distinguish tropical and temperate lakes (Talling 1965a, Burgis 1978, Melack 1979, Kalff and Watson 1986, Lewis 1987, Kilham and Kilham

TABLE 2. *Surface water chemistry of the African and Laurentian Great Lakes. Laurentian Great Lakes values represent summer measurements only. Data sources are USDOI (1968), Torrey (1976), Dobson* et al. *(1974), Weiler (1978), Thompson (1978), Beeton* et al. *(1999), and Barbiero and Tuchman (2001). African Great Lakes data sources are Hecky and Bugenyi (1992), and original data.*

	Victoria	Tanganyika	Malawi	Superior	Michigan	Huron	Erie	Ontario
Na^+ (µmol/L)	450	2,700	840	60	170	130	478	522
K^+ (µmol/L)	97	820	150	10	30	26	36	33
Ca^{2+} (µmol/L)	140	270	450	324	820	674	948	948
Mg^{2+} (µmol/L)	110	1,650	300	107	490	247	411	329
Cl^- (µmol/L)	110	750	100	40	310	190	410	600
SO_4^{2-} (µmol/L)	≤ 24	37	30	30	210	135	219	281
Alkalinity (meq/L)	0.92	6.52	2.30	0.83	2.2	1.58	1.74	1.8
Conductivity (µS/cm)	97	610	230	95	290	208	268	308
NO_3^- (µmol/L)	≤ 0.4	≤ 0.4	≤ 0.4	20	12	20	18	16

1989, Guildford *et al.* 2000, Hecky 2000), but limited attention has been given to large lakes. Ultimately, differences that result from latitude are due to differences in the quantity and seasonal variation of solar radiation, and the diminished Coriolis effect at lower latitudes (Lewis 1987, Talling and Lemoalle 1998). These fundamental differences lead to a number of latitudinal trends in the physical, chemical, and biological properties of large lakes. With regard to thermal structure and hydrodynamics, there are three important differences between large tropical and temperate lakes. Due to small thermal gradients and the large effect of temperature on water density in the 20° to 30°C range, thermal structure is temporally less stable in tropical lakes. As a result, small changes in heat flux or turbulence result in large, rapid changes in the depth of the surface mixed layer. Secondly, while thermal stratification is less stable than in large temperate lakes, it is more persistent, particularly at depths greater than 100 m. The Laurentian lakes pass through the temperature of maximum density twice annually which insures that density driven circulation can lead to complete turnover annually or even semi-annually. The African lakes lack this mechanism, and wind energy is insufficient to induce turnover in such deep lakes (Spigel and Coulter 1996, Hecky 2000). Lake Victoria mixes for only a brief period each year, and Lakes Malawi and Tanganyika are both meromictic with anoxic hypolimnia. Thirdly, due to the reduced Coriolis effect, wind-generated currents have a greater effect on mixing and can produce more persistent internal seiches in large tropical lakes. Lakes Malawi and Tanganyika are both oriented nearly parallel to the direction of the prevailing winds in East Africa, and internal seiches may persist throughout much of the

year in these lakes (Eccles 1974, Bootsma 1993, Coulter and Spigel 1991). These physical movements appear to play a large role in the distribution of dissolved gases, nutrients, and plankton (Coulter 1968, Bootsma 1993, Hamblin *et al.* 2003).

Surface water concentrations of major ions and some nutrients are presented in Table 2. A comparison of the tropical and temperate lakes reveals several major differences. As a result of its exceptionally long flushing time (Table 1), Lake Tanganyika is more saline than any of the other large lakes, as reflected in the high conductivity. However, salinity is affected by both flushing time and major ion inflow rates, and the long flushing times of the African lakes are countered by the relatively small river inflows and the low ionic content of inflowing river water. Dilution is also provided by the relatively large amount of direct rainfall on the lakes. As a result, the salinity of Lakes Malawi and Victoria is similar to that of the temperate Great Lakes. Among the temperate Great Lakes, the role of basin geology is apparent when comparing Lake Superior with the other four lakes. Despite its long flushing time, Lake Superior has a low ionic concentration, and the similarity between conductivities and flushing times in Lakes Superior and Victoria underscore the fact that, like the Superior basin, the African basins are made up largely of solution-resistant granitic minerals. In contrast the remaining Laurentian lakes receive waters rich in calcium and bicarbonate as a consequence of the extensive limestone deposits in their basins (Table 2).

Basin geology also results in tropical-temperate differences in the relative importance of various ions. While calcium is the dominant cation in the Laurentian Great Lakes, sodium and potassium

have greater relative and absolute concentrations in the large African lakes. The greater relative Na and K concentrations reflect the geology of African drainage basins (Kilham 1990), which are generally low in calcareous minerals. The greater absolute abundance is a result of the lakes' long flushing times. The implications of these chemical differences for biological processes are uncertain, but phytoplankton physiology and species composition are known to be affected by ion availability (Douglas and Smol 1995, Dempster and Sommerfeld 1998). Fryer and Iles (1972) have made the interesting observation that digestion of filamentous cyanobacteria by cichlid fishes appears to be made possible by the high sodium to calcium ratio in some African lakes.

Sulfate concentrations are low in the African Great Lakes, although they are also low in Lake Superior, again reflecting the important role of drainage basin geology. Concentrations as low as 3 μmol/L lhave been measured in Lake Victoria, where sulfur behaves more like a nutrient than a conservative ion. High rates of sulfur removal may also be facilitated by the anoxic hypolimnia and organic rich sediments of the African lakes, which favor sulfate reduction and the precipitation of sulfide minerals. Lake Malawi has been shown to have an unusually high removal rate for sulfate (Kelly *et al*. 1987). At one time sulfur limitation of algal growth was considered a possibility in Lake Victoria, but it now appears that this is unlikely (Lehman and Branstrator 1994).

Another chemical distinction between large tropical and temperate lakes is the low availability of dissolved nitrogen in tropical systems (Table 2). Within several of the Laurentian Great Lakes, surface nitrate concentrations have been increasing over the past century, probably due to atmospheric inputs (Bennett 1986). While atmospheric inputs of nitrogen to the African Great Lakes are also high (Bootsma *et al*. 1996, Langenburg *et al*. 2003), nitrogen does not accumulate in these lakes. This is likely due to the persistence of anoxic hypolimnia. Anoxia and warm temperatures promote rapid denitrification rates and enhance phosphorus mobilization in tropical lakes, and may explain the greater prevalence of nitrogen limitation in the tropics (Hecky *et al*. 1996, Downing *et al*. 1999). As a result, nitrogen fixers and species tolerant of low N:P ratios can make up a significant proportion of the phytoplankton and periphyton communities at certain times of the year (Hecky and Kling 1987, Kling *et al*. 2001), and nitrogen fixation appears to account for a large fraction of annual nitrogen input to these lakes (Hecky *et al*. 1996, Higgins *et al*. 2001, Mugidde *et al*. 2003).

The physical and chemical limnological characteristics associated with a tropical climate result in unique biological properties of the African Great Lakes. Warm temperatures result in high metabolic rates and rapid turnover rates of the plankton. Chlorophyll *a* concentrations in Lakes Malawi and Tanganyika are typically below 1 μg /L, and Secchi disk depths regularly exceed 15 m. By these standards, the lakes can be classified as oligotrophic. But despite low phytoplankton biomass, photosynthetic rates are remarkably high. Hecky and Fee (1981) estimated a mean photosynthetic rate of 1 g C/m^2/d for Lake Tanganyika, and rates in Lake Malawi are around 0.7 g C/m^2/d (Bootsma 1993). Thus, while phytoplankton abundance in these lakes is similar to that in Lake Superior (Vollenweider *et al*. 1974, Guildford *et al*. 2000, Barbiero and Tuchman 2001), photosynthetic rates are comparable to those in Lake Erie. According to classification standards that have been applied to the Laurentian Great Lakes (Vollenweider *et al*. 1974), Lakes Malawi and Tanganyika would be considered eutrophic. Accepted paradigms for temperate lakes may not readily apply to tropical lakes.

Another paradigm that large tropical lakes appear to defy is the notion that tropical ecosystems are temporally more stable than their temperate counterparts. The intensive studies on Lake George as part of the International Biological Program in the late 1960s supported the suggestion that, like their terrestrial counterparts, tropical aquatic systems are relatively stable over time (Ganf and Viner 1973). Other tropical-temperate comparisons have also indicated that seasonal variability is reduced in tropical lakes (Melack 1979, Ashton 1985). However, these analyses did not include large lakes. Seasonal changes of temperature and surface irradiance in the African Great Lakes are small compared to those for the Laurentian Great Lakes, but nutrient availability in the mixed layer of the African Great Lakes is likely much more variable than it is within the temperate lakes, due to the very high dissolved nutrient concentrations below the surface mixed layer (Bootsma and Hecky 1993, Edmond *et al*. 1993, Hecky *et al*. 1996). Periodic injections of these nutrients into the trophogenic zone result in phytoplankton variability that is comparable to that observed in the Laurentian Great Lakes (Table 3).

The conversion of phytoplankton production into fishery yield tends to be more efficient in tropical

TABLE 3. *Inter-lake comparison of phytoplankton biomass temporal variability (presented as coefficient of variation). For all lakes, volumetric concentration of phytoplankton biomass in surface waters was used to determine variation. The value for Lake Tanganyika is based on measurements made at one station near the north end of the lake. The value for Lake Malawi represents the variation of means (7 to 11 stations) for 11 cruises. The value for Lake Victoria was determined from pelagic chlorophyll concentrations, which Kling* et al. *(2001) found to be a good proxy for biomass. The variation for Lake Erie represents the mean of three basins. Variation in Lakes Erie, Ontario, Huron, and Superior are based on lake-wide monthly means of 25, 27, 22, and 34 stations, respectively (exact numbers of samples not given).*

Lake	Time Span	C.V. (%)	n	Source
Victoria	12 months	44	11	Kling *et al.* (2001)
Tanganyika	10 months	94	29	Hecky and Kling (1981)
Malawi	12 months	58	11	Bootsma (1993)
Superior	May–Nov.	26	—	Munawar and Munawar (1986)
Huron	Apr.–Dec.	54	—	Munawar and Munawar (1986)
Erie	Mar.–Dec.	63	—	Munawar and Munawar (1986)
Ontario	12 months	69	—	Munawar and Munawar (1986)

lakes than in temperate lakes. This is likely due to the year-round growth of tropical fishes (as opposed to the seasonal growth observed in most temperate fishes), and the greater proportion of low trophic level fishes in tropical fisheries. However, carbon transfer efficiency and fishery catches also appear to be influenced to a large degree by food web structure (Hecky 1984). The potential importance of trophic structure is highlighted by a comparison of Lakes Tanganyika and Malawi. Initial measurements suggested that phytoplankton production is comparable in the two lakes (Hecky and Fee 1981, Bootsma 1993), but that the fishery yield of Lake Tanganyika is several times greater than that of Lake Malawi. Early acoustic estimates of pelagic fish biomass in Lake Tanganyika were around 160 kg/ha (Roest 1977, Coulter 1991b) while that for Lake Malawi is 70 kg/ha (Menz *et al.* 1995). The reasons for this apparent difference in trophic efficiency remain a matter of debate. Suggested causes include the more efficient utilization of plankton production by pelagic clupeids in Lake Tanganyika (Turner 1982), and the lengthening of the pelagic food chain in Lake Malawi due to the presence of lakefly (*Chaoborus edulis*) larvae (Allison *et al.* 1995). The lakefly is also found in Lake Victoria which has a rather inefficient food web today, but it is absent from Lake Tanganyika. More recent estimates of photosynthesis and fish production in Lake Tanganyika (Sarvala *et al.* 1999) suggest that trophic efficiency may not be as high as previously thought. Similarly, recent fish biomass

surveys on Lake Malawi have revealed the existence of deep-water stocks that have the potential to significantly increase the lake's fishery yield (Menz and Thompson 1995). These ongoing changes in understanding these complex systems underscore the need for more spatially complete and temporally continuous measurements of ecological processes, made all the more urgent by the need to conserve the unique biota of these lakes and ensure that they continue to provide a sustainable food source to the growing human populations in the region.

THE DIRECTION OF RESEARCH ON THE AFRICAN GREAT LAKES

Various authors have documented the history of scientific research on the African Great Lakes (Beadle 1981, Talling 1995, Melack 1996, Talling and Lemoalle 1998). Several expeditions were conducted to each of the lakes between 1894 and 1905, which resulted in the documentation of a large number of animal and plant species. The first studies of physical and chemical properties were those of Worthington (1930, 1931) on Lake Victoria, and Beauchamp (1939, 1940, 1953) on Lakes Tanganyika and Nyasa. The most noteworthy findings of Beauchamp's work were that Lakes Malawi and Tanganyika were permanently stratified, had anoxic hypolimnia, and had very low phytoplankton concentrations compared to other tropical lakes that had been studied. The work of Talling (1957,

1965a, 1965b, 1966, 1969) on Lake Victoria was a major step in understanding the dynamics of photosynthesis in aquatic systems, and advanced the understanding of tropical algal ecology and its relation to physical and chemical conditions. Talling's work also provided critical baseline data that has allowed for the quantification of chemical, physical, and biological changes that have occurred in Lake Victoria over the past several decades (Hecky 1993, Bootsma and Hecky 1993).

Research programs on the African Great Lakes over the past 40 years have not followed the same agenda as those on the Laurentian lakes. Until recently, problems such as eutrophication and contaminant inputs received little attention in the African lakes, where much of the research has been motivated by the pragmatic need for improved fisheries production and management (Ogutu-Ohwayo 1990, Menz 1995, Mölsä *et al.* 1999), or by a more academic interest in the systematics, zoogeography, and behavior of the diverse cichlid fish communities (Genner *et al.* 1999, van Alphen and Seehausen 2001, Salzburger *et al.* 2002). In addition, the thick sediments underneath the African lakes provide a paleo-record that is unmatched in large temperate lakes with regard to temporal span and resolution. As a result, a significant amount of research has been carried out on the geology and sedimentology of the lakes. Much of this work has focused on paleoclimatic reconstruction for the past 10,000 to 40,000 years (Talbot and Lærdal 2000, Johnson *et al.* 2002), revealing regional changes in hydrology, temperature, and possibly wind that coincide with global changes in climate. Sediment cores have also proved useful in elucidating the potential causes of water quality changes that have occurred more recently (Hecky 1993, Verschuren *et al.* 2002).

Water-borne diseases are especially prevalent in the tropics. For diseases such as malaria, cholera, and schistosomiasis, the lakes may serve as vectors, especially in densely populated lakeshore regions (Cetron *et al.* 1996, Shapiro *et al.* 1999). In Lake Malawi, there appears to have been an increase in the incidence of schistosomiasis over the past three decades. While this is probably due in part to increased population density and poor hygiene, there is evidence that over-fishing may also have contributed. A comparison of several datasets collected from the 1970s to the 1990s suggests that the abundance of the snail that serves as a host for the schistosome parasite, *Bulinus globosus*, has increased, while the number of snail-eating fishes has de-

clined, probably due to intensive nearshore gillnetting and beach seining (Stauffer *et al.* 1997). While some research and education programs have been devoted to the management of schistosomiasis and other water-borne diseases in the African Great Lakes region, their huge negative impact on social and economic conditions warrants a much larger effort.

Recent changes in all three lakes have resulted in an increased realization that individual components of these systems cannot be understood in isolation, and that effective management must expand beyond conventional fisheries management to account for the interaction of physical, geological, chemical, and biological processes at the ecosystem scale (Mölsä *et al.* 1999). Although specific processes in tropical aquatic ecosystems, such as hydrodynamics, plankton production, and fisheries production have received some attention, there remains a need to integrate these processes in order to gain a better understanding of ecosystem functioning. One means of doing this is through the development of conceptual and numerical models, which can facilitate both the theoretical understanding and applied management of these ecosystems (Crisman and Streever 1996). As management problems move from the relatively simple issue of fishery control to the more complex issues of land use and climate change, models will play an important role in decision-making processes. For the developing riparian countries, it is critical that management strategies have maximum positive impact with minimal expense. Predicting the efficacy of various management options is obviously more cost effective than a trial and error approach. To this end, initial models that simulate physical and biogeochemical processes in the lakes and their catchments have been developed for Lakes Malawi and Victoria (Lam *et al.* 2001). The hope is that these models will serve as a basis for informed discussions about the present and future state of the lakes, and eventually be applied as decision-support tools for management of the lakes.

An understanding of ecosystem functioning and the development of integrated physical and biogeochemical models are also critical for the interpretation of sediment records. The sediment records available from the African Great Lakes, as well as smaller African lakes, are invaluable to an understanding of the magnitude and timing of global climate variation (Johnson 1996, Gasse 2000). Interpretation of many of the climate proxies measured in these sediments requires an understanding

of the mechanisms that link meteorology, hydrodynamics, chemistry, and biology. For example, the interpretation of diatom microfossil records (Stager *et al.* 1986, Haberyan and Hecky 1987, Gasse *et al.* 2002) relies on a general understanding of diatom autecology (Hecky and Kling 1987, Kilham *et al.* 1986, Owen and Crossley 1992). But there remains a need to better quantify the effects of physical and chemical conditions on diatom species composition (Kilham *et al.* 1986, Gasse *et al.* 2002) and biogenic silica deposition. While some empirical data are available to indicate how the lakes' plankton communities respond to meteorological changes over time scales of months to years, these observations do not necessarily reflect steady state conditions in these slowly flushing lakes (Bootsma *et al.* 2003), and therefore they must be used with caution when trying to interpret the climatic significance of long-term changes in the microfossil record. For this purpose, hydrodynamic and biogeochemical models that simulate over time scales of decades to centuries are necessary.

The need for tropical lake ecosystem models goes beyond lake management. As D.V. Anderson pointed out in his editorial preface to the 11th IAGLR conference proceedings, the study of large tropical lakes can increase the general understanding of the mechanisms that control the physical, chemical, and biological functioning of large, aquatic ecosystems. Paradigms that help to direct research and management priorities in the Laurentian Great Lakes are constrained by the geological, meteorological, and biological conditions that exist in those lakes. When those conditions change (e.g., following exotic species invasions or a change in climate), the paradigms often are of limited use in predicting ecosystem response. Thienemann (1932) observed this over half a century ago, when he discovered that the measurement of hypolimnetic oxygen deficit could not be used to trophically classify tropical lakes, as it was for temperate lakes. Currently there is much concern and uncertainty about potential impact of climate change on temperate aquatic ecosystems (Mortsch and Quinn 1996, Nicholls 1999). While the effects of a given change in climate on lake physical processes can probably be predicted with a good degree of certainty, potential changes in chemical cycles and biological properties are much more difficult to predict, due to the number and complexity of interacting processes that link meteorology to chemical and biological dynamics. By viewing the African Great Lakes as endpoints along a climatic gradient, it

may be possible to acquire insight into how physical changes such as warmer temperatures, prolonged stratification and hydrologic shifts will affect biota and ecosystem functioning in other lakes.

Following accelerated species extinction rates around the world, the implications of species losses for ecosystems has become a concern, and the question of how organisms are influenced by their environment has been turned around to ask what role species composition and biodiversity play in ecosystem functioning (Tilman 1999, McCann 2000). Already several decades ago, Fryer and Iles (1972) discussed the possible relationship between cichlid diversity and ecosystem stability in the African Great Lakes. However, despite the recognition that fish diversity might play a role in ecosystem processes such as energy transfer and nutrient cycling, and that the cichlid communities of the African Great Lakes present a unique opportunity to examine these relationships, the role of diverse fish communities in ecosystem functioning has received little attention in the African Great Lakes (Leveque 1995). Some of the recent papers presented in this issue and elsewhere (Higgins *et al.* 2001, André *et al.* 2003) suggest that further research on this topic in the African Great Lakes will be fruitful. The great biological diversity in these lakes, and the recent loss of much of this diversity from Lake Victoria, present opportunities to examine the relationships between community structure and ecosystem functioning in natural settings. The results of these studies may well provide insight to the long-term response of the Laurentian Great Lakes to changes in diversity and community structure resulting from exotic species invasions that have taken place over the past century and will likely continue in the future (Mills *et al.* 1993, 1994).

Truly large freshwater systems that immediately invite the epithet "great" are rare on the present earth. Studies of these large systems are logistically and intellectually challenging. These characteristics of rarity and challenge impose a special onus upon great lakes researchers to share and promote the results of these studies for the benefit of all the great lakes. This special issue of the Journal of Great Lakes Research is a welcome opportunity to share the results of recent research on the African Great Lakes with the great lakes research community.

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REFERENCES

Abdallah, A.M., and Barton, D.R. 2003. Environmental factors controlling the distributions of benthic invertebrates on rocky shores of Lake Malawi, Africa. *J. Great Lakes Res*. 29 (Suppl. 2):202–215.

Alimoso, S., Magasa, J., and Van Zalinge, N. 1990. Exploitation and management of fish resources in Lake Malawi. In *Fisheries of the African Great Lakes*, pp. 83–95. International Agricultural Centre, Wageningen, Netherlands. Occasional Paper 3.

Allison, E.H., Patterson, G., Irvine, K., Thompson, A.B., and Menz, A. 1995. The pelagic ecosystem. In *The fishery potential and productivity of the pelagic zone of Lake Malawi/Nyasa*, ed. A. Menz, pp. 351–367. Chatham, UK: Natural Resources Institute.

André, E.R., Hecky, R.E., and Duthie, H.C. 2003. Nitrogen and phosphorus regeneration by cichlids in the littoral zone of Lake Malawi, Africa. *J. Great Lakes Res*. 29 (Suppl. 2):190–201.

Ashton, P.J. 1985. Seasonality in Southern Hemisphere phytoplankton assemblages. *Hydrobiologia* 125: 179–190.

Barbiero, R.P., and Tuchman, M.L. 2001. Results from the U.S. EPA's biological open water surveillance program of the Laurentian Great Lakes: I. Introduction and phytoplankton results. *J. Great Lakes Res*. 27:134–154.

Beauchamp, R.S.A. 1939. Hydrology of Lake Tanganyika. *Int. Rev. ges. Hydrobiol*. 39:316–353.

_____. 1940. Chemistry and hydrography of Lakes Tanganyika and Nyasa. *Nature* 146:253–256.

_____. 1953. Hydrological data from Lake Nyasa. *J. Ecol*. 41: 226–239.

Beadle, L.C. 1981. *Inland waters of tropical Africa.* New York: Longman.

Beeton, A.M., Sellinger, C.E., and Reid, D.F. 1999. An introduction to the Laurentian Great Lakes ecosystem. In *Great Lakes fisheries policy and management; a binational perspective*, eds. W.W. Taylor and C.P. Ferreri, pp. 3–54. East Lansing, MI: Michigan State University Press.

Bennett, E.B. 1986. The nitrifying of Lake Superior. *Ambio* 15:272–275.

Beuning, K.R.M., Kelts, K., and Ito, E. 1997. Paleaohydrology of Lake Victoria, East Africa, inferred from $^{18}O/^{16}O$ ratios in sediment cellulose. *Geology* 25:1083–1086.

Bland, S.J.R., and Donda, S.J. 1995. *Common property and poverty: fisheries co-management in Malawi*. Malawi Fisheries Department, Fisheries Bulletin No. 30:1–16.

Bootsma, H.A. 1993. Algal dynamics in an African Great Lake, and their relation to hydrographic and meteorological conditions, Ph.D. thesis, Univ. of Manitoba, Winnipeg, Manitoba.

_____, and Hecky, R.E. 1993. Conservation of the African Great Lakes: A limnological perspective. *Conser. Biol*. 7:644–656.

_____, Bootsma, M.J., and Hecky, R.E. 1996. The chemical composition of precipitation and its significance to the nutrient budget of Lake Malawi. In *The limnology, climatology and paleoclimatology of the East African lakes*, eds. T.C. Johnson and E.O. Odada, pp. 251–265. Amsterdam, The Netherlands: Gordon and Breach Publishers.

_____, Hecky, R.E., Johnson, T.C., Kling, H.J., and Mwita, J. 2003. Inputs, outputs, and internal cycling of silica in a large, tropical lake. *J. Great Lakes Res*. 29 (Suppl. 2):121–138.

Brooks, J.L. 1950. Speciation in ancient lakes. *Quart. Rev. Biol*. 25:30–36, 131–176.

Burgis, M.J. 1978. Case studies of lake ecosystems at different latitudes: the tropics. The Lake George ecosystem. *Verh. Internat. Verein. Limnol*. 20:1139–1152.

Calder, I.R., Hall, R.L., Bastable, H.G., Gunston, H.M., Shela, O., Chirwa, A., and Kafundu, R. 1995. The impact of land use change on water resources in sub-Saharan Africa: a modeling study of Lake Malawi. *J. Hydrol*. 170:123–135.

Cetron, M.S., Chitsulo, L., Sullivan, J.J., Pilcher, J., Wilson, M., Noh, J., Tsang, V.C., Hightower, A.W., and Addiss, D.G. 1996. Schistosomiasis in Lake Malawi. *Lancet* 348:1274–1278.

Coche, A.G. 1974. Limnological study of a tropical reservoir, part I. In *Lake Kariba, a man-made tropical ecosystem in Central Africa*, eds. E.K. Balon and A.G. Coche, pp. 1–248. Monogr. Biologicae 24. The Hague: Junk.

Cohen, A.S., Soreghan, M.J., and Scholz, C.A. 1993. Estimating the age of ancient lakes: an example from Lake Tanganyika, East African Rift system. *Geology* 21:511–514.

_____, Kaufman, L., and Ogutu-Ohwayo, R. 1996. Anthropogenic threats, impacts and conservation strategies in the African Great Lakes: a review. In *The limnology, climatology and paleoclimatology of the East African lakes*, eds, T.C. Johnson and E.O. Odada, pp. 575–632. Amsterdam, The Netherlands: Gordon and Breach Publishers.

_____, Scholz, C.A., and Johnson, T.C. 2000. The international decade of East African lakes (IDEAL) drilling initiative for the African Great Lakes. *J. Paleolimnol*. 24:231–235.

Coulter, G.W. 1968. Hydrological processes and primary production in Lake Tanganyika. In *Proc. 11th Conf. Great Lakes Res.,* pp. 609–626. Internat. Assoc. Great Lakes Res.

_____. 1991a. Composition of the flora and fauna. In *Lake Tanganyika and its life*, ed. G.W. Coulter, pp. 200–274. Oxford, England: Oxford University Press.

_____. 1991b. Fisheries. In *Lake Tanganyika and its life*, ed. G.W. Coulter, pp. 139–150. Oxford, England: Oxford University Press.

_____, and Spigel, R.H. 1991. Hydrodynamics. In *Lake Tanganyika and its life*, ed. G.W. Coulter, pp. 49–75. Oxford, England: Oxford University Press.

Crisman, T.L., and Streever, W.J. 1996. The legacy and future of tropical limnology. In *Perspectives in tropical limnology*, eds. F. Schiemer and K.T. Boland, pp. 27–42. Amsterdam, The Netherlands: SPB Academic Publishing.

Croley, T.E., II, and Hunter, T.S. 1994. *Great Lakes Monthly Hydrologic Data*. NOAA Tech. Memo. TM-083, Great Lakes Environmental Research Laboratory, Ann Arbor, Michigan.

Dempster, T.A., and Sommerfeld, M.R. 1998. Effects of environmental conditions on growth and lipid accumulation in *Nitzschia communis* (Bacillariophyceae). *J. Phycol.* 34:712–721.

Dobson, H., Dobson, F.H., Gilbertson, M., and Sly, P.G. 1974. A summary and comparison of nutrients and related water quality in lakes Erie, Ontario, Huron, and Superior. *J. Fish. Res. Board Can.* 31:731–738.

Douglas, M.S.V., and Smol, J.P. 1995. Periphytic diatom assemblages from high arctic ponds. *J. Phycol.* 31:60–69.

Downing, J.A., McClain, M., Twilley, R., Melack, J.M., Elser, J., Rabalais, N.N., Lewis, W.M., Turner, R.E., Corredor, J., Soto, D., Yanez-Arancibia, A., Kopaska, J.A., and Howarth, R.W. 1999. The impact of accelerating land-use change on the N-Cycle of tropical aquatic ecosystems: Current conditions and projected changes. *Biogeochem.* 46:109–148.

Eccles, D.H. 1974. An outline of the physical limnology of Lake Malawi (Lake Nyasa). *Limnol. Oceanogr.* 19:730–742.

Edmond, J.M., Stallard, R.F., Craig, H., Craig, V., Weiss, R.F., and Coulter, G.W. 1993. Nutrient chemistry of the water column of Lake Tanganyika. *Limnol. Oceanogr.* 38:725–738.

FAO 1999. *The state of world fisheries and aquaculture*. Food and Agricultural Organization, Rome. FAO 43 AGRIS: M11: M12.

Finney, B.P., Scholz, C.A., Johnson, T.C., and Trumbore, S. 1996. Late quaternary lake-level changes of Lake Malawi. In *The limnology, climatology and paleoclimatology of the East African lakes*, eds. T.C. Johnson and E.O. Odada, pp. 495–508. Amsterdam, The Netherlands: Gordon and Breach Publishers.

Fryer, G., and Iles, T.D. 1972. *The cichlid fishes of the Great Lakes of Africa; their biology and evolution*. Edinburgh: Oliver and Boyd.

Ganf, G.G., and Viner, A.B. 1973. Ecological stability in a shallow equatorial lake (Lake George, Uganda). *Proc. R. Soc. Lond. B.* 184:321–346.

Gasse, F. 2000. Hydrological changes in the African tropics since the last glacial maximum. *Quat. Sci. Rev.* 19:189–211.

_____, Ledee, V., Massault, M., and Fontes, J.-C. 1989. Water-level fluctuations o f Lake Tanganyika in phase with oceanic changes during the last glaciation and deglaciation. *Nature* 342:57–59.

_____, Barker, P., and Johsnon, T. 2002. A 24,000 yr diatom record from the northern basin of Lake Malawi. In *The East African great lakes: limnology, palaeolimnology and biodiversity*, eds. E.O. Odada and D.O. Olago, pp. 393–414. Dordrecht, The Netherlands: Kluwer.

Genner, M.J., Turner, G.F., and Hawkins, S.J. 1999. Foraging of rocky habitat cichlid fishes in Lake Malawi: Coexistence through niche partitioning? *Oecologia* 121:283–292.

Goldschmidt, T., Witte, F., and Wanink, J. 1993. Cascading effects of the introduced Nile perch on the detritivorous/phytoplanktivorous species in the sublittoral areas of Lake Victoria. *Conserv. Biol.* 7:686–700.

Gonfiantini, R., Zuppi, G.M., Eccles, D.H., and Ferro, W. 1979. Isotope investigation of Lake Malawi. In *Isotopes in lake studies*, pp. 195–207. Vienna, Austria: International Atomic Energy Agency.

Grove, A.T. 1996. African river discharges and lake levels in the twentieth century. In *The limnology, climatology and paleoclimatology of the East African lakes*, eds. T.C. Johnson and E.O. Odada, pp. 95–100. Amsterdam, The Netherlands: Gordon and Breach Publishers.

Guildford, S.J., Bootsma, H.A., Fee, E.J., Hecky, R.E., and Patterson, G. 2000. Phytoplankton nutrient status and mean water column irradiance in Lakes Malawi and Superior. *Aquat. Ecosyst. Health Manage.* 3:35–45.

Haberyan, K.A., and Hecky, R.E. 1987. The late Pleistocene and Holocene stratigraphy and paleolimnology of Lakes Kivu and Tanganyika. *Palaeogogr. Palaeoclimatol. Palaeoecol.* 61:169–197.

Hamblin, P.F., Bootsma, H.A., and Hecky, R.E. 2003. Modeling nutrient upwelling in Lake Malawi/Nyasa. *J. Great Lakes Res.* 29 (Suppl. 2):34–47.

Hecky, R.E. 1984. African lakes and their trophic efficiencies: a temporal perspective. In *Trophic interactions within aquatic ecosystems*, ed. D.G. Meyers and J.R. Strickler, pp. 405–448. Amer. Assoc. Adv. Sci. Selected Symposium 85.

_____. 1993. The eutrophication of Lake Victoria. *Verh. Int. Verein. Theor. Ang. Limnol.* 25:39–48.

_____. 2000. A biogeochemical comparison of Lakes Superior and Malawi and the limnological consequences of an endless summer. *Aquat. Ecosyst. Health Manage.* 3:23–33.

_____, and Bugenyi, F.W.B. 1992. Hydrology and chemistry of the African Great Lakes and water quality issues: Problems and solutions. *Mitt. Internat. Verein. Limnol*. 23:45–54.

_____, and Fee, E.J. 1981. Primary production and rates of algal growth in Lake Tanganyika. *Limnol. Oceanogr*. 26:532–547.

_____, and Kling, H.J. 1981. The phytoplankton and protozooplankton of the euphotic zone of Lake Tanganyika: species composition, biomass, chlorophyll content and spatio-temporal distribution. *Limnol. Oceanogr*. 26:548–564.

_____, and Kling, H.J. 1987. Phytoplankton ecology of the great lakes in the rift valleys of Central Africa. *Arch. Hydrobiol. Beih., Ergebn. Limnol*. 25:197–228.

_____, Bootsma, H.A., Mugidde, R.M., and Bugenyi, F.W.B. 1996. Phosphorus pumps, nitrogen sinks, and silicon drains: plumbing nutrients in the African Great Lakes. In *The limnology, climatology and paleoclimatology of the East African lakes*, eds. T.C. Johnson and E.O. Odada, pp. 205–224. Amsterdam, The Netherlands: Gordon and Breach Publishers.

Herdendorf, C.E. 1982. Large lakes of the world. *J. Great Lakes Res*. 8:379–412.

Higgins, S.N., Hecky, R.E., and Taylor, W.D. 2001. Epilithic nitrogen fixation in the rocky littoral zones of Lake Malawi, Africa. *Limnol. Oceanogr*. 46:976–982.

Johnson, T.C. 1996. Sedimentary processes and signals of past climatic change in the large lakes of the East African rift valley. In *The limnology, climatology and paleoclimatology of the East African lakes*, eds. T.C. Johnson and E.O. Odada, pp. 367–412. Amsterdam, The Netherlands: Gordon and Breach Publishers.

_____, Scholz, C.A., Talbot, M.R., Kelts, K., Ricketts, R.D., Ngobi, G., Beuning, K., Ssemmanda, I., and McGill, J.W. 1996. Late Pleistocene desiccation of Lake Victoria and rapid evolution of cichlid fishes. *Science* 273:1091–1093.

_____, Brown, E.T., McManus, J., Barry, S., Barker, P., and Gasse, F. 2002. A high-resolution paleoclimate record spanning the past 25,000 years in southern East Africa. *Science* 296:113–114, 131–132.

Kalff, J., and Watson, F. 1986. Phytoplankton and its dynamics in two tropical lakes: a tropical and temperate zone comparison. *Hydrobiologia* 138:161–176.

Kelly, C.A., Rudd, J.W.M., Hesslein, R.H., Schindler, D.W., Dillon, P.J., Driscoll, C.T., Gherini S.A., and Hecky, R.E. 1987. Prediction of biological acid neutralization in lakes. *Biogeochemistry* 3:129–140.

Kidd, C.H.R. 1983. *A water resources evaluation of Lake Malawi and the Shire River*. UNDP Project MLW/77/012, World Meteorological Organization, Geneva.

Kilham, P. 1990. Mechanisms controlling the chemical composition of lakes and rivers: Data from Africa. *Limnol. Oceanogr*. 35:80–83.

_____, and Kilham, S.S. 1989. Endless summer: internal loading processes dominate nutrient cycling in tropical lakes. *Freshwat. Biol*. 23:379–389.

_____, Kilham S.S., and Hecky, R.E. 1986. Hypothesized resource relationships among African planktonic diatoms. *Limnol. Oceanogr*. 31:1169–1181.

Kling, H.J., Mugidde, R., and Hecky, R.E. 2001. Recent changes in the phytoplankton community of Lake Victoria in response to eutrophication. In *The great lakes of the world (GLOW): food-web, health and integrity*, eds. M. Munawar and R.E. Hecky, pp. 47–65. Leiden, The Netherlands: Backhuys Publishers.

Konings, A. 1995. *Malawi cichlids in their natural habitat*. 2nd ed. Germany: Cichlid Press.

Langenburg, V.T., Nyamushahu, S., Roijackers, R., and Koelmans, A.A. 2003. External nutrient sources for Lake Tanganyika. *J. Great Lakes Res*. 29 (Suppl. 2):169–180.

Lam, D.C.L., Leon, L., Hecky, R., Bootsma, H., and McCrimmon, R.C. 2002. A modelling approach for Lake Malawi/Nyasa/Niassa: integrating hydrological and limnological data. In *The East African great lakes: limnology, palaeolimnology and biodiversity*, eds. E.O. Odada and D.O. Olago, pp. 189–208. Dordrecht, The Netherlands: Kluwer.

Lehman, J.T., and Branstrator, D.K. 1994. Nutrient dynamics and turnover rate of phosphate and sulfate in Lake Victoria, East Africa. *Limnol. Oceanogr*. 39:931–945.

Leveque, C. 1995. Role and consequences of fish diversity in the functioning of African freshwater ecosystems: a review. *Aquat. Living Resour*. 8:59–78.

Lewis, W.M. 1983. Temperature, heat and mixing in Lake Valencia, Venezuela. *Limnol. Oceanogr*. 28:273–286.

_____. 1987. Tropical limnology. *Ann. Rev. Ecol. Syst*. 18:158–184.

McCann, K.S. 2000. The diversity-stability debate. *Nature* 405:228–233.

Melack, J.M. 1979. Temporal variability of phytoplankton in tropical lakes. *Oecologica* 44:1–7.

_____. 1996. Recent developments in tropical limnology. *Verh. Internat. Verein. Limnol*. 26: 211–217.

Menz, A. 1995. *The fishery potential and productivity of the pelagic zone of Lake Malawi/Niassa*. Chatham, UK: Natural Resources Institute.

_____, and Thompson, A.B. 1995. *Management report of the UK/SADC pelagic fish resouce assessment project, Lake Malawi/Nyasa*. Chatham, UK: Natural Resources Institute.

_____, Bulirani, A., and Goodwin, C.M. 1995. Acoustic estimation of fish biomass. In *The fishery potential and productivity of the pelagic zone of Lake Malawi/Nyasa*, ed. A. Menz, pp. 307–349. Chatham, UK: Natural Resources Institute.

Michel, A.E., Cohen, A.S., West, K., Johnston, M.R., and Kat, P.W. 1992. Large African lakes as natural

laboratories for evolution: examples from the endemic gastropod fauna of Lake Tanganyika. *Mitt. Internat. Verein. Limnol.* 23:85–99.

Mills, E.L., Leach, J.H., Carlton, J.T., and Secor, C.L. 1993. Exotic species in the Great Lakes: A history of biotic crises and anthropogenic introductions. *J. Great Lakes Res.* 19:1–54.

_____, Leach, J.H., Carlton, J.T., and Secor, C.L. 1994. Exotic species and the integrity of the Great Lakes: Lessons from the past. *Bioscience* 44:666–676.

Mölsä, H., Reynolds, J.E., Coenen, E.J., and Lindqvist, O.V. 1999. Fisheries research towards resource management on Lake Tanganyika. *Hydrobiologia* 40:1–24.

Mortsch, L.D., and Quinn, F.H. 1996. Climate change scenarios for Great Lakes Basin ecosystem studies. *Limnol. Oceanogr.* 41:903–911.

Mugidde, R., Hecky, R.E., Hendzel, L.L., and Talyor, W.D. 2003. Pelagic nitrogen fixation in Lake Victoria (East Africa). *J. Great Lakes Res.* 29 (Suppl. 2):76–88.

Munawar, M., and Munawar, I.F. 1986. The seasonality of phytoplankton in the North American Great Lakes, a comparative synthesis. *Hydrobiologia* 138:85–115.

Nicholls, K.H. 1999. Effects of temperature and other factors on summer phosphorus in the inner Bay of Quinte, Lake Ontario: Implications for climate warming. *J. Great Lakes Res.* 225:250–262.

Nicholson, S.E. 1996. A review of climate dynamics and climate variability in eastern Africa. In *The limnology, climatology and paleoclimatology of the East African lakes*, eds. T.C. Johnson and E.O. Odada, pp. 25–56. Amsterdam, The Netherlands: Gordon and Breach Publishers.

Ogutu-Ohwayo, R. 1990. The reduction in fish species diversity in Lakes Victoria and Kyoga (East Africa) following human exploitation and introduction of non-native fishes. *J. Fish. Biol.* Suppl. A:207–208.

Owen, R.B., and Crossley, R. 1992. Spatial and temporal distribution of diatoms in sediments of Lake Malawi, Central Africa, and ecological implications. *J. Paleolimnol.* 7:55–71.

_____, Crossley, R., Johnson, T.C., Tweddle, D., Kornfield, I., Davison, S., Eccles, D.H., and Engstrom, D.E. 1990. Major low levels of Lake Malawi and their implications for speciation rates in cichlid fishes. *Proc. Royal Soc.* 240:519–553.

Ribbink, A.J., Marsh, A.C., Marsh, B.A., and Sharp, B.J. 1983. A preliminary survey of the cichlid fishes of rocky habitats in Lake Malawi. *S. Afr. J. Zool.* 18:147–310.

Roest, F. 1977. *Stolothrissa tanganicae: population dynamics, biomass evolution and life history in the Burundi waters of Lake Tanganyika.* United Nations Food and Agriculture Organization, CIFA Technical Paper 5:42–63.

_____. 1992. The pelagic fisheries resources of Lake Tanganyika. *Mitt. Internat. Verein. Limnol.* 23:11–15.

Rosendahl, B.R. 1987. Architecture of continental rifts with special reference to East Africa. *Ann. Rev. Earth Planet. Sci.* 15:445–504.

Rzoska, J. 1976. Lake Victoria, physical features, general remarks on chemistry and biology. In *The Nile, biology of an ancient river*, ed. J. Rzoska, pp. 167–175. The Hague: Dr. W. Junk.

Salzburger, W., Meyer, A., Baric, S., Verheyen, E., and Sturmbauer, C. 2002. Phylogeny of the Lake Tanganyika cichlid species flock and its relationship to the Central and East African haplochromine cichlid fish faunas. *System. Biol.* 51:113–135.

Sarvala, J., Salonen, K., Järvinen, M., Aro, E., Huttula, T., Kotilainen, P., Kurki, H., Langenberg, V., Mannini, P., Peltonen, A., Plisnier, P.-D., Vuorinen, I., Mölsä, H., and Lindqvist, O. 1999. Trophic structure of Lake Tanganyika: carbon flows in the pelagic food web. *Hydrobiologia* 407:149–173.

Seehausen, O. 2000. Explosive speciation rates and unusual species richness in haplochromine cichlid fishes: effects of sexual selection. *Adv. Ecol. Res.* 31:237–274.

_____, Van Alphen, J.J.M., and Witte, F. 1997. Cichlid fish diversity threatened by eutrophication that curbs sexual selection. *Science* 277:1808–1811.

Shapiro, R.L., Otieno, M.R., Adcock, P.M., Phillips, H.P.A., Hawley, W.A., Kumar, L., Waiyaki, P., Nahlen, B.L., and Slutsker, L. 1999. Transmission of epidemic *Vibrio cholerae* O1 in rural western Kenya associated with drinking water from Lake Victoria: An environmental reservoir for cholera? *Am. J. Trop. Med. Hyg.* 60:271–276.

Spigel, R.H., and Coulter, G.W. 1996. Comparison of hydrology and physical limnology of the East African Great Lakes: Tanganyika, Malawi, Victoria, Kivu and Turkana (with reference to some North American Great Lakes). In *The limnology, climatology and paleoclimatology of the East African lakes*, eds. T.C. Johnson and E.O. Odada, pp. 103–139. Amsterdam, The Netherlands: Gordon and Breach Publishers.

Stager, J.C., Reinthal, P.N., and Livingstone, D.A. 1986. A 25,000 year history for Laek Victoria, East Africa and some comments on its significance for the evolution of cichlid fishes. *Freshwat. Biol.* 16:15–19.

Stauffer, J.R. Jr., Arnegard, M.E., Cetron, M., Sullivan, J.J., Chitsulo, L.A., Turner, G.F., Chiotha, S., and McKaye, K.R. 1997. Controlling vectors and hosts of parasitic diseases using fishes. *Bioscience* 47:41–49.

Talbot, M.R., and Lærdal, T. 2000. The late Pleistocene—Holocene palaeolimnology of Lake Victoria, East Africa, based upon elemental and isotopic analyses of sedimentary organic matter. *J. Paleolim.* 23:141–164.

_____, and Livingstone, D.A. 1989. Hydrogen index and carbon isotopes of lacustrine organic matter as lake level indicators. *Palaeogogr. Palaeoclimat. Palaeoecol.* 70:121–137.

Talling, J.F. 1957. Diurnal changes of stratification and photosynthesis in some tropical African waters. *Proc. R. Soc.* (B) 147: 57–83.

_____. 1965a. Comparative problems of phytoplankton production and photosynthetic activity in a tropical and a temperate lake. *Mem. Ist. Ital. Hydrobiol.* 18, Suppl.: 399–424.

_____. 1965b. The photosynthetic activity of phytoplankton in East African lakes. *Int. Rev. ges. Hydrobiol.* 50: 1–32.

_____. 1966. The annual cycle of stratification and phytoplankton growth in Lake Victoria (East Africa). *Int. Rev. ges. Hydrobiol.* 51: 545–621.

_____. 1969. The incidence of vertical mixing, and some biological and chemical consequences, in tropical African lakes. *Verh. Internat. Verein. Limnol.* 17: 998–1012.

_____. 1990. Diel and seasonal energy transfer, storage and stratification in African reservoirs and lakes. *Arch. Hydrobiol. Beih., Ergebn. Limnol.* 33:651–660.

_____. 1995. Tropical limnology and the Sunda expedition. In *Perspectives in tropical limnology*, eds. F. Schiemer and K.T. Boland, pp. 19–26. Amsterdam: SPB Academic Publishing.

_____, and Lemoalle, J. 1998. *Ecological dynamics of tropical inland waters*. Cambridge: Cambridge University Press.

Thienemann, A. 1932. Tropische Seen und Seetypenlehre. *Arch. Hydrobiol.* Suppl. 9:205–231.

Thompson, A.B. 1995. Fisheries potential. In *The fishery potential and productivity of the pelagic zone of Lake Malawi/Nyasa*, ed. A. Menz, pp. 369–386. Chatham, UK: Natural Resources Institute.

Thompson, M.E. 1978. Major ion loadings to Lake Superior. *J. Great Lakes Res.* 4:361–369.

Tiercelin, J.-J., and Mondeguer, A. 1991. The geology of the Tanganyika trough. In *Lake Tanganyika and its life*, ed. G.W. Coulter, pp. 7–48. Oxford, England: Oxford University Press.

Tilman, D. 1999. The ecological consequences of changes in biodiversity: a search for general principles. *Ecology* 80:1455–1474.

Torrey, M.S. 1976. Environmental status of the Lake Michigan region. Vol. 3, *Chemistry of Lake Michigan.* Argonne National Laboratory, Argonne, IL. ANL/ES-40.

Turner, J.L. 1982. Lake flies, water fleas and sardines. In *Biological studies on the pelagic ecosystem of Lake Malawi*, pp. 165–182. FAO Tech. Rep. 1, FI:DP/MWL/75/019.

Twongo, T. 1996. Growing impact of water hyacinth on nearshore environments in Lakes Victoria and Kyoga (East Africa). In *The limnology, climatology and paleoclimatology of the East African lakes*, eds. T.C. Johnson and E.O. Odada, pp. 633–642. Amsterdam, The Netherlands: Gordon and Breach Publishers.

U.S. Department of the Interior. 1968. *Water quality investigations, Lake Michigan basin: physical and chemical quality conditions.* Fed. Water Pollut. Control Admin. Tech. Rep., Great Lakes Region, Chicago.

van Alphen, J.J.M., and Seehausen, O. 2001. Sexual selection, reproductive isolation and the genic view of speciation. *J. Evol. Biol.* 14:874–875.

Verschuren, D., Johnson, T.C., Kling, H.J., Edginton, D.N., Leavitt, P.R., Brown, E.T., Talbot, M.R., and Hecky, R.E. 2002. History and timing of human impact on Lake Victoria, East Africa. In *Proc. Royal Soc. Biol. Sci. Ser. B. 269*, pp. 289–294.

Vollenweider, R.A., Munawar, M., and Stadelmann, P. 1974. A comparative review of phytoplankton and primary production in the Laurentian Great Lakes. *J. Fish. Res. Board Can.* 31:739–762.

Weiler, R.R. 1978. Chemistry of Lake Superior. *J. Great Lakes Res.* 4:370–385.

Willoughby, N.G., Watson, I.G., and Twongo, T. 1996. Preliminary studies on the effects of water hyacinth on the diversity, abundance and ecology of the littoral fish fauna in Lake Victoria, Uganda. In *The limnology, climatology and paleoclimatology of the East African lakes*, eds. T.C. Johnson and E.O. Odada, pp. 643–655. Amsterdam, The Netherlands: Gordon and Breach Publishers.

Witte, F., Goldschmidt, T., Wanink, J., Van Oijen, M., Goudswaard, K., Witte-Maas, E., and Bouton, N. 1992. The destruction of an endemic species flock: Quantitative data on the decline of the haplochromine cichlids of Lake Victoria. *Env. Biol. Fish* 34:1–28.

Worthington, E.B. 1930. Observations on the temperature, hydrogen-ion concentration, and other physical conditions of the Victoria and Albert Nyanzas. *Int. Rev. ges. Hydrobiol.* 24: 328–357.

_____. 1931. Vertical movements of freshwater macroplankton. *Int. Rev. ges. Hydrobiol.* 25: 394–436.