NUTRIENTS AND PLANKTON BIOMASS IN THE RIFT LAKE SOURCES OF THE WHITE NILE: LAKES ALBERT AND EDWARD

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1. Abstract

The rift lakes Albert and Edward, as well as Lake George, Uganda, were sampled at nearshore and offshore sites during March 1995 with attention to water column chemistry, plankton biomass, and production rates. Biomass of phytoplankton exceeds that of zooplankton in both rift lakes, and the predictive relationship between light attenuation and particulate chlorophyll is consistent with that of Lake Victoria. Cyclopoid copepods dominate Albert and Edward; calanoids are rare (<1 m^{-3}) and Cladocera represent less than ten percent of zooplankton biomass. Although previously reported to be present in other lakes in the Nile system, *Thermodiaptomus galebi* was not confirmed in Lake Albert before this study. Adult males and ovigerous females of the species were collected in Lake Albert and immature females were sampled in Lake Edward. *Mesocyclops ogunnus* was collected from Lake Albert, which is a new record for this species from East African Rift Valley lakes. Present water temperatures of Lake Albert are elevated by about 0.5 °C compared with historical records, a circumstance which parallels changes recorded for Lake Victoria. Both Albert and Edward have lower levels of Total P and nitrate than historical accounts have reported. In shallow Lake George, heterocyst-forming cyanobacteria and centric diatoms were rare compared with historical records, a recent condition that may be the result of metal contamination, especially by copper from mining activities in the Ruwenzoris.

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2. Introduction

The Western Rift of East Africa, north of the Virunga volcanoes, contains two ancient lakes that attracted scientific attention since their discovery by Europeans more than a century ago. Underlain by sediments of great antiquity, Lakes Albert and Edward together with Lake Victoria constitute the major lake sources of the White Nile and contribute to the rich limnology of central East Africa. These lakes have not been subject to comparative examination of limnological properties for over two decades, despite changes in land use, fisheries exploitation, population growth, and regional climate. In order to identify modern conditions, we undertook limnological sampling and process rate experiments at these lakes in 1995.

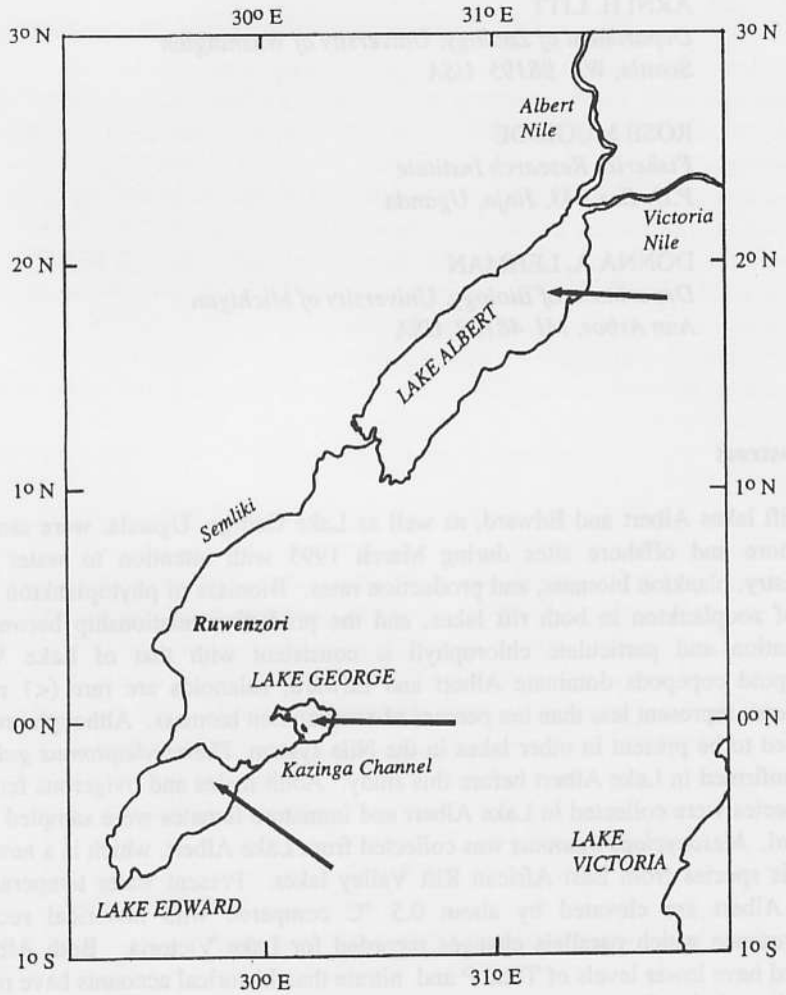


Figure 1. Lakes Albert, Edward, and George, with sampling sites indicated.

Lake Albert is a characteristic half-graben lake of maximum depth 58 m, and 5300 km^2 surface area, lying at surface elevation of 615 m (Fig. 1). The lake receives its main inflow at the south from the Semliki River, which descends from Lake Edward, and which river is both augmented and diluted by tributary streams from the northern slopes of the Ruwenzoris (Viner 1975). The Victoria Nile enters Lake Albert at its northernmost end, where it joins the northward outflow of the Albert Nile.

Lake Edward is a smaller (2325 km^2) and deeper (112 m) tilted basin. The lake reaches its maximum depth within 5 km of the western (Congo) shore, and slopes gradually to the Uganda shore. The lake receives drainage from the southwestern Ruwenzoris, from the Rwanda highlands, and from the Virunga volcanoes to the south. Some inflow occurs through the Kazinga Channel from a shallow (2 m) but optically deep and hypereutrophic northeastern basin, Lake George. Lake George had been well studied during the 1960s as part of a Royal Society component of the International Biological Programme (Burgis et al. 1972). Subsequently the lake has become an area of environmental concern because of heavy metal contamination by copper and cobalt from mining operations in the Ruwenzoris (Denny et al. 1995).

3. Methods

Lake Albert was sampled nearshore (5 m) and offshore (AL1: 40 m) from Butiaba, Uganda in the northeastern half of the lake. Lake Edward was sampled nearshore close to the mouth of the Kazinga Channel (ED1, 4 m) as well as at two offshore locations (ED2, 18 m and ED3, 25 m).

In situ profiles of temperature, oxygen, pH, and conductivity were obtained with an Endeco/YSI 6000 CTD equipped with internal data logger. Oxygen and pH electrodes were calibrated each day of use and in situ profiles of dissolved oxygen were further calibrated against surface water measurements by Winkler titration. Conductivities at in situ temperatures were converted to specific conductance at 25 °C by using a temperature coefficient of 2.3% $°C^{-1}$ (Talling and Talling 1965). Underwater irradiance (µE PAR) was measured with a LiCor cosine-corrected quantum sensor. Discrete water samples were collected by Van Dorn bottle. Samples were filtered on shore within 4 h of collection. SRP and SRSi were measured immediately by spectrophotometric methods (Hach). Filters for chlorophyll and particulate chemistry were dried over silica gel and were shipped to Ann Arbor for analysis. Chlorophyll filters were ground in 90% acetone; pigment was measured by extracted fluorescence, corrected for pheopigment. Both unfiltered water samples and filtrate were also shipped to Ann Arbor. Chloride, nitrite, nitrate, and sulfate were measured by ion chromatography. Alkalinity was measured by Gran titration. Sodium, potassium, magnesium, and calcium were measured by flame atomic absorption spectroscopy. Iron and manganese were measured by graphite furnace atomic absorption. Total dissolved P (DP) and particulate P were measured after persulfate oxidation and Total P (TP) was calculated as the sum of the two.

Zooplankton were sampled with four replicate vertical hauls by nets of both 100 and 60 µm aperture, 0.5 m mouth opening, and 5:1 aspect ratio (Research Nets, Inc.).

Zooplankton dry mass by taxon was estimated by drawing individuals as encountered from plankton collections, rinsing them in deionized water, and then drying them to constant mass at 60 °C. Mass determination was by electrobalance (Cahn 29).

Kinetics of phosphate uptake were measured for nearshore and offshore plankton assemblages. Lake water aliquots received additions ranging from 0 to 2 μM Na_2HPO_4 and concentration changes were measured over ca. 2 h at ambient temperature (ca. 25 °C) in subdued light. Maximum rates of uptake and half-saturation constants were determined by non-linear regression (SYSTAT 5.03).

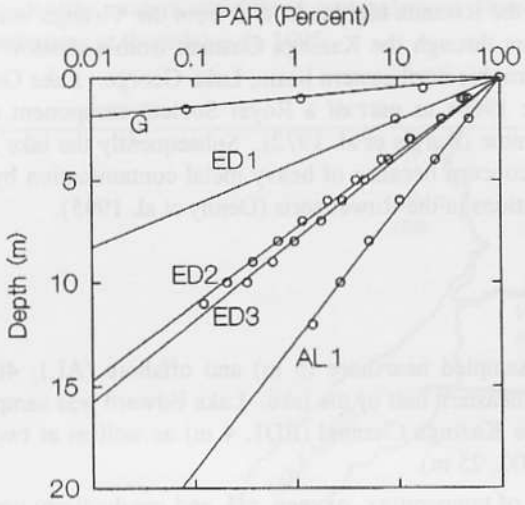


Figure 2. Photosynthetically active irradiance versus depth, as percentage of surface readings, for Lakes Albert, Edward, and George, 1995.

4. Results

4.1. PHYSICAL AND CHEMICAL PROPERTIES

4.1.1. *Light Attenuation*

Vertical attenuation of light varies among lakes, and between nearshore and offshore Lake Edward (Fig. 2). With the exception of Lake George, the range of attenuation coefficients was similar to observations from offshore Lake Victoria (Lehman et al. 1998). The nearshore station ED1 was near the mouth of the Kazinga Channel, linking Edward with its upstream hypereutrophic extension, Lake George. Light attenuation was primarily a function of particulate chlorophyll concentration (Fig. 3) such that a common linear model applies to the three large basins Albert, Edward, and Victoria. Light attenuation could thus be used to predict algal biomass for these lakes when direct measurements are lacking. Light attenuation in Lake George is considerably greater than predicted by the model that fits the deeper lakes. This appears to result from high

abiotic turbidity in Lake George. The residual deviation of light attenuation in Lake George (2.54 m^{-1}) from the linear model prediction is similar in magnitude to the high background attenuation value of 2.55 m^{-1} that Ganf (1974) reported for Lake George water, independent of its chlorophyll content.

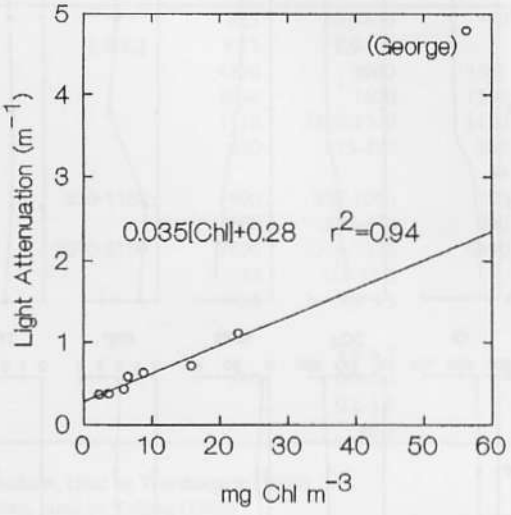


Figure 3. Vertical attenuation of PAR versus chlorophyll for Lakes Albert, Edward, George, and modern Victoria. Modern Victoria data from R. Mugidde (Lehman et al. 1998).

4.1.2. *Lake Albert*

Measurements for Lake Albert at the offshore station AL1 reveal a lake that is about 0.5 °C warmer throughout (Fig. 4) than measured by Talling during March 1961, or during any other of his longitudinal lake surveys (Talling 1963). The lake is well-mixed on a diel basis to a depth of about 25 m. In other respects, the lake is more dilute in terms of specific conductance and concentrations of major ions, and lower in phosphate and nitrate than measured decades ago by Talling and others (Table 1).

Historical values for particulate chlorophyll in Lake Albert are lacking for comparison with our modern profile (Fig. 4), but Talling (1965) reported light attenuation coefficients for green light, the most penetrating spectral component. The values cited by Talling range from 0.35 to 0.72 m^{-1}, including 0.50 m^{-1} during March of 1961. Our estimate for light attenuation (Fig. 2) during the same month of 1995 was 0.36 m^{-1}. As we noted above, the linear model of Fig. 4 can be reformulated to predict chlorophyll from light attenuation. Such a reformulated model predicts that chlorophyll levels in March 1961 were about 6.4 mg m^{-3}, or nearly three times higher than in March 1995. If it is true that historical light attenuation in Lake Albert was controlled by variation in algal abundance, this comparison indicates that chlorophyll levels in Lake Albert have declined.

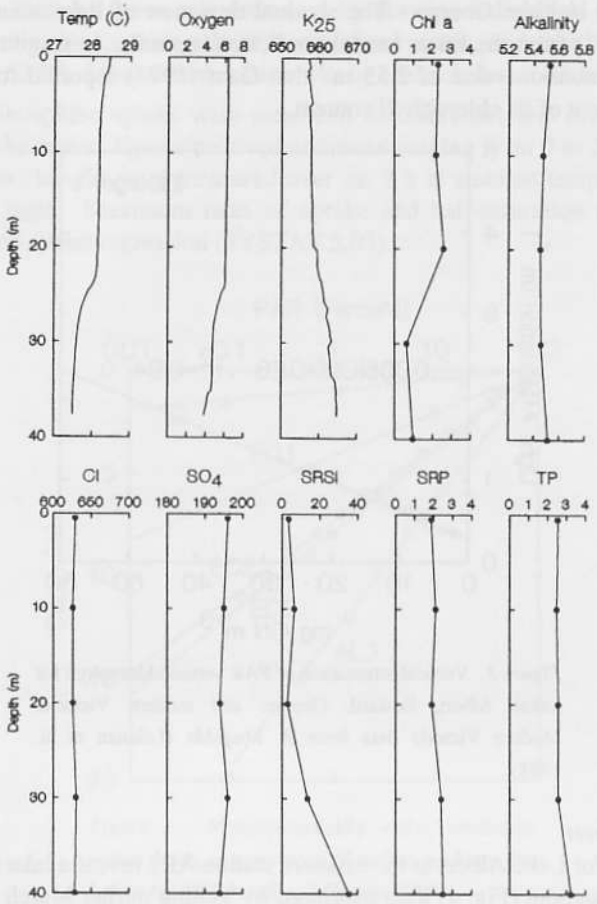


Figure 4. Temperature, oxygen (mg L^{-1}), chlorophyll (mg m^{-3}), and chemical properties: Lake Albert, March 1995. Chemical units are as in Table 1.

4.1.3. *Lake Edward*

Lake Edward also differs from historical record (Fig. 5, Table 2). Talling (1965) reported light attenuation of 1.3 m^{-1} from a 5.5 m northeast station near the Kazinga Channel. Our empirical relationship between attenuation and chlorophyll (Fig. 3) implies that the value corresponds with ca. 29 mg m^{-3} Chl, similar to the 22.7 mg m^{-3} we found at a 2.5 m station immediately offshore of the Channel mouth (at 1.11 m^{-1} light attenuation). Offshore stations at 18 and 25 m had Chl of 8.8 and 6.5 mg m^{-3}, corresponding to measured light attenuation coefficients of 0.63 and 0.58 m^{-1}, respectively. Present P concentrations in Lake Edward are about one half of historical reports and modern sulfate concentrations are lower, as well (Table 2). Lower modern values for sulfate parallel observations made by Hecky and Bugenyi (1992) and by Lehman and Branstrator (1994) for Lake Victoria, where modern sulfate is lower than previously reported. Hecky and Bugenyi speculate that some of the difference may be analytical, owing to modern methods (ion chromatography).

TABLE 1. Chemical composition of Lake Albert surface water. Samples for 29 March 1995 are from offshore station AL1 (40 m depth). Values are µM unless indicated.

	1923[1]	1953[2]	1960-61[3]	1969[4]	1995
K_{25} (µS)		825	803-870	770	660
pH	7.8-9.2	9.12	8.9-9.0		
Na		4220	3960	3567	3430
K		1690	1670	1333	1070
Mg		1310	1300-1340	1150	1010
Ca		230	225-270	260	216
F				44	37
Cl	850-1160	900	930-1080	770	630
SO_4		260	280-470	290	195
Alk (µEq)	8070-8150	7800	7250-7330	6390	5500
SiO_2		57	0.7-18.3		3.4
SRP		4.2	3.9-5.5		1.88
DP					2.17
TP			3.9-6.5		2.54
NO_3		0.6	0.3-2.4		<0.1
Fe			0.8-1.6		0.08
Mn			<0.2		

[1]From Tottenham, cited by Worthington (1930)
[2]From Elskens, cited by Talling (1963)
[3]From Talling (1963), n= 5 sampling dates, and from Talling and Talling (1965)
[4]From Kilham (1972)

TABLE 2. Composition of Lake Edward surface water. Samples for 25 March 1995 are from an offshore station at 0° 12.596' S, 29° 46.799' E (25 m depth). Values and methods as in Table 1.

	1954[1]	1961[2]	1964[3]	1969[4]	1995
K_{25} (µS)	1043	1031	1026	508-580	880
pH	8.89	9.1	9.1	7.9-8.2	8.9
Na	4870	4780	2450	2175-2262	3750
K	2030	2310	2120	818-941	1620
Mg	1850	1990		833-962	1630
Ca	242	310	280	330-340	310
F				32-35	44
Cl	760	1010		440-474	580
SO_4	365	320		350-400	250
Alk (µEq)	10100	9850	9900	4070-4740	7870
SiO_2	33	108		210-270	150
SRP	1.0	0.6			0.6
DP					0.8
TP		4.1			1.4
NO_3	1.6	1.7			<0.1
Fe		4.2			0.06
Mn		<0.2			

[1]From Elskens, cited by Talling (1963)
[2]From Talling and Talling (1965)
[3]From Beadle (1966)
[4]From Kilham (1972)

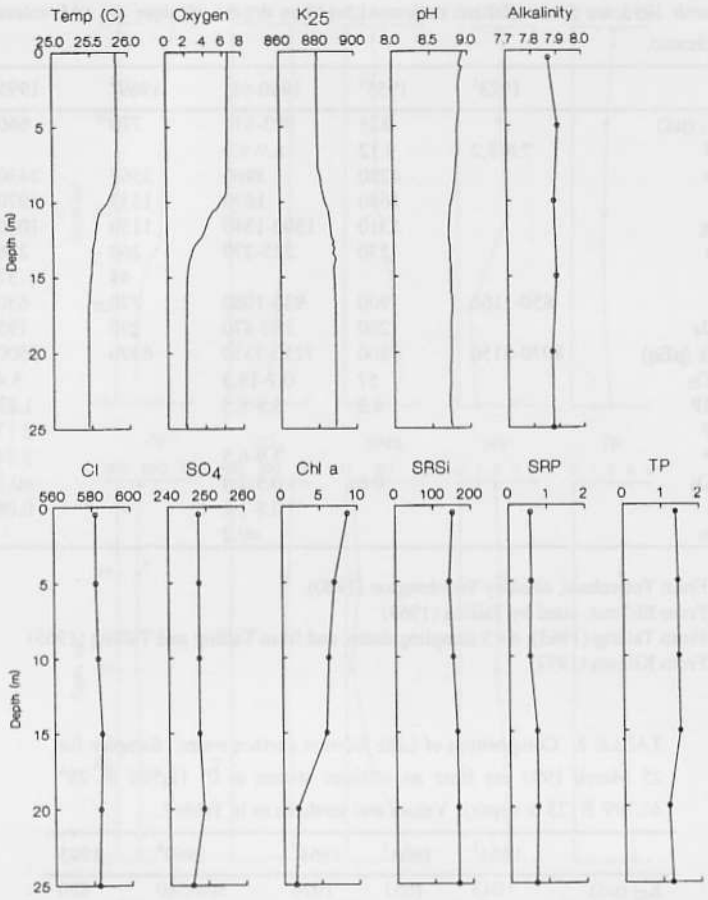


Figure 5. Distribution of temperature, oxygen, chlorophyll, and chemical properties in Lake Edward, March 1995. Units as in Fig. 4.

4.2. PLANKTON COMMUNITIES

Cyclopoid copepods dominate Lakes Albert (Fig. 6) and Edward (Fig. 7). The lakes exhibit similar species richness of crustacean zooplankton, but differ in species assemblages (Table 4). In particular, large unhelmetted *Daphnia lumholtzi* var. *monacha* are present in Lake Albert, consistent with observations by Green (1967, 1971). The species was rare in Lake Edward, and smaller *Daphnia longispina* occurred there instead. *Thermodiaptomus galebi* is very rare in both lakes; only immature specimens were found in Lake Edward despite exhaustive searching. We assume that the immature individuals are *T. galebi* because previous authorities identified the taxon from the lake (Dussart 1989). We found ovigerous *T. galebi* females and adult males in

Lake Albert, despite prior literature assertions that calanoids were absent (Verheye and Dumont 1984).

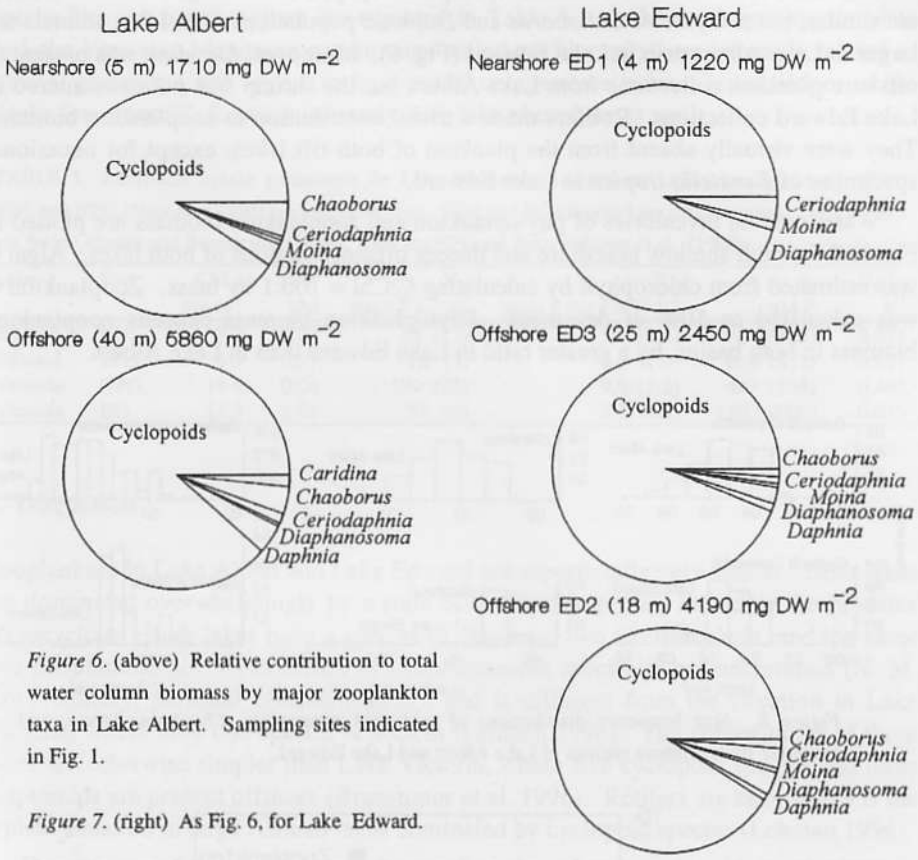


Figure 6. (above) Relative contribution to total water column biomass by major zooplankton taxa in Lake Albert. Sampling sites indicated in Fig. 1.

Figure 7. (right) As Fig. 6, for Lake Edward.

TABLE 4. Crustacean zooplankton taxa in Lakes Albert and Edward, March 1995

Lake Albert	Lake Edward
Mesocyclops aequatorialis aequatorialis	*Mesocyclops aequatorialis similis*
Mesocyclops ogunnus	*Mesocyclops aequatorialis* hybrid
Thermocyclops neglectus	*Thermocyclops oblongatus*
	Thermocyclops consimilis
Thermodiaptomus galebi	*Thermodiaptomus (galebi)*
Daphnia lumholtzi monacha	*Daphnia lumholtzi monacha*
	Daphnia longispina
Diaphanosoma excisum	*Diaphanosoma excisum*
Diaphanosoma mongolianum	*Diaphanosoma mongolianum*
Ceriodaphnia cornuta	*Ceriodaphnia cornuta rigaudi*
Ceriodaphnia dubia	*Ceriodaphnia dubia*
Moina micrura	*Moina micrura*
Caridina nilotica	

Size distributions of the dominant cyclopoid copepod assemblages in the two lakes are similar, but analyses of *Chaoborus* and *Daphnia* populations reveal that animals are larger in Lake Albert than in Lake Edward (Fig. 8). Moreover, *Caridina* was present in offshore plankton collections from Lake Albert, but the shrimp was not encountered in Lake Edward collections. Rotifers made a trivial contribution to zooplankton biomass. They were virtually absent from the plankton of both rift lakes, except for occasional specimens of *Keratella tropica* in Lake Edward.

Water column inventories of phytoplankton and zooplankton biomass are plotted in Figure 8 for both shallow nearshore and deeper offshore stations of both lakes. Algal C was estimated from chlorophyll by calculating C:Chl = 100:1 by mass. Zooplankton C was calculated as 50% of dry mass. Phytoplankton biomass exceeds zooplankton biomass in both basins, by a greater ratio in Lake Edward than in Lake Albert.

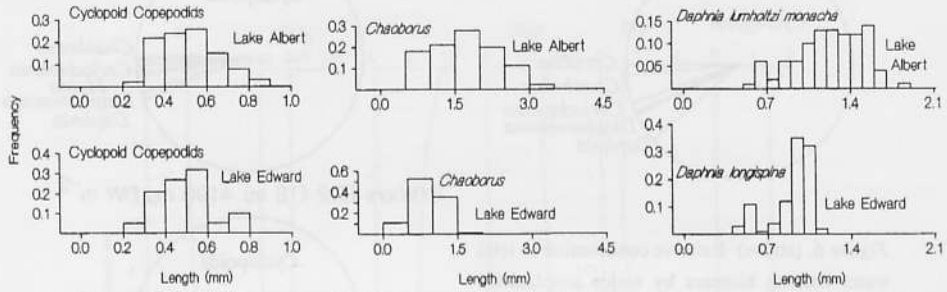


Figure 8. Size frequency distributions of cyclopoid copepodids, *Chaoborus* larvae, and *Daphnia* from offshore stations of Lake Albert and Lake Edward.

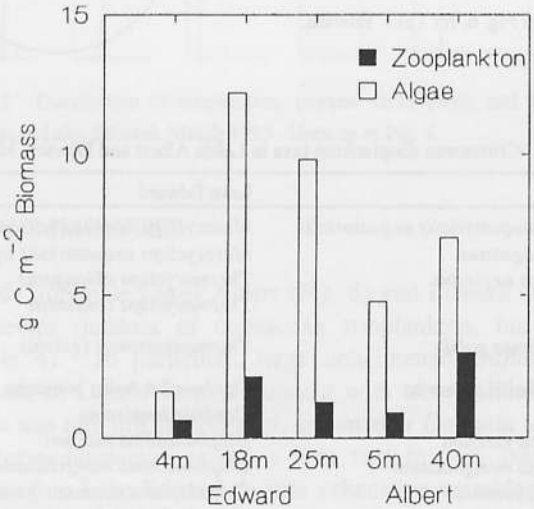


Figure 9. Total biomass of phytoplankton and zooplankton at nearshore and offshore stations in Lakes Albert and Edward.

4.3. PHOSPHATE UPTAKE

Uptake kinetics for phosphate are reported in Table 5, together with comparison data for Lake Victoria. Maximum uptake rates scaled to chlorophyll are inversely related to ambient phosphate and appear to be a useful comparative index. Initial slopes of the uptake functions (V_m/k_s) vary inversely with lake phosphate as well.

TABLE 5. Phosphate uptake parameters for Lake Edward and nearshore Lake Victoria, March 1995. ED1 and NPG (Napoleon Gulf) are nearshore sites. ED3 and BG (Bugaia) are offshore sites. Data for BG are from Lehman and Branstrator (1994). Data for NPG are from Lehman et al. (1998).

Lake	Site	Chl *a* mg m^{-3}	SRP µM	V_m nmol P L^{-1} h^{-1}	V_m nmol P (µg Chl)$^{-1}$ h^{-1}	k_s nM P	V_m/k_s h^{-1}
Edward	ED1	7.2	0.20	28 (17)	3.9 (2.4)	841 (1185)	0.033
Edward	ED3	6.9	0.57	18 (7)	2.6 (1.0)	664 (855)	0.027
Victoria	NPG	18.8	0.04	180 (23)	9.6 (1.2)	447 (168)	0.403
Victoria	BG	11.3	1.65	23 (4)	2.0 (0.4)	1200 (600)	0.019

5. Discussion

Zooplankton in Lake Albert and Lake Edward are superficially very similar. Both lakes are dominated overwhelmingly by a suite of cyclopoid species, including the predator *Mesocyclops*. Both lakes have a species of *Daphnia*, two *Ceriodaphnia*, and the same two *Diaphanosoma*. Coexistence of *Diaphanosoma* species is not uncommon (N. M. Korovchinsky, personal communication), and is different from the situation in Lake Victoria, where only one species is present (Lehman 1996). The communities of these lakes are otherwise simpler than Lake Victoria, where five cyclopoid species and three diaptomids are present offshore (Branstrator et al. 1996). Rotifers are rare, which is the typical situation in large African lakes dominated by cyclopoid species (Lehman 1996).

Despite superficial similarities, the smaller size of non-cyclopoid zooplankton in Lake Edward compared with Lake Albert suggests that visual planktivory is more intense in Edward. That notion is reinforced by the lower ratio of zooplankton biomass to phytoplankton biomass in Lake Edward. Presence of an effective piscivore, Nile perch, in Lake Albert may cause reductions in the numbers of planktivorous fish that occur in that lake. As early as the 1960s, Green (1967) argued that there was reduced intensity of predation by fish on zooplankton in mid-lake regions of Lake Albert.

Zooplankton biomass at offshore stations in both Lake Albert and Lake Edward exceed the seasonal mean values reported for Lake Victoria by Branstrator et al. (1996), but the values are within the range of annual variation observed for Lake Victoria. In all three of the lakes, zooplankton biomass falls in a range from approximately 2 to 6 g DW m^{-2}. Water column depths that were sampled differed among the lakes, however, and ranged from 25 m in Edward to 40 m in Albert, to 50 m in Victoria. As a consequence of averaging the areal abundances over different depth ranges, computed volumetric abundances of zooplankton are somewhat higher in Edward than in the other two lakes. We did not investigate the vertical distribution of

the plankton in the lakes, and thus actual in situ concentrations are only approximated by water column averages.

Previous literature reports that *Diaptomus* is not present in Lake Albert are erroneous. It is unlikely that our discovery represents a new colonization event. The animals are extremely rare, on the order of one individual per cubic meter. We confirmed their presence only by diligent and sustained search of large sample volumes. An immature diaptomid copepod had already been discovered in a Lake Albert collection during 1993 with an identical net (V. Kiggundu and J. Lehman, personal observation), but its species identity could not be established at that time. The fact that calanoids are so scarce in these lakes, compared with Lake Victoria, points again to higher levels of visual planktivory in the rift lakes.

Lake Albert seems to be more transparent now than 30 years ago, evidently because of reduced algal chlorophyll. Phosphate concentrations are also lower, but that is probably not the cause of increased transparency. Talling had reported extreme phosphate concentrations (Table 1), and stoichiometric considerations dictate that P could not be a limiting factor in biomass production, then or now. The elevated temperature of the lake water is intriguing, because it is reminiscent of similar warming of Lake Victoria (Hecky 1993; Lehman 1996). Whether or how altered mixing in response to the thermal regime may have affected lake production, nutrient supplies to the epilimnion, and algal biomass cannot be answered by our limited temporal data.

We found lower values of Total P in Lake Edward than previous reports had indicated. We cannot yet determine if the reduction is paralleled by chlorophyll because historical data are not readily available for comparison. All three lakes exhibit modern values of sulfate lower than historical reports. This apparent reduction is a regional feature in common with Lake Victoria. It is not yet clear how much of this difference is real, a consequence of lessened inputs or possibly increased chemical reduction in the sediments, or how much is the result of improvements in analytical methodology.

Kinetic characteristics of the algae in Lake Edward suggest that phosphate is not growth limiting. Inverse variation of both V_m and V_m/k_s with SRP in these tropical lakes is consistent with expectations from temperate lakes. Values for Lake Edward are intermediate between inshore and offshore Lake Victoria, where bioassay experiments (Lehman and Branstrator 1993, 1994) demonstrated that P is not the proximate limitation for biomass production.

5.1. CONDITION OF LAKE GEORGE

Lake George, as well as much of eastern Lake Edward, lies within Queen Elizabeth (Ruwenzori) National Park. Restoration of political stability to Uganda in the late 1980s after a decade of strife has stimulated conservation efforts for wildlife within the National Park. In addition, copper mining has recently resumed along the Nyamwamba River, which flows into Lake George. The Kilembe mines first began operation in 1956, and shortly before they closed in 1979 elevated copper concentrations were measured along a gradient extending from Lake George, along the Kazinga Channel

which links George to Edward, and then across northern Lake Edward to its outflow as the Semliki River (Bugenyi 1979).

The IBP investigations of the 1960s preceded evidence of metal pollution. They established that nitrogen was a limiting resource to the algae of the lake, and that total community respiration approximately balanced photosynthesis on a 24-h basis (Ganf and Viner 1973). Nitrogen income was dominated by fluvial inputs and nitrogen fixation by diazotrophic cyanobacteria. Hydrologic input is dominated by flow from the Ruwenzoris (Viner and Smith 1973), and the chemistry of the streams is representative of headwaters draining predominant silicate rocks (Kilham 1984).

The high pH of Lake George is the result of photosynthesis by suspended phytoplankton (Ganf and Horne 1975). Withdrawal of CO_2 from the water by photosynthesis elevates the pH. During the 1960s, the lake exhibited a diurnal pH variation from approximately 8.75 to 9.98 (Ganf 1972). More recently, pH as high as 11.2 has been reported from nearshore waters, with open lake values consistently near pH 10 (Denny et al. 1995). By elevating the pH, photosynthesis can accelerate net chemical weathering of silica from sediments, and there appears to be a trend toward higher silica concentrations in recent years (Table 3). Biogenic precipitation of amorphous silica by diatoms, a process that typically reduces silica levels in lakes, may become partly inhibited by toxic effects of the polluting metals, especially copper. Copper is known to inhibit silica uptake and silicification by diatoms (Reuter 1983).

TABLE 3. Chemical composition of Lake George surface water. Samples for 24 March 1995 were collected mid-lake at 0° 0.30' N, 30° 13.27' E (2 m depth). Values are µM unless indicated.

	1961[1]	1967[2]	1969[3]	1995
K_{25} (µS)	224	234-262	234-338	240
pH	9.6		8.2	10.0
Na	587	848-892	674-1240	620
K	108	97-118	243-271	90
Mg	333	300-321	300-412	300
Ca	505	362-500	520-565	450
F			25	18
Cl	248	214-259	364-567	240
SO_4	116	150-188	131-200	45
Alk (µEq)	1910	1250-2000	1780-2290	1730
SiO_2	300	330-340	375-410	370
SRP	<0.6	1.8-4.2		1.3
DP				1.3
TP	13.3			
NO_3			n.d.[4]	<0.1
Fe		4.5		0.10
Mn		4.7		

[1]Talling and Talling (1965)
[2]Viner (1969)
[3]Kilham (1972)
[4]Viner (1975) reports NO_3 as not detectable

Copper also inhibits the nitrogen-fixation processes of diazotrophic, heterocyst-forming cyanobacteria (Elder and Horne 1975), including the taxa *Anabaena* and *Aphanizomenon*, which formerly were important elements of the flora (Ganf 1974b). Our recent samples were dominated by colonial coccoid cyanobacteria (Chroococcales), which do not produce heterocysts, but nonheterocystous cyanobacteria can fix nitrogen in the dark when there is no production of nitrogenase-disabling oxygen by photosynthesis, or in the light either by spatial separation between aerobic and anerobic portions of colonies or by temporal separation of photosynthesis and nitrogen fixation in different phases of the cell cycle (Carpenter and Price 1976; Stal and Krumbein 1985; Mitsui et al. 1986). Small pennate diatoms are present, but not as biomass dominants. Centric diatoms, especially *Aulacoseira* (formerly *Melosira*) species, were rare. A similar situation was reported for Lake Edward during 1972 (Hecky and Kling 1987); Chroococcales dominated the phytoplankton and diatoms were significantly abundant only at a southern site, remote from the metal contamination later identified in the north.

Nitrogen fixation formerly provided nearly half of the nitrogen income for Lake George (Horne and Viner 1971). Unlike regenerated nutrients, such "new" nutrient permits net biological production and export of biogenic material from the water column to the sediments. The prospect that metal pollution may increase with mining development suggests the need for additional analyses of the productive ecosystem.

6. Conclusions

The most conspicuous changes to lakes Albert and Edward during the previous 30 years appear to have been (1) reductions in algal biomass, measured as particulate chlorophyll, and (2) reduced water column inventories of P and inorganic N. These changes are consistent with increased temperature of Lake Albert, and suggest reduced mixing of the surface layer, possibly under influence of reduced wind stress. Given sufficient silica to support fast-sinking diatoms, increased physical stability can lead to accelerated sedimentation of particulate matter, including Chl, P, and N, from surface layers. This tendency is opposed only when there is a floristic change to more buoyant taxa, as in modern Lake Victoria. We regard climatic variation to be a master controlling variable for lakes of East Africa, and its signal may be registered through changes in primary production and algal biomass as well as nutrient conditions.

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