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Conservation of the African Great Lakes: A Limnological Perspective

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Abstract: *The limnology of Lakes Malawi, Tanganyika, and Victoria is discussed with the objective of examining how the physical, chemical, and biological properties of the lakes will determine the response of these ancient great lake ecosystems to human activities. Of the physical properties discussed, large dilution capacities and long flushing times can make the detection and removal of chemical pollutants in these lakes difficult. The outflows of all three lakes are small because of high evaporation losses, and as a result lake levels are responsive to climate changes that would alter evaporation:precipitation ratios. Increased nutrient input to these lakes will likely result in a decrease in the volume of oxygenated water and available fish habitat. Plankton community composition will also change, probably toward dominance by cyanobacteria. While the effects of eutrophication on fish production are difficult to predict, changes in plankton composition would almost certainly be accompanied by changes in fish community structure. Recent studies of water chemistry and plankton productivity in Lake Victoria provide evidence of possible eutrophication. Because land use has a diffuse but potentially large impact on these lakes, conservation strategies must take into account human activities within entire drainage basins. This requires cooperation between riparian countries and technological and financial input from the international community. An immediate need is the establishment of monitoring programs to determine the impact, real or potential, of human activities around the lakes.*

Conservación de los Grandes Lagos Africanos:
Una perspectiva limnológica

Resumen: *La limnología de los lagos Malawi, Tanganyika y Victoria es discutida con el objetivo de examinar como las propiedades físicas, químicas y biológicas de estos lagos determinan la respuesta de estos antiguos ecosistemas de grandes lagos a las actividades humanas. Dentro de las propiedades físicas discutidas, una gran capacidad de dilución y un largo período de dispersión pueden hacer que la detección y remoción de polutantes en estos lagos sea difícil. El efluente de los tres lagos es pequeño por la pérdida producida por la alta evaporación, como resultado el nivel de los lagos es sensible a cambios climáticos que pueden alterar la relación entre evaporación y precipitación. Un incremento en la entrada de nutrientes a estos lagos puede resultar en un decrecimiento en el volumen de oxígeno en el agua y hábitat disponible para los peces. La composición de las comunidades de Plankton también puede cambiar, probablemente hacia una dominancia de cianobacterias. Si bien los efectos de eutroficación en la producción de los peces es difícil de predecir, cambios en la composición del plankton pueden casi siempre ir acompañados de cambios en la estructura de la comunidad de peces. Estudios recientes de la química del agua y productividad del plankton en el Lago Victoria suministraron evidencia de una posible eutroficación. Estrategias en cuanto a conservación tienen que considerar las actividades humanas dentro de toda la cuenca, por que el uso de la tierra tiene un impacto potencial difuso pero de gran alcance sobre estos lagos. Esto requiere cooperación entre países lindantes e ingresos económicos y tecnológicos por parte de la comunidad internacional. El establecimiento de programas de monitoreo para determinar*

el impacto real o potencial de las actividades humanas alrededor de los lagos es una necesidad inmediata.

Introduction

Lakes Malawi, Tanganyika, and Victoria are perhaps best known for their faunal diversity (Brooks 1950; Fryer & Iles 1972). From a limnological perspective, however, the distinguishing attributes of these lakes are their large size and tropical location, and it is to these features, along with their great ages, that their diverse faunas may partly be attributed (Brooks 1950; Hecky 1984). Understanding the limnology of these lakes is necessary to predict the effects of human activities on water quality, biodiversity, ecological responses to human activities, and fish production. Further, it will enable us to determine whether or not patterns observed in small tropical lakes or large temperate lakes can be more generally applied over size or climatic gradients. The relatively small role of natural watershed influences on energy and mass cycling in large lakes, and the small climatic variability experienced in the tropics, make the African Great Lakes useful as models of oceanic ecosystems (Eccles 1988; Hecky 1991).

Despite their shared characteristics, there are some major limnological differences among Africa's three largest lakes. Lake Victoria is substantially shallower, younger geologically (Hecky 1984), and has faster water renewal than the other two. Lakes Tanganyika and Malawi are similar in morphology and clarity, and both are meromictic, but they are markedly different with regard to hydrology, nutrient dynamics (Hecky & Bugenyi 1992), plankton composition (Hecky & Kling 1987), and trophic structure (Hecky 1984). Therefore, the effects of human activities may be quite different in each lake, and the ability to predict these effects and decisions on how to prevent or mitigate them require an understanding of the limnology of each lake.

Human benefits gained from these lakes include (1) water supply, for drinking, agriculture, industry, and hydroelectricity production; (2) fish production, which serves as a source of food and cash income; (3) aesthetic value, which attracts tourists, supports an aquarium trade in cichlid fishes, and has other noneconomic benefits; (4) scientific value. Coulter et al. (1986) listed a number of current human activities that may threaten these values in the African Great Lakes. These include overfishing, pollution, catchment development (which can be considered a precursor of some forms of pollution), and alien species introductions. The objective of this paper is to discuss the physical, chemical, and biological properties of Lakes Malawi, Tanganyika, and Vic-

toria, and how these properties will determine the response of these lakes to human activities.

Hydrology and Hydrodynamics

The fate of a pollutant in a lake depends on a variety of processes, including degradation, sedimentation, volatilization, resuspension, and flushing. The relative importance of each of these processes varies according to the type of pollutant and physico-chemical conditions. However, flushing rate is a dominant factor controlling the fate of many aquatic pollutants. For example, the rapid eutrophication of Lake Erie and the relatively short time required to reverse the eutrophication can be largely attributed to the small volume and rapid flushing rate of that lake (Ragotzkie 1988). Although adsorption onto particles and subsequent sedimentation is sometimes considered a "detoxification" mechanism in the short term (see Neely 1985; Eisenreich et al. 1988), toxins in surficial sediment may accumulate and become reintroduced to the food web either through deposit feeders or sediment resuspension. Removal of sediment-bound pollutants from a lake also depends on flushing rate (Cornett & Chant 1988).

Due to their large volume and relatively small outflow, Lakes Malawi, Tanganyika, and Victoria all have long flushing times (Table 1). The potential influence of these long flushing times on pollution retention is illustrated in Fig. 1. While this model is simplistic, it serves to illustrate two points. First, even though pollution input rates may be relatively high, dilution in these large lakes may result in the pollutant going undetected for many years. Second, once hazardous concentrations of a pollutant are reached in these lakes, elimination of pollution sources will not have immediate beneficial results unless mechanisms other than flushing are efficient at removing that pollutant.

A second hydrological variable of relevance to the conservation and use of these lakes is lake level. Changes in lake level have important implications for fish speciation (Fryer & Iles 1972), industrial use (particularly hydroelectric generation), and possibly fish production (Fryer & Iles 1972:448). Because of the dominant roles of precipitation and evaporation in the water budgets of all three lakes (Table 1), levels are very sensitive to climatic changes (Haberyan & Hecky 1987; Owen et al. 1990). Under conditions where evaporation exceeds water input, closed lakes will decrease in surface area until evaporation—which is related to surface

Table 1. Morphometric and hydrological data for Africa's three largest lakes.

	Malawi	Tanganyika	Victoria
Catchment Area (km ²)	100,500	220,000	195,000
Lake Area (km ²)	28,800	32,600	68,800
Maximum Depth (m)	785 ^a	1470 ^a	79 ^b
Mean Depth (m)	292 ^a	580 ^a	40
Volume (km ³)	8400 ^a	18,900 ^a	2760 ^b
Outflow (O) (km ³ y ⁻¹)	11 ^c	2.7 ^d	20 ^b
Inflow (I) (km ³ y ⁻¹)	29 ^c	14 ^d	20 ^b
Precipitation (P) (km ³ y ⁻¹)	39 ^c	29 ^d	100 ^b
Evaporation (km ³ y ⁻¹)	55 ^e	44 ^d	100 ^b
Flushing time (V/O) (years)	750	7000	140
Residence time (V/(P+I)) (years)	140	440	23

^a Gonfiantini et al. (1979).^b Rzoska (1976).^c Owen et al. (1990).^d Coulter and Spigel (1991).^e Eccles (1974).

area—balances input. In the steep-sided Lakes Tanganyika and Malawi, even a small reduction in surface area can require a significant drop in lake level. For example, in order to achieve a 10% decrease in surface area, the necessary drop in lake level is 12 m for Victoria, 32 m for Malawi, and 56 m for Tanganyika.

The susceptibility of lake levels to change is reflected in historic lake-level records. Hutchinson (1957) com-

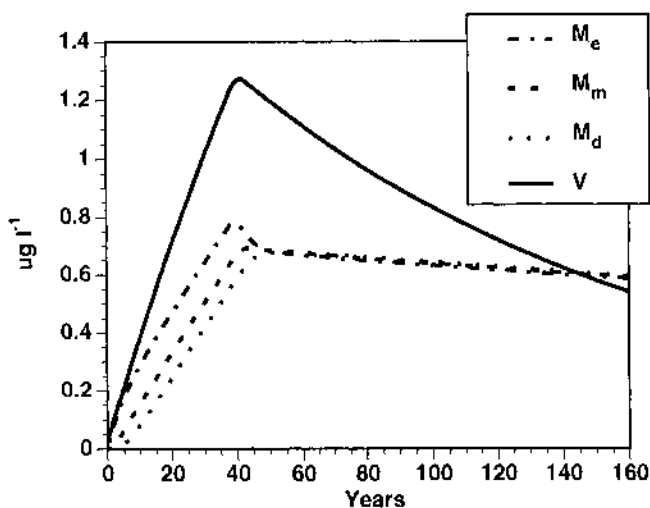


Figure 1. Pollution scenario for Lakes Victoria and Malawi in which all inflowing rivers contain $5 \mu\text{g l}^{-1}$ pollutant for 40 years, followed by complete cessation of pollution input. The model uses the hydrological parameters of Table 1; it assumes that the only loss of pollutant is via outflow and that all inflow enters surface waters. V = Victoria; M_e = Malawi epilimnion; M_m = Malawi metalimnion; M_a = Malawi monimolimnion. Mixing rates between Lake Malawi strata are from Gonfiantini et al. (1979).

pared fluctuations of the three lakes during the early 1900s. While Victoria and Tanganyika have fluctuated over a range little greater than 2 m since the beginning of the century, Malawi has steadily risen to a level that is presently about 6 m higher than the 1912 low (Crossley et al. 1984). This rise is largely due to the lack of an outflow from Lake Malawi during the early part of the century, a condition that also existed in Tanganyika for at least part of the 1800s (Hutchinson 1957). Superimposed on the rising trend in Malawi are small peaks and troughs that Hutchinson (1957) suggested correspond to similar fluctuations in the other two lakes. More recent lake-level records (Drayton 1979; Kite 1981; Tiercelin & Mondeguer 1991) also show simultaneous fluctuations in the three lakes. In the early 1960s, all three lakes rose, and in 1964 Tanganyika and Victoria both reached their highest levels to date during this century. Malawi and Victoria rose rapidly again in 1979, when Malawi reached its highest level during recorded history (we have no data for Tanganyika beyond 1964). These similarities in lake-level fluctuations support Hutchinson's (1957) suggestions that the levels of all three lakes are affected by regional climatic conditions.

For many lakes and reservoirs, damming is an effective method of controlling water levels. This is not true for these three lakes. Assuming unchanged inflow and evaporation for Lake Tanganyika, a decrease in rainfall on the lake surface of greater than 9% would result in a lowering of lake level, even if outflow was completely stopped. Under this scenario, Lakes Victoria and Malawi could withstand a 20% and a 28% rainfall decrease, respectively. In reality, even smaller rainfall decreases will result in lake-level drops, since any decrease in rainfall will be accompanied by less inflow and more evaporation. For example, based on the relationships among rainfall, evaporation, and inflow reported by Owen et al. (1990), a more realistic tolerance limit for Malawi is

13%. If precipitation:evaporation ratios change due to global warming, these lakes will respond, perhaps in dramatic fashion.

The third physical aspect of lakes that deserves discussion is mixing processes. The movement of water in lakes controls the distribution of oxygen and nutrients, to which the distribution and abundance of organisms are closely linked. In a stratified lake, bottom water can become oxygen-depleted. Due to the inverse relationship between oxygen saturation concentration and temperature, and the increased metabolic rate of decomposers at high temperatures, tropical lakes are especially susceptible to oxygen depletion (Lewis 1987). Stratification also results in the loss of nutrients from the mixed surface layer to the deep waters, where they accumulate due to the sinking of particulate organic material. In these lakes with long residence time, phytoplankton production in the euphotic zone depends to a large extent on the return of nutrients from deep waters via mixing (Hecky et al. 1991). However, rapid mixing may also result in fish deaths due to anoxia or exposure to toxic concentrations of reduced compounds.

In temperate lakes, the transition between stratification and destratification is largely the result of variations in solar radiation and air temperature, which control the temperature difference between the mixed surface layer and the deep hypolimnion (monimolimnion in permanently stratified lakes). In the tropics, annual variation of solar radiation is much reduced, and air temperature and wind are the most important factors controlling thermal structure and mixing. Lewis (1983) has demonstrated the importance of minimum daily air temperature controlling stratification in Lake Valencia. When air temperature is low, heat is lost from surface waters due to evaporation, conduction, and back radiation, resulting in lower stability. In the African Great Lakes, air temperatures are lowest during the May through August dry monsoon season, when the strong and persistent southeast trade winds blow. These winds add kinetic energy to the surface mixed layer and make a major contribution to evaporative heat loss (Talling 1966; Coulter & Spigel 1991). As a result of the decreased stability and the added kinetic energy, the layer increases in depth. In Lakes Malawi and Tanganyika, mixing does not presently extend below 250–300 m. However, upwelling does occur at their upwind (southerly) ends due to tilting of the thermocline under prolonged wind stress (Eccles 1974; Coulter & Spigel 1991). Lake Victoria, due to its lesser depth, undergoes complete mixing at least once a year.

While temperature profiles provide information on current mixing regimes, the potential for Lakes Malawi and Tanganyika to mix completely over longer periods is also of interest. Because of the slow exchange rates between surface and deep waters in these lakes, the

deep waters are anoxic and rich in CO_2 , NH_3 , and H_2S . Rapid upwelling could thus have catastrophic effects on fish and other organisms. For example, the relatively low diversity of fish species in Lake Kivu can be attributed to fish kills resulting from catastrophic mixing events caused by volcanism and hydrothermal activity (Verbeke 1957; Hecky 1984; Haberyan & Hecky 1987). There is circumstantial evidence for deep mixing in Lake Malawi in 1937 (Eccles 1974) and 1946 (Beauchamp 1953), but it is unlikely that these events represented complete overturn (Eccles 1974). Beauchamp (1953) and Eccles (1974, 1988) suggested that the monimolimnion of Lake Malawi may gradually warm over several decades, resulting in occasional overturn. Eccles (1988) presented evidence for monimolimnetic warming between 1939 and 1976, but this was insufficient to bring about complete mixing. Based on the existence of finely laminated sediments, Haberyan and Hecky (1987) suggest that deep mixing (to 400 m) has not occurred within at least the last 10,000 years in Lake Tanganyika.

While complete overturn appears to be a very rare event in Lakes Malawi and Tanganyika, fish kills may still be caused by local upwelling (Coulter 1963; Eccles 1974). In all three lakes, the movement of internal waves and their breaking on contact with the lake bottom can be expected to result in the death of fish that are living near their lower oxygen threshold. While such an event is unlikely to result in the complete extermination of widespread pelagic species, it poses a particular threat to those nearshore species with very restricted distributions.

Nutrient Dynamics

One of the most common ways in which humans affect aquatic ecosystems is through altering nutrient dynamics. The potential impact of such activities on large water bodies is attested to by the changes observed in the Laurentian Great Lakes during the 1960s and 1970s (Ragotzkie 1988), and those recently occurring in the Baltic Sea (Larsson et al. 1985; Hansson & Rudstam 1990).

Predicting the effects of an altered nutrient regime requires an understanding of which nutrients limit algal growth, the relative importance of various nutrient sources, and how the relative availability of different nutrients affects algal community composition. While phosphorus is the nutrient most often limiting algal growth and biomass in temperate lakes (Vollenweider 1976; Schindler 1977; Hecky & Kilham 1988), this is not necessarily the case in tropical lakes. In Lakes Malawi, Tanganyika, and Victoria, concentrations of nitrogen and phosphorus in surface waters are low (Fig.

2). Talling and Talling (1965) suggested that low nitrate concentrations in Victoria indicated the potential for nitrogen limitation. In culture assays carried out by Evans (1961) on samples from Victoria, phosphorus addition was found to increase the abundance of the diatom *Melosira*, while other algal species, particularly green Chlorococcales, were more responsive to nitrogen and sulphate addition. Thus, it is unlikely that a single nutrient continuously controls algal growth. This is supported by more recent investigations of particulate nutrient ratios, which have been shown to be useful indicators of the nutrient status of phytoplankton (Healey & Hendzel 1980; Table 2). While phytoplankton in Victoria appear slightly deficient in N, neither N nor P is strongly limiting, based on particulate nutrient ratios. Similarly, particulate nutrient ratios in Malawi suggest moderate N and P deficiency in the phytoplankton com-

munity (Table 2). Little work has been done to identify limiting nutrients in Tanganyika, but the fact that the N:P regeneration ratio is close to 16:1 (Hecky 1991), the optimal ratio for phytoplankton, suggests that in this lake also neither nutrient alone strongly limits growth rates.

Knowledge of the relative importance of various nutrient sources is essential to predicting the impact of disturbances in the lakes. The three potential external sources of nutrients for phytoplankton growing in the mixed layer are rivers, atmospheric deposition, and the nutrient-rich deep waters. The data for Lake Victoria are insufficient to allow estimates of riverine input and internal recycling rates, but it is possible to make preliminary estimates of nutrient flux from the three sources for Tanganyika (Hecky 1991) and Malawi (Table 3). Because they are anoxic, the monimolimnia of Lakes Tanganyika and Malawi are nitrogen sinks. Very little ammonia regenerated in the monimolimnion reaches the euphotic zone (Fig. 2), because it is oxidized to nitrate when it mixes with oxic waters. The nitrate is denitrified and lost as N_2 and N_2O , as indicated by the decrease in NO_3^- concentration with depth in the region above the anoxic boundary (Fig. 2). Consequently, phytoplankton nitrogen demands must be met by input from rivers, atmospheric deposition, and biological nitrogen fixation. The N supply rates required to balance P input (which is equivalent to phytoplankton P uptake) can be calculated by using particulate N:P ratios (Table 2) and P input estimates (Table 3). This is slightly different from the approach used by Hecky et al. (1991), but the discussion below is unaffected by the slight difference in results using both approaches. In both lakes, atmospheric and riverine input contribute a small proportion of the total N requirement. There are two possible mechanisms by which the balance of required N can be supplied. The first is nitrogen fixation. In Lake Tanganyika, nitrogen-fixing cyanobacteria (blue-green algae) are most abundant from September to October, but they account for a significant portion of total phytoplankton biomass in the southern basin throughout much of the year (Hecky & Kling 1981). In Lake Victoria, Talling (1966) recorded *Anabaena* dominance from September to January, and nitrogen-fixing cyanobacteria are now abundant throughout the year (Hecky 1993), indicating that nitrogen fixation is also probably an important source of nitrogen in that lake. In Lake Malawi, cyanobacteria are an important component of the phytoplankton; but although blooms of *Anabaena* have been reported (Beauchamp 1953) and this genus can occasionally make up significant proportions of total phytoplankton biomass, nitrogen-fixing cyanobacteria are generally low in abundance (Hecky & Kling 1987; Bootsma 1993). This indicates that a second mechanism—internal recycling within the surface mixed

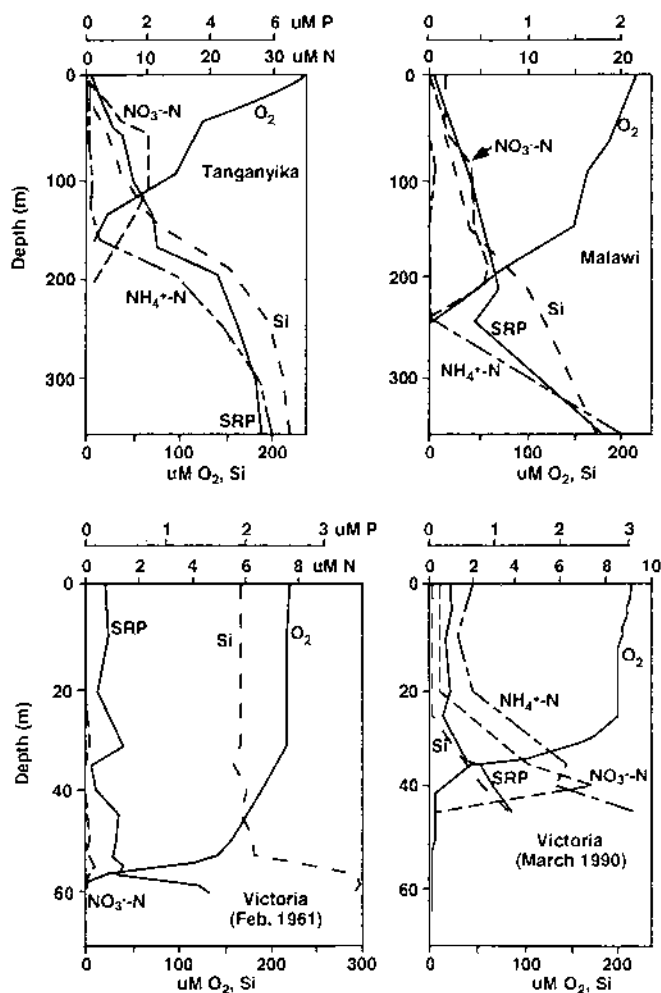


Figure 2. Nutrient and oxygen profiles for the three African Great Lakes. Data sources: Tanganyika—Coulter (1977); Malawi—original data; Victoria 1961—Talling (1966); Victoria 1990—original data. SRP = soluble reactive phosphorus.

Table 2. Mean particulate C, N, and P concentrations and elemental ratios for Lakes Malawi and Victoria compared to nutrient deficiency indicators.

	<i>n</i>	<i>C</i>	<i>N</i>	<i>P</i>	<i>C:N</i>	<i>C:P</i>	<i>N:P</i>
Lake Malawi	120	15.3	1.2	0.08	13.2	251	18.5
Lake Victoria	16	68.3	8.2	0.64	8.5	110	13
Moderate P Deficiency					NA	129–258	NA
Severe P Deficiency					NA	>258	>22
Moderate N Deficiency					8.3–14.6	NA	NA
Severe N Deficiency					>14.6	NA	NA

Concentrations are given as $\mu\text{mol l}^{-1}$, and ratios are mole:mole. Malawi data are original. Victoria data from Hecky and Bugenyi (1992). Deficiency indices after Healey and Hendzel (1980). NA = not applicable.

layer—may be important in supplying N. If N is recycled more efficiently than P in the surface mixed layer, then the N required to balance P input (Table 3) does not have to be all new N. There is evidence that N recycling is more efficient than P recycling in the water column (Miyajima 1992) and in lake sediments (Levine & Schindler 1992). It would be expected that the influence of this differential recycling efficiency is more significant in Malawi than Tanganyika, since a higher proportion (about 40% versus 25%) of the bottom of Malawi is in contact with the surface mixed layer.

The estimates of vertical diffusion presented in Table 3 are speculative. Values for Tanganyika are based on a single nutrient profile and an estimate of eddy diffusivity calculated from the methane oxidation measurements of Rudd (1980), while Malawi values are based on two nutrient profiles, in August and February, and estimates of mixing made by Gonfiantini et al. (1979). These data are obviously sparse, but it is nevertheless clear that vertical diffusion accounts for a large percentage of phosphorus flux into the upper layers of Tanganyika and Malawi. Estimates of annual N demand depend directly on assumptions about vertical mixing rates, and values presented here should be considered qualitative.

Unless phosphorus is entering the monimolimnion from sublacustrine springs, vertical diffusion represents recycled phosphorus, whereas riverine and atmospheric fluxes represent new input that balances losses to sed-

imentation and outflow. Although riverine and atmospheric inputs are relatively small on an annual basis, they have the potential to alter total phosphorus availability over periods of decades to centuries. Because of the large dilution capacity of these lakes, increased input of pollutants will not be immediately reflected in pollutant concentrations within the lakes. Early detection of cultural eutrophication requires monitoring of atmospheric and riverine nutrient input. Such programs are not in effect at present.

Continuous, long-term monitoring is necessary to determine whether or not there are any real temporal trends in the trophic status of a lake (Goldman 1988). Such data are available for none of the African Great Lakes. However, the large differences in phytoplankton abundance, phytoplankton species composition, primary production, water clarity, and nutrient concentrations between the time of Talling's work (Talling 1965, 1966; Talling & Talling 1965) and recently (Ochumba & Kibaara 1989; Komárek & Kling 1991; Hecky & Bugenyi 1992; Mugidde 1993), and the continuous increase in sediment P deposition and depletion of dissolved Si over the past 30 years (Hecky 1993), are strong evidence of real change in Lake Victoria. Although it has been hypothesized that exotic fish introductions, such as those that have occurred in Victoria (Ogutu-Ohwayo 1990a), can cause changes in nutrient dynamics and plankton community structure (Carpenter et al. 1986),

Table 3. Speculative estimates of nutrient loading to the surface mixed layer of Lakes Tanganyika and Malawi.

Source	Lake Malawi			Lake Tanganyika		
	<i>N</i>	<i>P</i>	<i>Si</i>	<i>N</i>	<i>P</i>	<i>Si</i>
Rivers	0.023	0.001	0.22	0.005	0.002	0.16
Rain	0.006	0.0001	0	0.086	0.017	NM
Dry Fallout	0.081	0.002	NM	NM	NM	NM
Vertical Mixing	0.0	0.023	1.64	0.0	0.19	6.6
Total	0.068	0.0251	1.862	0.091	0.209	6.76
N Deficit	0.407			3.2		—

Details of the estimates for L. Tanganyika are given in Hecky et al. (1991). Riverine loading for L. Malawi is calculated as the average of 13 river samples (total dissolved N and P, and SiO_2) times total annual river inflow. Rain loading was estimated from measurements of rainfall and rain chemistry (SRP, NO_3^- -N, and NH_4^+ -N) during 1990–1991 at the lakeshore near Monkey Bay. Dry atmospheric loading was estimated by measuring the accumulation of SRP, NO_3^- -N, and NH_4^+ -N in deionized water during 24-hour exposures (nine replicates between August and November 1990). Vertical mixing and diffusion were estimated from nutrient depth profiles and annual exchange rates between monimolimnion, chemolimnion, and mixolimnion as calculated by Gonfiantini et al. (1977). All values given as moles $\text{m}^{-2} \text{y}^{-1}$. NM = not measured.

the fact that increased P sedimentation rates have not been accompanied by a decrease in P concentration in the water column (Fig. 2) indicates that P flux into the lake has increased. We have no data on nutrient concentrations in Victoria tributaries, but the concentration of soluble reactive phosphorus (SRP) in rain on the north shore of Victoria was much higher in 1991 than in 1958–1959 (Table 4). Lewis (1981) recorded a SRP deposition rate of $0.96 \text{ mmol m}^{-2} \text{ y}^{-1}$ for Lake Valencia (Venezuela), which was much higher than rates reported for other tropical and temperate regions (Lewis 1981), but is less than one third of that measured near Lake Victoria in 1991. Similarly, the 1991 SRP concentration is more than an order of magnitude greater than that measured in rain from the Central Amazon Basin (Lesack & Melack 1991). While the comparison of recent measurements near Victoria with those made by Visser (1961) is hampered by differences in sampling and analytical methods, as well as by a lack of knowledge of inter-annual variability, the difference is large enough to suggest that there has been a real increase in atmospheric P flux into the lake. The cause of this apparent change is uncertain. Unlike nitrogen and sulphur, however, both of which appear to have changed little since 1961, phosphorus has no abundant volatile form and is more closely associated with particulates. Increased atmospheric P concentrations may be caused by a greater atmospheric particulate load, which could be the result of burning or increased soil erosion by wind due to deforestation and cultivation. In areas where these activities are intense, nutrient concentrations in surface runoff are also likely to be high (Viner et al. 1981).

In Africa, burning, deforestation, and increased agricultural activity are all results of increased population density. Therefore, a discussion of population density and its potential influence on the lakes would be useful. Catchment basin morphometry is a major determinant of both the potential for human habitation and the potential for detrimental influences of basin development. The low relief of land near the shores of Lake Victoria (Fig. 3) make much of this area amenable to human

Table 4. Concentrations of nutrients in rain near Lakes Victoria and Malawi ($\mu\text{mol l}^{-1}$).

Lake	N	P	SO_4^-
Victoria (1958–1959)	64 (62)	0.053	19 (59)
Victoria (1991)	66 (11)	3.4 (34)	46 (10)
Malawi	8.6 (20)	0.18 (23)	2.5 (15)

Data from 1958–1959 for Lake Victoria are median values (Visser 1961). Data for Lake Victoria in 1991 and Lake Malawi are volume weighted means. Values in brackets represent sample size (Visser did not report sample size for SRP). Nitrogen was measured as dissolved inorganic N, phosphorus as soluble reactive P.

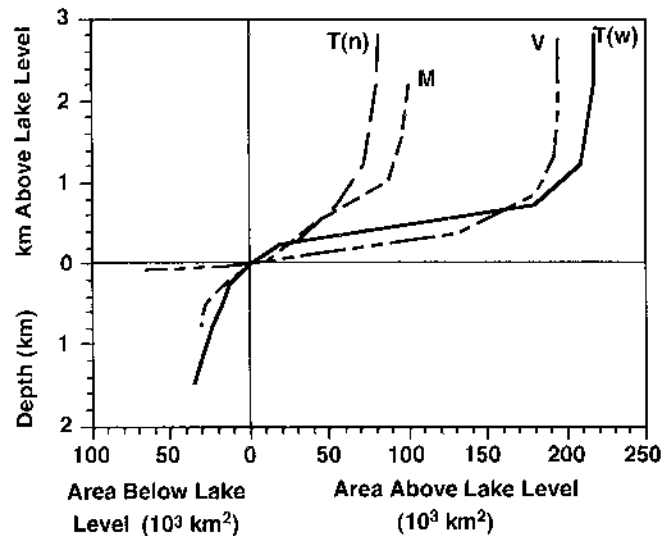


Figure 3. Hypsographic curves for the three lakes and their drainage basins. $T(w)$ = entire Tanganyika drainage basin. A separate curve for the Tanganyika drainage basin ($T(n)$) was determined by excluding the eastern plains (area east of dashed line in Fig. 4) in order to provide a more accurate description of nearshore topography. Note changing scales on each axis.

habitation, and population densities around much of the lakeshore are very high (Fig. 4). Although the low relief results in less potential for erosion and direct runoff into the lake, this advantage is countered by the close proximity of dense populations to the lake, especially around Winam Gulf, where eutrophication is most severe (Mavuti & Litterick 1991). Cattle must also cause high nutrient input in some nearshore areas. In 1970 densities as great as 160 km^{-2} , similar to human population densities, were recorded around Winam Gulf (Kenya Government atlas). The dense population in the southwestern portion of the basin is further away from the lake, and the ability of streams and rivers to buffer anthropogenic nutrient input (Meyer 1979; Mulholland 1992) may reduce the effect of these populations on riverine input to the lake, but the mountainous relief in this part of the watershed makes it especially susceptible to soil erosion; any increases in atmospheric nutrient content resulting from burning, deforestation, and cultivation in the Rwanda-Burundi highlands may affect both Lakes Victoria and Tanganyika.

Lakes Malawi and Tanganyika have steep nearshore topographies (Fig. 3) that are very susceptible to erosion after disturbance (for example, the northeast shore of Tanganyika) but are not attractive for dense human populations or cattle grazing. Nevertheless, cultivation and deforestation increasingly occur on some of the steep slopes around these lakes, and although such practices are currently not extensive, the potential exists for

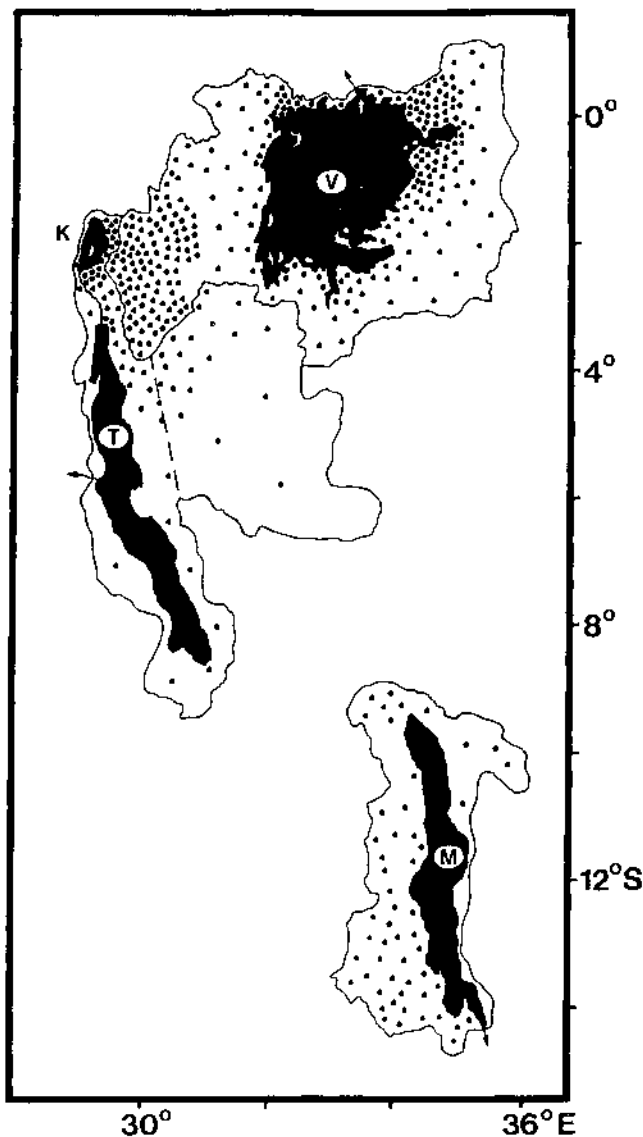


Figure 4. Human population densities in the lake drainage basins. Estimates made using official government figures. Where recent data were not available, a population growth rate of 2.8% per annum was applied to determine 1992 population densities. V = Victoria; K = Kivu; T = Tanganyika; M = Malawi. One dot = 100,000 persons.

land degradation and local increases in sediment and nutrient input in the very near future. Except for the extreme northern end of Tanganyika, nearshore population densities are presently low around the entire lake (Fig. 4). The population density in the Malawi catchment basin is almost twice as high as that for Tanganyika, but the majority of the population lives on the uplands remote from the lake, and development of nearshore slopes is minimal but accelerating. If current population growth trends continue, cultivation and deforestation on the steep slopes will definitely increase in all the Great Lake watersheds of Africa.

Moderate increases in nutrient availability and phytoplankton productivity in Lakes Tanganyika and Malawi would not necessarily be detrimental in themselves. Indeed, they can be beneficial and actually increase fish production (see Stockner & Shortreed 1988). The impact of any increase in phytoplankton productivity will largely depend on phytoplankton species composition. If phytoplankton can readily be utilized by zooplankton and fish, then nutrients and biomass will accumulate at higher trophic levels than are useful for human consumption (Hecky 1984). But if phytoplankton biomass cannot be utilized by higher trophic levels, phytoplankton biomass will increase and the direct cycling of energy and nutrients between phytoplankton and bacteria, especially during and after sedimentation, will become more important. The potentially detrimental effects of more sedimenting phytoplankton and detritus include a rise of the anoxic boundary depth (Fig. 2), due to increased oxygen demand, and more rapid light attenuation, which will reduce the depth of the euphotic zone. Both of these effects may result in shrinkage of available fish habitat.

Eutrophication would almost definitely result in changes in phytoplankton species composition. The nature of these changes will be determined by the absolute and relative input rates of N, P and Si, by hydrodynamics, and by the complex interplay between internal nutrient cycling and trophic structure. In the Laurentian Great Lakes, eutrophication has been observed to result in lower Si concentrations (Schelske et al. 1986; Schelske 1988) due to the rapid growth and subsequent sedimentation of diatom frustules. The increased productivity in Lake Victoria in 1991 (Mugidde 1993) relative to 1960–1961 (Talling 1965, 1966) appears to have had the same effect (Fig. 2). While diatoms were still abundant in Victoria during 1990, they consisted primarily of thinly silicified *Nitzschia* (H. Kling, personal communication), whereas Talling (1966) reported dominance by *Melosira*, a large, heavily silicified diatom.

Eutrophication often results in cyanobacteria dominance, although other factors such as temperature (Tilman et al. 1986; Varis et al. 1989), light (Zevenboom 1982), and pH (Shapiro 1973) may also affect the competitive ability of these organisms. This relationship between nutrient input and phytoplankton species composition is apparent in Lake Victoria, where evidence of increased nutrient input (Hecky 1993) is accompanied by higher cyanobacteria biomass (Ochumba & Kibaara 1989; H. Kling, personal communication) relative to that observed during 1960–1961 (Talling 1966). Because denitrification will minimize the influence of additional N input in Lakes Tanganyika and Malawi, eutrophication in these lakes will result in a greater increase in P availability than N availability, and nitrogen-fixing cyanobacteria would also become dominant in these lakes. Such a shift in phytoplankton species composition

might be expected to result in a lower efficiency of energy transfer to higher trophic levels, since cyanobacteria are generally considered a poor food source (Lampert 1981; Heerkloss et al. 1984; Haney 1987). The ability of some tilapiines to digest cyanobacteria (Moriarty 1973; McDonald 1987), however, suggests that eutrophication may result in a more productive fishery dominated by herbivorous fishes. While this would be beneficial with regard to food production, such an environment would not be favorable for zooplanktivorous fish species, since cyanobacteria are a poor food source for zooplankton.

Trophic Dynamics

While some organisms will be affected directly by changes occurring in the African Great Lakes, others will be affected indirectly, and any attempt to predict the overall impact of changes requires an understanding of trophic relationships. The feeding habits of the near-shore cichlids have been the subject of numerous studies, particularly in Lake Malawi (Fryer 1959; Ribbink et al. 1983; Reinthal 1989, 1990). An apparent paradox is the ability of these fishes to occupy very narrow trophic niches while retaining the capacity to exploit a wide range of food resources, and it is this combination of specialization and flexibility to which their diversity has been partly attributed (Liem 1980; Ribbink et al. 1983). Eutrophication often results in the simplification of aquatic ecosystems. Species diversity decreases (Rapport 1989; Schindler 1990) and food chains become less complex, but not necessarily shorter. The trophic flexibility of many cichlids suggests that a greater homogeneity of food types resulting from eutrophication would not be detrimental in itself. Indeed, Fryer (1959) and Ribbink et al. (1983) found it difficult to differentiate between rock-dwelling cichlids based on stomach contents. However, spatial partitioning appears to be an important mechanism by which high species diversity is maintained (Ribbink et al. 1983; Reinthal 1990), and an increase in nearshore sedimentation rates, along with a decrease in depth of the oxic-anoxic boundary, would undoubtedly diminish habitat availability and heterogeneity, leading to competitive exclusion.

The pelagic food webs of the three lakes are quite different. While algal biomass and productivity are apparently similar in Lakes Malawi and Tanganyika, in Lake Tanganyika zooplankton biomass is lower, the dipteran *Chaoborus* is absent, and the biomass of planktivorous and piscivorous fish is greater, resulting in a more productive fishery (Hecky 1984). The transfer efficiency (ratio of fishery carbon yield to algal carbon production) of Tanganyika (0.45%; Hecky et al. 1981) is higher than that estimated for Malawi (0.15%; Degnbol & Mapila 1982) and approaches that of marine systems.

This may be due to additional carbon input at the bottom of the food chain in the form of bacteria growing on dissolved organic material and reduced substances (Hecky et al. 1981). This input ultimately depends on energy fixed by photosynthesis, however, and the fact that estimates of bacterial production are close to those of algal production (Hecky et al. 1981) implies that, on an annual basis, the lake may not be in steady state with regard to photosynthetically fixed carbon. Considering the large size of this lake and the relatively small volume of river inflow, it is unlikely that allochthonous input of organic carbon could account for high bacterial production. A similar state of nonequilibrium may exist in Lake Malawi, where Degnbol and Mapila (1982) measured areal respiration rates greater than photosynthetic rates. The possibility that the lakes are currently in transition with regard to carbon and energy flux must be considered in any attempt at predicting their long-term productivity.

An alternative explanation for the relatively high fishery production and transfer efficiency in Lake Tanganyika is the presence of the clupeids, *Limnothrissa miodon* and *Stolothrissa tanganyicae* (Hecky 1991). Being members of the herring family, they are well-adapted pelagic planktivores, unlike the small cyprinid *Engraulicypris sardella* of Lake Malawi, which is not truly pelagic (Fryer & Iles 1972; Turner 1982). The absence of an efficient planktivore in the waters of Malawi may explain the greater diversity and abundance of crustacean zooplankton in that lake. Turner (1982) has suggested that the presence of *Chaoborus* in Malawi is evidence of poor utilization of zooplankton by *E. sardella*.

Melack (1976) calculated a transfer efficiency of 0.10% for Lake Victoria, based on the algal production measurements of Talling (1965) and the fish biomass estimates of Kudhongania and Cordone (1974). The success of the introduced Nile perch *Lates niloticus* (Ogutu-Ohwayo 1990a) might be expected to reduce transfer efficiency due to the addition of a trophic level (Fryer 1972; Fryer & Iles 1972; Coulter et al. 1986). However, Nile perch appear to be able to exploit a broad range of prey types (Ogutu-Ohwayo 1990b). This, combined with the fact that the herbivorous *Oreochromis niloticus* continues to make up a significant portion, and the planktivorous *R. argentea* an increasing proportion, of the total catch, while total fish landings have increased 10-fold from 1970 to 1990 (Ogutu-Ohwayo 1990a), suggests that the transfer efficiency may not have changed significantly, despite drastic changes in community structure.

In all three lakes, production estimates are available only for the two extremes of the food chain: the phytoplankton and the fish. Current estimates of photosynthetic rates are limited in time and space, and they should not be accepted as long-term, lake-wide aver-

ages. Estimates of fish biomass and production are extremely difficult to make in these lakes due to their great size and the unconsolidated nature of their fisheries. All these uncertainties make the above comparisons very tentative. In order to more accurately predict potential changes in these lakes and better manage their resources, longer time series are required of quantitative measurements of the interactions between their biological components.

The Lakes' Future

In the past, low population densities and concomitant low intensities of agriculture, industry, and fishing allowed the African Great Lakes to maintain their pristine condition with little or no management. This is no longer the case. Even if human population densities stabilize in the near future, increased exploitation of the lakes and their catchment basins, as well as industrial development, are inevitable. Parks and conservation areas can be very effective in controlling fishing and watershed use in limited areas. For example, in Malawi a large expansion of agriculture between 1970 and 1980 resulted in a 50% increase in surface runoff in the upper Bua River catchment, while runoff in the upper Dwangwa catchment, which is largely protected by Kasungu National Park, maintained relatively constant flow rates during this period (Kombe 1984). Unlike the case in most terrestrial systems, however, spatial interaction is very high in lakes because of the continuity of water, so unwise land use and lake use practices in one area may produce deleterious effects throughout an entire lake. Obviously, a reserve along the lakeshore cannot protect the adjacent aquatic ecosystem from the effects of a species introduction or eutrophication. Each lake and its drainage basin must be managed as a whole. As each of these lakes is bordered by at least three countries, effective lake management will require international cooperation. In this regard it would be useful to establish international organizations for each lake similar to the now defunct Lake Victoria Fisheries Survey and the East African Freshwater Fisheries Research Organisation (Ogutu-Ohwayo 1990a).

A hinderance often experienced in aquatic conservation is the "out of sight, out of mind" phenomenon (Ray 1986). It is difficult to make legislators and the general public realize the importance of protecting the environment of organisms that they never see in their natural habitat. Researchers and managers must make information on the African Great Lakes more available and more presentable to nonscientists. A second hinderance in developing countries is the limited availability of funds. For the governments of countries surrounding the African Great Lakes, the immediate welfare of the riparian populations is a priority. While fisheries management

and research are easy to justify in this context, the resources required for research and management activities that have less immediate or less direct benefits are often not available. These resources must be supplied by the international community on the basis of scientific, cultural, and humanitarian justification.

The African Great Lakes are an important source of income and food, and the surrounding populations have an interest in the production of these ecosystems. However, ecologically friendly lake use and land use practices do not necessarily ensue as a result of this interest, either because the primary objective is short-term gain or because of lack of ecological knowledge. Both of these impediments to conservation may be addressed through public education, which is an important function of national parks (Bootsma 1992).

Effective management requires ongoing information on the status of an ecosystem; this can be obtained only by regular monitoring. In particular, monitoring of nutrient dynamics, primary production, and community structure is useful in detecting ecosystem change (Odum et al. 1979; Rapport et al. 1985). Indeed, it was the study of such properties that revealed the changes in Lake Victoria. Sufficient spatial and temporal coverage of such large lakes is difficult and expensive using conventional sampling techniques, but there is good potential for the application of remote sensing and automated measurements. Management also requires an understanding of ecosystem function. While separate physical, chemical, and biological components of the African Great Lakes have received attention since the beginning of the century, studies examining their interaction have been few. The ecology of the African Great Lakes is as unique as the organisms that inhabit them. The lakes are of immense socioeconomic value to the countries surrounding them, but they also must be seen by the rest of the world as a heritage to maintain.

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