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Phytoplankton community structure and environment in the Kenyan waters of Lake Victoria

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SUMMARY

1. Phytoplankton species composition, numerical abundance, spatial distribution and total biomass measured as chlorophyll *a* concentration were studied in relation to environmental factors in September 1994 (dry season) and March 1995 (rainy season), respectively, in the Kenyan waters of Lake Victoria; 103 species were recorded.
2. Blue-green algae (Cyanophyceae) were most diverse, followed by diatoms (Bacillariophyceae), green algae (Chlorophyceae) and dinoflagellates (Dinophyceae).
3. Twinspan separated the phytoplankton communities in the Nyanza Gulf and those in the open lake during both seasons. During the dry season, the Nyanza Gulf was strongly dominated by blue-greens, while diatoms dominated in the open lake. During the rainy season, blue-greens remained dominant in the Nyanza Gulf although the number of species found was lower than during the dry season; in the open lake, blue-greens replaced diatoms as the dominant group and there were more species than in the dry season.
4. Canonical correspondence analysis indicated that the phytoplankton species distribution was significantly correlated with turbidity during the dry season and with SiO₂ during the rainy season. Chlorophyll *a* concentrations ranging from 2.0 to 71.5 mg m⁻³ in the dry season and 2.0–17.2 mg m⁻³ in the rainy season confirm earlier reports of increasing phytoplankton biomass in Lake Victoria since the 1960s.

Keywords: chlorophyll *a*, Kenya, Lake Victoria, phytoplankton, species distribution

Introduction

Since the first sampling of Lake Victoria by Stuhlmann in 1892 (Schmidle 1898, 1902), some twenty publications on its algal flora have resulted in a list of a total of 601 taxa of algae (mainly phytoplankton), belonging to 117 genera (Cocquyt *et al.*, 1993). Information on the main environmental features was first given in the pioneer work of Worthington (1930) and quantitative studies on the phytoplankton began

with the work of Fish (1955, 1956, 1957), followed by Talling (1957a,b, 1962, 1966) and Evans (1961, 1962a,b). More recently, Talling (1987) integrated the available information on seasonal population dynamics and photosynthetic production in Lake Victoria. Akiyama *et al.* (1977) have related the phytoplankton seasonality to the physico-chemical parameters in the Mwanza Gulf.

According to observations in offshore waters of the lake made in the early 1960s (Talling, 1966, 1987), diatoms increased in numerical abundance during periods of isothermal mixing of the whole water column. On the other hand, helioid cyanobacteria ('blue-green algae' or Cyanophyceae) dominated the epilimnion during thermal stratification, while *Ceratium brachyceros*, a dinoflagellate, varied erratically.

Green algae generally remained sparse throughout the year. A few other taxa occurred in small numbers.

Recent investigations have revealed significant changes in the chemical characteristics and phytoplankton community of Lake Victoria (Hecky & Bugenyi, 1992; Hecky, 1993; Gophen *et al.*, 1995). Phytoplanktonic biomass has increased overall and blooms of cyanobacteria, which had already been observed early in the century (Ostenfeld, 1908), have now become common (Ochumba & Kibaara, 1989). Correlatively with their dominance, there is a relative reduction in diatoms and other groups. These changes may be associated with climatic, physical, chemical and biological processes, together with human activities which are increasingly taking place in the catchment and in the lake itself. Crul (1995) reviewed the conditions in the catchment of Lake Victoria. A detailed description of the sources and quantities of pollutants and fertilizers brought in the Kenyan part of Lake Victoria is given by Kirugara & Nevejan (1996).

Indigenous fish species have declined markedly, partly as a result of predation and competition from fish species introduced to the lake in late 1950s and early 1960s (Welcomme, 1967; Ogutu-Ohwayo, 1990). A reduction in native phytoplanktivorous fish has been partly blamed for increases in algal biomass (Witte *et al.*, 1992).

In order to elucidate the influence of environmental factors on the distribution and abundance of phytoplankton in Lake Victoria, we investigated the recent phytoplankton community structure of the Kenyan part of the lake. Therefore, we sought to find any differences in the phytoplankton between the dry and rainy seasons, and between the inshore waters and the open lake, and to relate these to environmental conditions.

Methods

The Kenyan part of Lake Victoria comprises the north-eastern part of the main lake and the semi-enclosed Nyanza Gulf (also called the Winam Gulf or the Kavirondo Gulf). It receives the flow of several rivers, most of them rising from the slopes of the western ridge of the East African Rift valley. The main geographical, hydrological and physical characteristics of Lake Victoria and Nyanza Gulf have been summarized by Burgis *et al.* (1987), Mavuti & Litterick (1991) and Crul (1995).

The climate of the catchment area is of the equatorial type (Walter *et al.*, 1960). The mean annual temperatures in areas close to the lake range between 22.8 and 23.3 °C, and the mean daily temperature of the hottest month ranges between 29.3 and 31.6 °C. There are two main rainy seasons, the long rains occurring from March to May and the short rains from November to December.

Samples were taken in September 1994 and in March 1995 at thirteen sites from a previously established monitoring programme of the Kenya Marine and Fisheries Research Institute (Fig. 1). These included nine coastal stations with a maximum depth of 4.1 m, mainly located in the Nyanza Gulf (numbers 1, 2, 3, 9, 10, 17 and 26), and in the vicinity of the River Nzoia (number 53) and the Yala Swamp (number 54); four offshore stations, where the water depth ranged between 5.2 and 50 m, and which were situated in the main open lake (numbers 32 and 34) as well as in the Nyanza Gulf (numbers 4 and 31), were also sampled.

Light penetration was estimated with a 20-cm diameter, black-white Secchi disc. Turbidity was measured with a Hach turbidimeter 2100 P. Water temperature and dissolved oxygen were measured with a Yellow Spring Instruments dissolved oxygen meter YSI 57. pH was determined with a Digital mini-pH meter 49 and conductivity with a Microprocessor conductivity meter LF 96. Water samples were collected with a 3-L Van Dorn sampler at the surface, and at depths of 2, 4, 10, 20, 30 and 40 m depending on the maximum depth of each station. Portions of the water sample were analysed for alkalinity by titration with 0.02 N HCl to pH 4.5 using methyl orange indicator (GEMS, 1992). Spectrophotometric methods were used to determine phosphate-phosphorus (i.e. SRP and ascorbic) and nitrate-nitrogen (i.e. cadmium reduction and diazoic complex), as outlined by Mackereth *et al.* (1978) and silicate (heteropoli blue) according to APHA (1985).

For phytoplankton analysis, 250 mL of water was placed in a polyethylene bottle and fixed immediately with Lugol's iodine solution. After 48 h decantation, the lower layer (20–25 mL) containing the sedimented algae was put in a glass vial and stored in a dark cool box. The known volume of concentrated sample was used for identification and counting of phytoplankton under an inverted microscope. Phytoplankton species were identified using the methods of Huber-Pestalozzi

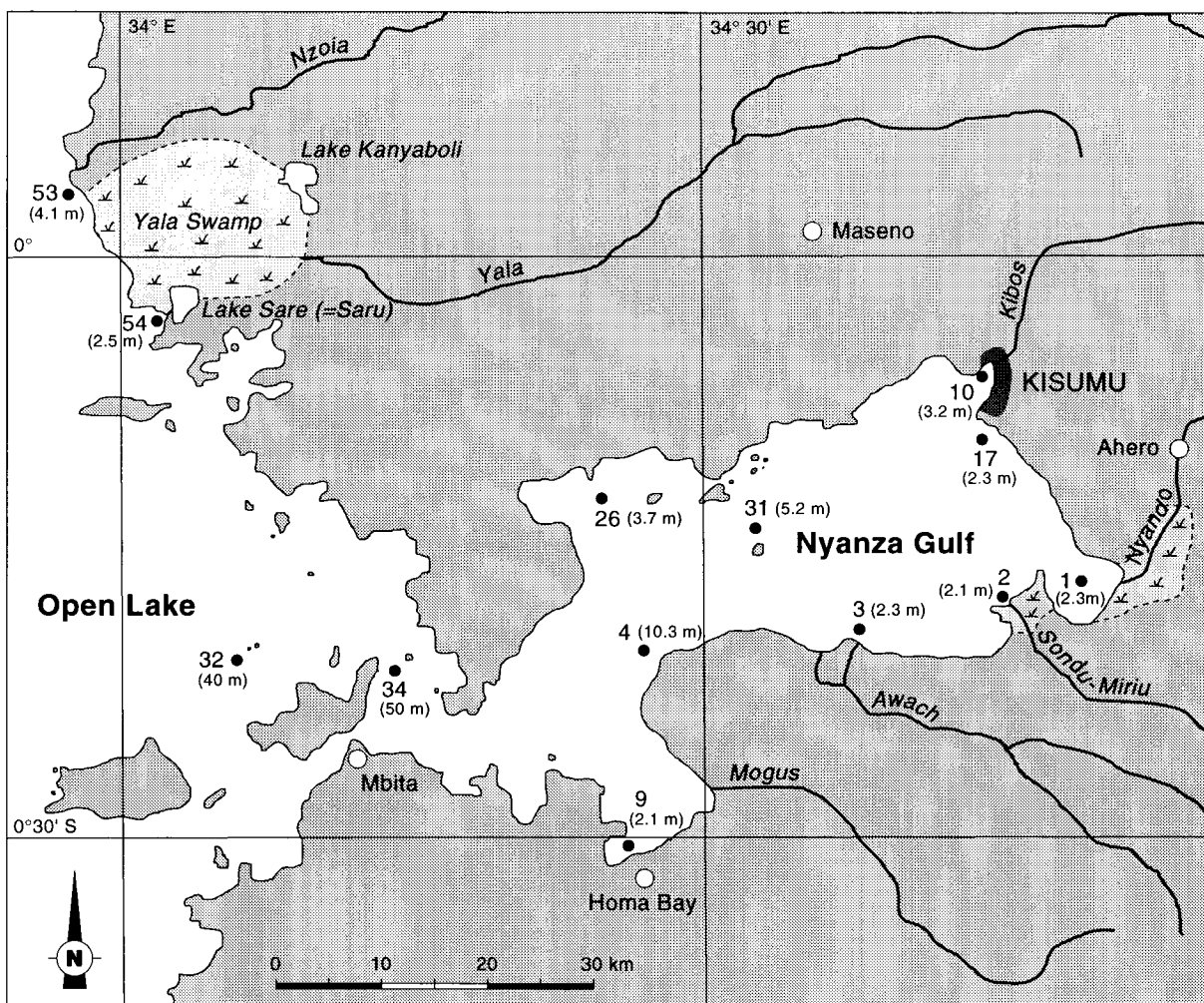


Fig. 1 Map showing the positions of the sampling stations in the Kenyan part of Lake Victoria. The brackets indicate depth. The gulf stations are numbers 1, 2, 3, 9, 10, 17 and 26 (coastal), and 4 and 31 (offshore). The open lake stations are numbers 53 and 54 (coastal), and 32 and 34 (offshore).

(1938) for Cyanobacteria, those of Hustedt (1942), Germain (1981) and Krammer & Lange-Bertalot (1986, 1988) for Bacillariophyceae, those of Ettl (1983), Komárek & Fott (1983) and Ettl & Gärtner (1988) for Chlorophyceae, and the methods of Huber-Pestalozzi (1968) and Popovsky & Pfiester (1990) for Dinophyceae. In addition, the keys of Pankow *et al.* (1990) as well as some earlier publications on East African Lakes (see references in the checklist of Cocquyt *et al.*, 1993) were consulted. Nomenclatural authorities and abbreviations for species are given in Table 1.

Phytoplankton density (numbers mL^{-1}) were estimated by counting all individuals whether these

organisms were single cells, colonies or filaments, for example.

To determine the phytoplankton distribution and community structure, percentage species contribution was subjected to two-way indicator species analysis (twinspan) (Hill, 1979), using the default options of the computer program. This is a classification program based on a subsequent dichotomous classification technique expressing the occurrences of the organisms in an ordered two-way table constructed from the sites-taxa matrix. The results can be viewed as a dendrogram showing clusters of stations with similar species composition. The indicator species

identified are not necessarily dominant, but demarcate the conditions in which the other taxa of the group are likely to be found.

To investigate the relationships between species, stations and environmental factors, numerical abundance data were $\ln + 1$ transformed and subjected to canonical correspondence analysis (CANOCO or CCA) using down weighing of rare species (Jongman *et al.*, 1987; ter Braak, 1988, 1990). This is a technique concurrently performing the regression and the ordination of the data. The significance of the correlations between environmental factors and the species distribution was tested by Monte Carlo permutation.

Environmental factors measured included Secchi depth, turbidity, temperature, dissolved oxygen, pH, alkalinity, conductivity, SiO_2 , $\text{PO}_4\text{-P}$ and $\text{NO}_3\text{-N}$. Only the surface samples, for which most environmental data were available, were used in the CCA analysis to study the correlations with environmental factors on phytoplankton distribution.

For determination of chlorophyll *a* concentration, water volumes of 50–500 mL were filtered immediately through GF/C glass fibre filters after the addition of 0.2 mL saturated MgCO_3 suspension (GEMS, 1992). Filters were extracted in cold 90% acetone for 18–24 h. Light extinction of the extract was measured in a Spectronic 21 D digital spectro-photometer at wavelengths of 665, 645 and 630 nm. The extinctions were corrected for turbidity by subtracting the corresponding reading at 750 nm and the corrected value used to calculate chlorophyll *a* concentration according to Strickland & Parsons (1968).

Results

Species composition

A total of 103 species of phytoplankton belonging to forty-five genera were collected and identified. Out of these species, ninety-three were recorded in September 1994 and eighty-four in March 1995 (Table 1).

The Cyanobacteria were most diverse with thirty-five species, followed by the Bacillariophyceae (diatoms) with thirty-four, the Chlorophyceae (green algae) with thirty-three and the Dinophyceae (dinoflagellates) represented by a single species.

In addition, there were numerous picoplankters (cell diameter < 2 μm) which could not be identified

or counted properly with the inverted microscope. These occurred, particularly in the dry season, in several forms including single cells, colonies and chains of cells.

Dry season

Without exception, twinspan separated stations in the Nyanza Gulf (left side cluster; indicator species *Aulacoseira nyassensis* and *Microcystis flos-aquae*) from those in the open lake (right hand cluster; indicator species *Nitzschia acicularis* and *Planktolyngbya subtilis*) (Fig. 2a). Within the Nyanza Gulf, stations on the south coast (numbers 1, 2, 3 and 9) were usually separated from those on the north coast (numbers 10, 17, 26 and 31) and the more offshore situated station 4. Stations 3 (2 m depth) and 31 (0 m) were the only 'misfit' samples. There were two clusters in the open lake: that on the left, consisting of stations 34 (upper samples) and 32 (deep samples); and that on the right, consisting of stations 34 (deep samples) and 32 (upper samples), and stations 54 and 53.

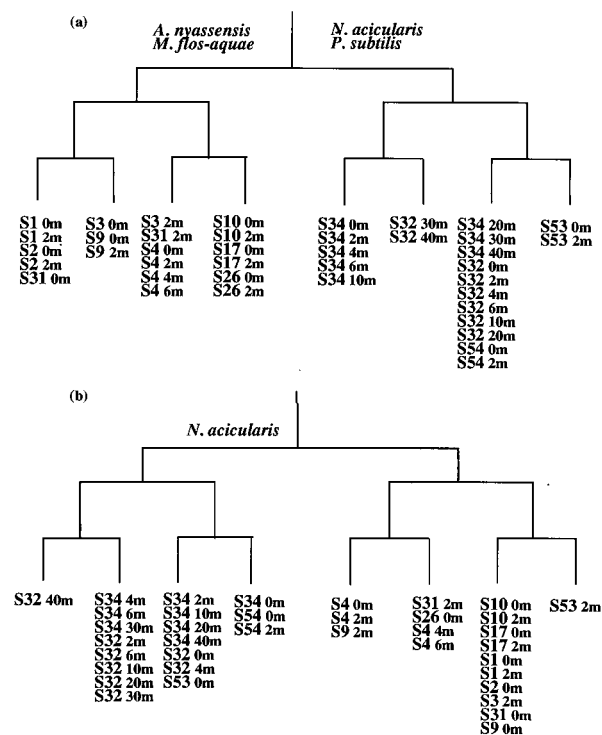


Fig. 2 Dendrogram showing the twinspan classification of samples from stations (numbers and depths) based on numerical abundance of phytoplankton species: (a) September 1994 (dry season); and (b) March 1995 (rainy season).

Table 1 Abbreviations and list of phytoplankton species recorded in September 1994 (dry season) and March 1995 (rainy season): (+) present; and (–) absent

Abbreviation	Species	Season	
		Dry	Rainy
<i>Cyanobacteria (Cyanophyceae)</i>			
Ana cir	<i>Anabaena circinalis</i> Rabh. ex Born. & Fl.	+	+
Ana flo	<i>A. flos-aquae</i> Bréb. ex Born. & Fl. var. <i>flos-aquae</i>	+	–
Ana spi	<i>A. spiroides</i> Klebahn	+	+
Ana spe	<i>Anabaena</i> sp.	+	+
Anp cir	<i>Anabaenopsis circularis</i> (G. S. West) Mill.	+	+
Anp tan	<i>A. tanganyikae</i> (G. S. West) Mill.	+	+
Aph del	<i>Aphanocapsa delicatissima</i> West & West	+	–
Aph ela	<i>A. elachista</i> West & West var. <i>elachista</i>	+	+
Apt mic	<i>Aphanothece microscopica</i> Näg.	+	+
Apt stag	<i>A. stagnina</i> (Spreng.) A. Br.	+	+
Chr lim	<i>Chroococcus limneticus</i> Lemm.	+	–
Chr min	<i>C. minutus</i> (Kütz.) Näg.	+	–
Chr mid	<i>C. minor</i> (Kütz.) Näg.	+	+
Chr 10	<i>C. tenax</i> (Kirchn.) Hieron.	+	+
Chr tur	<i>C. turgidus</i> (Kütz.) Näg. var. <i>turgidus</i>	+	+
Chr tum	<i>C. turgidus</i> Näg. var. <i>maximus</i> Nyg.	+	+
Coe kue	<i>Coelosphaerium kuetzingianum</i> Näg.	+	–
Coe pol	<i>C. pallidum</i> Lemm.	+	–
Gom apo	<i>Gomphosphaeria aponina</i> Kütz.	+	+
Lep lag	<i>Leptolyngbya lagerheimii</i> (Gom.) Anagn. & Komárek	+	+
Mer ele	<i>Merismopedia elegans</i> A. Br. ex Kütz. var. <i>elegans</i>	+	–
Mer gla	<i>M. glauca</i> (Ehr.) Näg.	+	+
Mer pun	<i>M. punctata</i> Meyen	+	+
Mer 10	<i>M. tenuissima</i> Lemm.	+	+
Mer spe	<i>Merismopedia</i> sp.	–	+
Mic aer	<i>Microcystis aeruginosa</i> (Kütz.) Kütz.	+	+
Mic flo	<i>M. flos-aquae</i> (Wittr.) Kirchn.	+	+
Mic rob	<i>M. robusta</i> (Clark) Nyg.	+	+
Mic vir	<i>M. viridis</i> (A. Br.) Lemm.	+	+
Mic wes	<i>M. wesenbergii</i> Kom.	+	+
Pla cir	<i>Planktolyngbya circumcreta</i> (G. S. West) Anagn. & Komárek	+	+
Pla con	<i>P. contorta</i> (Lemm.) Anagn. & Komárek	+	–
Pla nya	<i>P. nyassae</i> (Schmidle) Anagn. & Komárek	+	+
Pla sub	<i>P. subtilis</i> (W. West) Anagn. & Komárek	+	+
Spi lax	<i>Spirulina laxissima</i> G. S. West	+	+
<i>Chlorophyceae</i>			
Ank fal	<i>Ankistrodesmus falcatus</i> (Corda) Ralfs var. <i>falcatus</i>	+	+
Bot bra	<i>Botryococcus braunii</i> Kütz.	+	+
Cha spe	<i>Characium</i> sp.	+	–
Clo lon	<i>Closteriopsis longissima</i> (Lemm.) Lemm.	+	+
Coe ast	<i>Coelastrum astroideum</i> De-Not.	+	+
Coe mic	<i>C. microporum</i> Näg. var. <i>microporum</i>	+	+
Coe pro	<i>C. proboscideum</i> Bohl. in Wittr. & Nordst.	+	+
Cos lac	<i>Cosmarium lacunatum</i> G.S. West	–	+
Coe mon	<i>C. moniliforme</i> (Turp.) Ralfs	–	+
Cos spe	<i>Cosmarium</i> sp.	+	+
Dic sub	<i>Dictyosphaerium subsolitarium</i> Van Goor	+	+
Eud ele	<i>Eudorina elegans</i> Ehr.	+	–
Kir spe	<i>Kirchneriella</i> sp.	+	+
Lag cit	<i>Lagerheimia citrifomis</i> (Snow) Collins	+	+
Lag lon	<i>L. longiseta</i> (Lemm.) Wille	+	–
Ooc bor	<i>Oocystis borgei</i> Snow	+	–

Table 1 Continued

Abbreviation	Species	Season	
		Dry	Rainy
Ooc lac	<i>O. lacustris</i> Chod.	+	+
Ooc sol	<i>O. solitaria</i> Wittr.	+	+
Pan mor	<i>Pandorina morum</i> (O. F. Müll.) Bory	+	+
Ped dup	<i>Pediastrum duplex</i> Meyen var. <i>duplex</i>	+	+
Ped sim	<i>P. simplex</i> Meyen var. <i>simplex</i>	+	+
Scu acu	<i>Scenedesmus acuminatus</i> (Lagerh.) Chod.	+	+
Scu eco	<i>S. ecornis</i> (Ehr. ex Ralfs) Chod.	+	+
Scu obt	<i>S. obtusus</i> Meyen	-	+
Scu per	<i>S. perforatus</i> Lemm.	+	+
Scu qua	<i>S. quadricauda</i> (Turp.) Bréb. <i>sensu</i> Chod.	+	+
Scu spe	<i>Scenedesmus</i> sp.	-	+
Sid kol	<i>Siderocelis kolkwitzii</i> (Naum.) Fott	+	+
Sta ana	<i>Staurastrum anatinum</i> Cooke & Wills var. <i>anatinum</i>	+	+
Sta ans	<i>S. anatinum</i> Cooke & Wills var. <i>subglabrum</i> G.S. West	+	+
Sta gra	<i>S. gracile</i> Ralfs var. <i>nyansae</i> G.S. West	+	-
Sta mut	<i>S. muticum</i> Bréb. ex Ralfs	+	-
Sta uke	<i>S. ukerevense</i> Thom.	+	+
<i>Bacillariophyceae</i>			
Ach spe	<i>Achnanthes</i> sp.	+	+
Aul aga	<i>Aulacoseira agassizii</i> (Ostenf.) Sim.	+	+
Aul amb	<i>A. ambigua</i> (Grun.) Sim.	+	+
Aul gra	<i>A. granulata</i> (Ehr.) Sim. var. <i>granulata</i>	+	+
Aul nya	<i>A. nyassensis</i> (O. Müll.) var. <i>victoriae</i> O. Müll.	+	+
Coc pla	<i>Cocconeis placentula</i> Ehr. var. <i>placentula</i>	+	+
Cyc men	<i>Cyclotella meneghiniana</i> Kütz.	+	+
Cyc oce	<i>C. ocellata</i> Pantocsek	+	+
Cyc spe	<i>Cyclotella</i> sp.	+	+
Cym aff	<i>Cymbella affinis</i> Kütz.	+	+
Dia elo	<i>Diatoma elongatum</i> (Lyngb.) Ag.	+	+
Gom spe	<i>Gomphonema</i> sp.	-	+
Mas smi	<i>Mastogloia smithii</i> Thwaites	-	+
Nav obl	<i>Navicula oblonga</i> (Kütz.) Kütz.	+	+
Nav pup	<i>N. pupula</i> var. <i>pupula</i> Kütz.	+	+
Nav rhy	<i>N. rhynchocephala</i> Kütz.	-	+
Nav vul	<i>N. vulpina</i> Kütz.	+	+
Nit aci	<i>Nitzschia acicularis</i> (Kütz.) W. Smith var. <i>acicularis</i>	+	+
Nit acc	<i>N. acicularis</i> (Kütz.) W. Smith var. <i>closteroides</i> Grun.	+	+
Nit spi	<i>N. spiculoides</i> Hust.	+	-
Pin vir	<i>Pinnularia viridis</i> (Nitzsch) Ehr.	+	+
Rhi cur	<i>Rhizosolenia curvisetata</i> Hust.	+	+
Rhi lon	<i>R. longiseta</i> Zach.	+	+
Rhi vic	<i>R. victoriae</i> Schröder	-	+
Rho gib	<i>Rhopalodia gibberula</i> (Ehr.) O. Müll.	+	-
Ste ast	<i>Stephanodiscus astraea</i> (Ehr.) Grun. var. <i>astraea</i>	+	+
Sur ful	<i>Surirella fuellebornii</i> O. Müll. var. <i>elliptica</i> O. Müll.	+	+
Sur lin	<i>S. linearis</i> W. Smith var. <i>linearis</i>	+	-
Sur nya	<i>S. nyassae</i> O. Müll. var. <i>nyassae</i>	+	+
Sur spe	<i>Surirella</i> sp.	+	-
Syn cun	<i>Synedra cunningtonii</i> G.S. West.	+	+
Syn pul	<i>S. pulchella</i> Ralfs ex Kütz.	-	+
Syn uln	<i>S. ulna</i> (Nitz.) Ehr. var. <i>ulna</i>	+	+
Tab fen	<i>Tabellaria fenestrata</i> (Lyngb.) Kütz. var. <i>fenestrata</i>	+	+
<i>Dinophyceae</i>			
Cer bra	<i>Ceratium brachyceros</i> Dad.	+	-

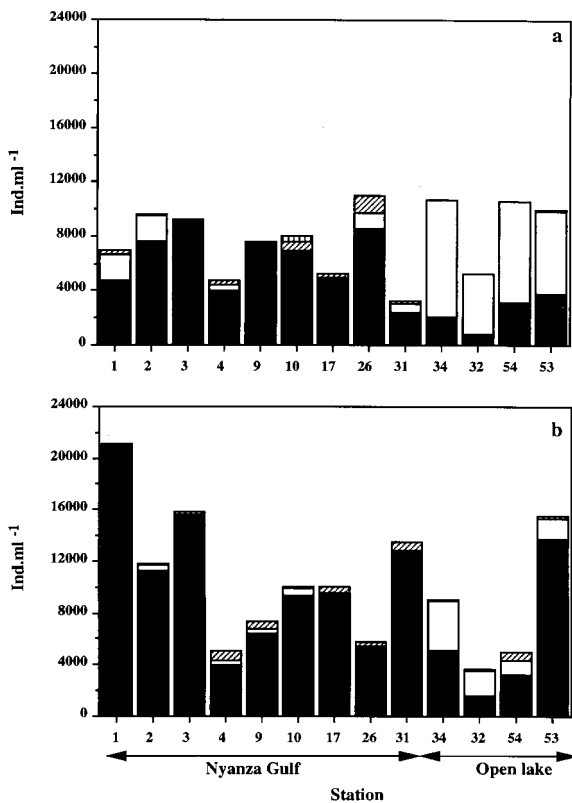


Fig. 3 Numerical abundance of phytoplankton in surface waters: (a) September 1994 (dry season); and (b) March 1995 (rainy season). Key: (dark-shaded areas) Cyanobacteria; (white areas) Bacillariophyceae; (obliquely hatched areas) Chlorophyceae; and (vertically hatched areas) Dinophyceae.

During the dry season, the total numerical abundance of phytoplankton cells showed no consistent differences between Nyanza Gulf stations and open lake stations, but cyanobacteria, with *Microcystis aeruginosa*, *Anabaena flos-aquae*, *A. circinalis*, *Microcystis flos-aquae*, *Anabaenopsis circularis* and *Chroococcus* spp. dominant, were prominent within the Gulf, while diatoms, with *Nitzschia acicularis* as the most important species, dominated in the open lake (Fig. 3a). The most abundant diatoms in the Nyanza Gulf included *Aulacoseira nyassensis*, which occurred in large numbers particularly at the mouths of the rivers Nyando and Sondu-Miriu. *Aulacoseira agassizii*, *Navicula* spp., *Synedra* spp., *Cocconeis placentula* and *Cyclotella* spp. also appeared in appreciable numbers in bays. Furthermore, blue-greens such as *Anabaena* spp., *Anabaenopsis tanganyikae*, *Planktolyngbya* spp., *Leptolyngbya lagerheimii* and *Spirulina laxissima* were also fairly abundant in the

offshore main lake. *Ceratium brachyceros*, the only dinoflagellate, occurred in a few shallow water stations within the Nyanza Gulf.

Cyanobacteria also contributed the largest number of species at most stations (Fig. 4a). Only in the Nyanza Gulf (stations 4, 10, 17, 26, and to some extent, 31) did diatoms and green algae contribute similar number of species as the cyanobacteria.

In the dry season, at the deep water stations 32 and 34, algae (particularly diatoms) were most abundant between 0 and 10 m depth, with a decline in the lower layers (Fig. 5a). The green alga (*Staurastrum anatinum*) was observed from 2 to 6 m depth at station 34 only. At station 34, the maximum abundance was observed at 4 m depth with *Nitzschia acicularis*, *Microcystis aeruginosa* and *Planktolyngbya subtilis* as the most important species. At station 32, the most important species were *N. acicularis*, *M. aeruginosa*, *P. subtilis* and *Spirulina laxissima*.

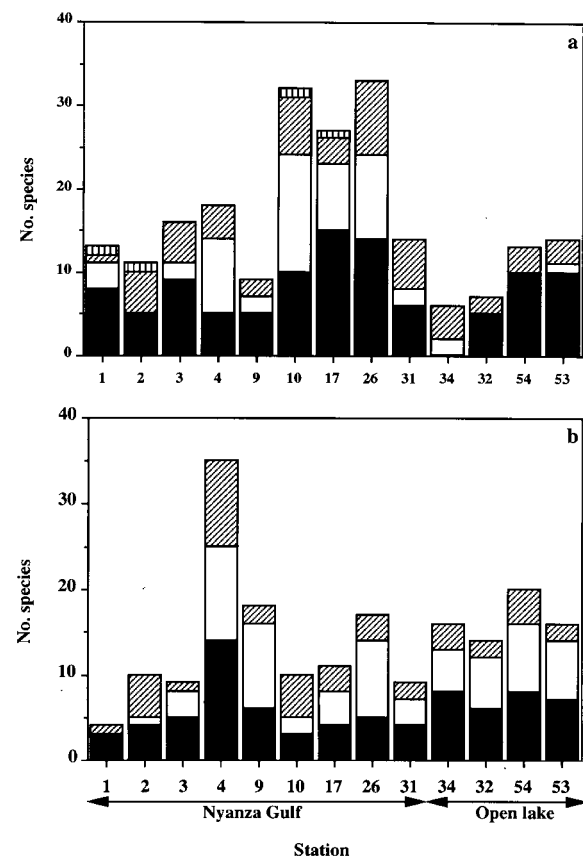


Fig. 4 Phytoplankton species composition in surface waters: (a) September 1994 (dry season); and (b) March 1995 (rainy season). For key, see the legend for Fig. 3.

Rainy season

During the rainy season, twinspan (Fig. 2b) produced essentially the same splitting of Nyanza Gulf stations (right hand cluster; no indicator species) and open lake stations (left hand cluster; indicator species *Nitzschia acicularis*) as during the dry season. An exception was station 53 (2 m depth) which now grouped with the Gulf stations (Fig. 2b). After the first separation, a number of sub-clusters were also

formed. For the Nyanza Gulf, western (numbers 4, 9 and 26) and eastern stations (numbers 1, 2, 3, 10 and 17) were separated, rather than the north-south split found during the dry season. In addition, station 9 (0 m depth) was a 'misfit' in the eastern cluster, and stations 31 (2 m depth) and 31 (0 m) occurred in the western and eastern clusters, respectively. In the open lake, no significant further specific sub-clustering were discerned, indicating a higher homogeneity of the populations than during the dry season.

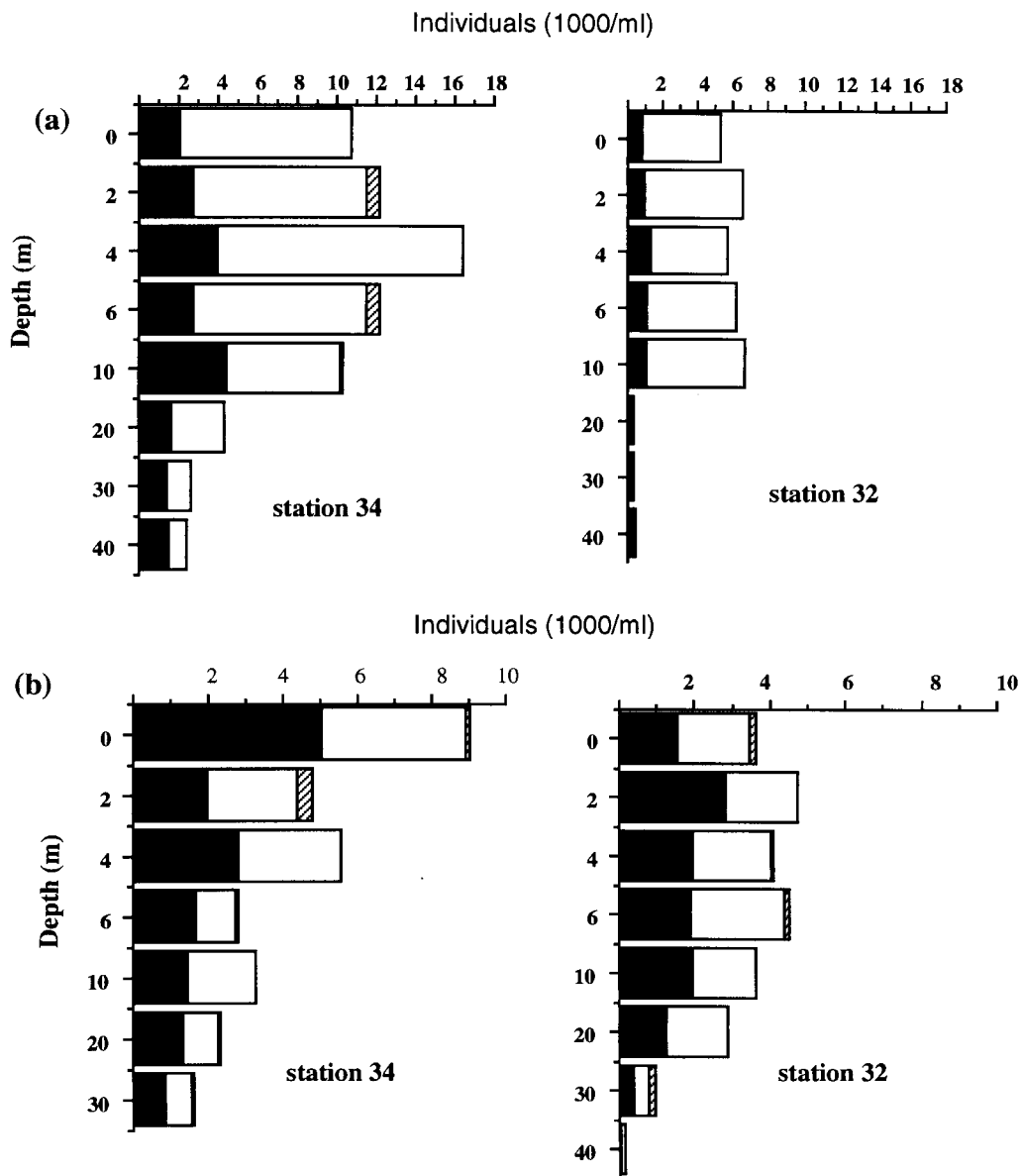


Fig. 5 Vertical distribution of phytoplankton abundance in station numbers 34 and 32: (a) September 1994 (dry season); and (b) March 1995 (rainy season). For key, see the legend for Fig. 3.

Table 2 Eigenvalues for the first canonical axis, species–environmental factors correlation and *P*-values from the canonical correspondence analysis for phytoplankton species in September 1994 (dry season) and March 1995 (rainy season)

Variable	Season	
	Dry	Rainy
Eigenvalue for axis 1	0.60	0.61
Cumulative percentage variance of species–environment correlation	78	77
<i>P</i> -value:		
Turbidity	0.04	0.39
Temperature	0.64	0.49
PO ₄ -P	0.68	0.47
SiO ₂	0.42	0.01
NO ₃ -N	0.52	0.47

Phytoplankton abundance was dominated by cyanobacteria both in Nyanza Gulf and in the open lake, except at stations 32 and 34. Nevertheless, at the latter points, diatoms and green algae were more abundant than in the Nyanza Gulf (Fig. 3b). The dinoflagellate *C. brachyceros* was not found in the rainy season.

In the rainy season, the relative importance of cyanobacteria in the deep water stations increased to equal that of diatoms (Fig. 5b). At station 34, higher phytoplankton abundance was observed between the surface and 4 m depth. The maximum abundance occurred at the surface, *N. acicularis*, *M. aeruginosa*, *P. subtilis*, *Anabaenopsis tanganyikae* and *S. laxissima* being the most important species. At station 32, a more or less even distribution of the phytoplankton abundance was observed from the surface to 20 m, with *N. acicularis*, *M. aeruginosa*, *Planktolyngbya nyassae* and *Anabaenopsis tanganyikae* as the most important species.

Relationships of phytoplankton to environmental factors

The results of the CCA analysis basically confirmed the grouping of stations as shown by twinspan (Table 2). Monte Carlo permutations (ninety-nine unrestricted permutations) showed that only one environmental factor was significantly correlated with phytoplankton species distribution in each season: turbidity in the dry season and SiO₂ in the rainy season. The variations of these two factors are shown in Fig. 6a,b and will be commented upon in the 'Discussion' below.

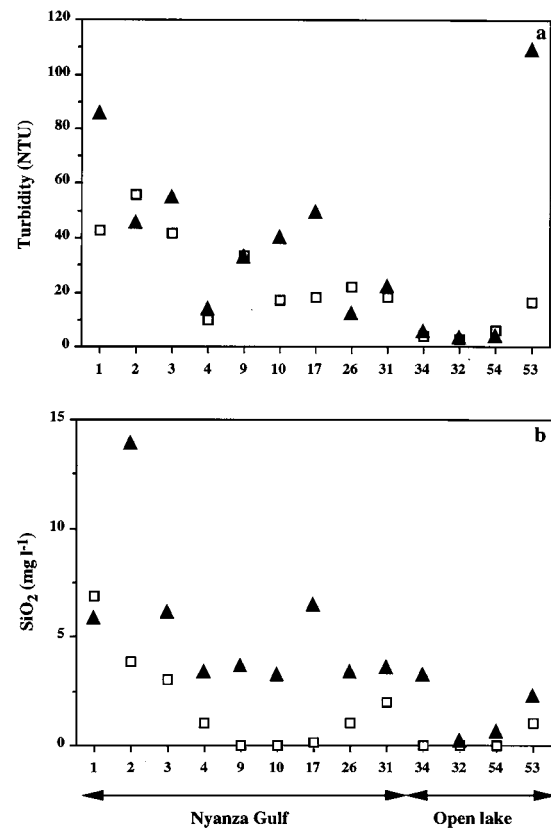


Fig. 6 (a) Turbidity and (b) SiO₂ in surface waters: (o) dry season; and (s) rainy season.

Chlorophyll *a* concentrations

During the dry season, chlorophyll *a* concentration was higher in the Nyanza Gulf than in the open lake (Mann Whitney *U*-test, *P* < 0.05) (Fig. 7). Generally, relatively higher values were found in bays within the Gulf and mouths of rivers. When all depths sampled are considered, the concentrations ranged from 9.3 to 71.5 mg m⁻³ in the Gulf (the latter value at the bottom of station 2 near the Sondu-Miriu mouth). In the open lake, the concentration ranged from 2.0 to 21 mg m⁻³ (except for the shallow station 53 near the Nzoia River mouth, with a value of 30.2 mg m⁻³).

An overall decrease in the concentration of chlorophyll *a* occurred during the rainy season, with values ranging from 8.8 to 17.2 mg m⁻³ in the Nyanza Gulf and from 2.0 to 13 mg m⁻³ in the open lake (at station 34, a maximum of 12 mg m⁻³ was observed at 6 m depth, and at station 32, a maximum of 13 mg m⁻³ at 4 m depth).

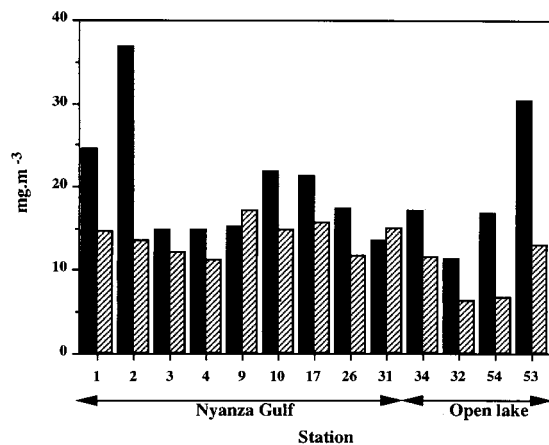


Fig. 7 Concentration of chlorophyll *a* in surface waters: (dark-shaded) September 1994 (dry season); and (obliquely hatched) March 1995 (rainy season).

Discussion

The analysis of phytoplankton samples from the Kenyan waters of Lake Victoria taken in September 1994 and March 1995 reveals some similarities and some differences with the situation observed prior to and during the 1960s.

A first similarity is the occurrence of most of the important species already reported in the literature (e.g. West, 1907; Ostefeld, 1908; Woloszynska, 1914; Bachmann, 1933; Thomasson, 1955; particularly Talling, 1966, 1987). These include the very small-sized *Aphanocapsa* spp., *Microcystis flos-aquae* and *M. wesenbergii*, *Planktolyngbya* spp., *Anabaena flos-aquae*, *Anabaenopsis tanganyikae*, *Aulacoseira agassizii*, *A. ambigua* and *A. nyassensis*, *Stephanodiscus astraera*, *Rhizosolenia victoriae*, *Nitzschia acicularis*, *Pediastrum duplex* and *P. simplex*, and *Ceratium brachyceros*.

Another fact, which is repeatedly mentioned and illustrated by Talling (1987; Fig. 6), is the distinction between inshore (bays and gulfs) and offshore (open lake) waters. This distinction appears as the first separation in our twinspan analysis both in the dry and the rainy seasons (Fig. 2a,b).

Although we analysed only samples taken in September and March, we observed a clear seasonal difference in the numerical abundance of the important phytoplankton species, as already emphasized by Talling (1966, 1987) from his counts made month by month in 1960–1961. Talling (1966) reported that diatoms were most abundant in the offshore open

lake during periods of isothermal mixing of the water column. *Surirella nyassae*, *Nitzschia acicularis*, *Aulacoseira nyassensis* and *A. agassizii* were the most important diatom species. Cyanobacteria dominated during periods of thermal stratification with *Anabaena flos-aquae*, *Anabaenopsis tanganyikae*, *Planktolyngbya circumcreta* and *Microcystis wesenbergii* as the most abundant. The green algae were present in low numbers throughout the year. The dinoflagellate *Ceratium brachyceros* also occurred in small numbers.

Although the data treated here did not allow us to describe the dynamics of the phytoplankton on a complete annual cycle, several conclusions may reasonably be drawn from the comparison of samples taken at two contrasted seasons from thirteen stations, both in- and offshore, in the Nyanza Gulf and the open lake. The phytoplankton of the Nyanza Gulf was numerically dominated by cyanobacteria followed by the diatoms, green algae and the flagellates, in that order, both during the dry and rainy seasons.

The north–south split between the Gulf stations observed in the dry season seemed to be the result of a higher number of species in the northern stations (numbers 10, 17 and 26) rather than differences in numerical abundance of the different groups. The unexpected position of our samples from station 3 (2 m) and 31 (0 m) could be caused by diel water currents. In the open lake, diatoms were dominant during the dry season, followed by blue-greens and green algae, whereas no dinoflagellates were observed. Station 34 deep waters and station 32 upper layers occurred in the same sub-cluster as a result of having a similar number of species rather than differences in total numerical abundance.

During the rainy season, twinspan produced the same separation between the open lake stations as in the dry season, but within the Gulf, the stations were separated in a west–east split rather than a north–south one. Again, the main contributing factor to this separation seemed to be a difference in number of species rather than a difference in total numerical abundance or group contribution (Figs 2b & 4b). The ‘western’ stations (4, 9, 26) had more species than the ‘eastern’ stations, and thus, their species richness was comparable to the species richness observed in the open lake stations during the dry season.

In the rainy season, there was a strong increase in the cyanobacteria and a decrease in the diatoms, both in the number of individuals and in the percentage

composition, at the deep stations of the open lake. This made the latter less different from the Nyanza Gulf than during the dry season. Also, the phytoplankton of station 53, which is shallow and situated near the mouth of the river Nzoia, had abundant cyanobacteria ($\approx 14\,000$ individuals mL^{-1}) which were dominant (about 90%) and resembled those of similar Gulf stations (numbers 1, 2, 3 and 10) to which it was grouped by twinspan until the second level (Fig. 2b). This may be attributed to the similarity of these stations, which are shallow, in a coastal location, and have an increased river flow causing turbulence and high turbidity in the rainy season (110 NTU at station 53).

The CCA showed that turbidity was the only environmental factor which was significantly correlated with phytoplankton species distribution during the dry season. As might be expected, most shallow and coastal stations had a higher turbidity than more offshore and deeper stations (Fig. 6). The turbidity was also higher in the rainy season than in the dry season, a consequence of higher run-off, turbulence and resuspension of sediment. At the southern coastal stations of the Nyanza Gulf (numbers 1, 2, 3 and 9), turbidity reached values above 25 NTUs. In the rainy season, turbidity at the north-eastern coastal stations of the Gulf (numbers 10 and 17) was higher than in the dry season, making the light conditions at these stations more comparable to that of the south-eastern stations (numbers 1, 2 and 3) than during the dry season. This is reflected in separated twinspan sub-clusters of phytoplankton composition in the dry season and their grouping in the rainy season. As might be expected, at deep water stations 32 and 34, surface turbidity was found low in both seasons. The species shown by CCA to be most positively correlated with turbidity included *Ankistrodesmus falcatius*, *Cyclotella ocellata* and *Aulacoseira nyassensis*. In particular, we found large numbers of *A. nyassensis* in the turbid waters at the mouths of the rivers Nyando and Sondu-Miriu, and the species appeared in the twinspan analysis as an indicator for the Nyanza Gulf in dry season. Kilham *et al.* (1986) showed that this large-pored species definitely has low light requirements, but it is possible that it could have benefited from other factors, mainly nutrients like Si and $\text{NO}_3\text{-N}$, which covaried with turbidity or could have been brought to the surface by turbulence in shallow water.

Canonical correspondence analysis showed that SiO_2 was the only factor significantly correlated with species distribution during the rainy season, and covaried with temperature and turbidity, but not with $\text{NO}_3\text{-N}$ concentration. During the rainy season, the concentration of SiO_2 was higher in most of the Nyanza Gulf stations than in the open lake. Within the Gulf, the highest concentration was measured at stations 1, 2, 3 and 17, all situated on the eastern side of the Gulf. Other 'eastern' stations (numbers 9 and 10) had similar SiO_2 concentrations to 'western' stations 4, 31 and 26. Canonical correspondence analysis showed that eight diatom species, among which *Synedra ulna*, *Aulacoseira ambigua*, *Diatoma elongatum* and *Rhizosolenia curvisepta*, were positively correlated with SiO_2 concentrations. On the other hand, *Nitzschia acicularis* and *Stephanodiscus astraea* showed negative correlation to SiO_2 . This agrees with Kilham *et al.* (1986), who ranked these two species among those with, respectively, moderate and low Si requirements.

In the rainy season, $\text{NO}_3\text{-N}$ concentration had increased by a factor of ten in comparison to the dry season values, reaching values of over $100\ \mu\text{g L}^{-1}$ at most stations within the Gulf and open lake. While this increase is remarkable, values ranging from 10 to $112\ \mu\text{g L}^{-1}$ have previously been reported from an offshore station (Talling, 1966). Two main trends distinguish the recent situation from that before or during the 1960s: a more marked dominance by cyanobacteria and a higher mean concentration of chlorophyll *a*. In the Nyanza Gulf, a high density of *Microcystis aeruginosa* was observed both in September (up to 8100 colonies mL^{-1}) and in March (up to $20\,893$ colonies mL^{-1}). In the open lake, large numbers of *Anabaena*, *Anabaenopsis*, *Planktolyngbya* and *Spirulina laxissima* were observed in both the two months. High densities of the most abundant diatom *Nitzschia acicularis* was also observed in the open lake in both September (up to $12\,200$ cells mL^{-1}) and March (up to 3731 cells mL^{-1}); such numbers are much higher than those observed by Talling (1957b, 1966).

We found that the concentrations of chlorophyll *a* in the main lake ranged from 2 to $21\ \text{mg m}^{-3}$ during the dry season and from 2 to $13\ \text{mg m}^{-3}$ during the rainy season. In the Nyanza Gulf, it ranged from 9.3 to $71.5\ \text{mg m}^{-3}$ during the dry season and from 8.8 to $17.2\ \text{mg m}^{-3}$ during the rainy season. High values

were also observed in the recent past by Ochumba & Kibaara (1989) in Kenyan waters of the main lake (8–77.6 mg m⁻³) as well as by Mugidde (1993) in Ugandan waters (8.4–40 mg m⁻³ offshore and 22.2–67.1 mg m⁻³ in Pilkington Bay). Thus, we can confirm the general increase in chlorophyll *a* concentration observed in the lake since 1960–1961, a period in which values of 1.2–5.5 mg m⁻³ at offshore stations and about 20 mg m⁻³ in the Nyanza Gulf were recorded by Talling (1965, 1966).

Besides the major phytoplankton groups reported in this study, picoplankton organisms were numerous in Lake Victoria, particularly during the dry season and could also have contributed to the higher chlorophyll *a* concentrations. Similar observations were made by Talling (1966, 1987), who reported the occurrence of large numbers of coccoid blue-greens in the offshore waters of the lake in 1960–1961.

In addition to a general increase in phytoplankton biomass, our observations confirm the increasing importance of cyanobacteria in Lake Victoria, also reported by Ochumba & Kibaara (1989), Hecky & Bugenyi (1992) and Hecky (1993). Species like *Microcystis aeruginosa* and *Anabaena flos-aquae* have the ability to form scums or blooms on the surface of water because of their well-known buoyancy. Paerl *et al.* (1983) also report that such cyanobacteria have large amounts of carotenoids, which serve as accessory pigments in photosynthesis and provide protection to chlorophyll from photooxidation. Thus, these species are adapted to areas with high illumination and can attain high photosynthetic efficiencies. These factors, in addition to high temperatures and nutrient concentrations in Lake Victoria, give these two and other similar species a competitive advantage, and it is likely that these organisms will continue to dominate.

The overall effect of the cyanobacteria on the ecology of Lake Victoria is complex. Several species, mainly the bloom-forming *Anabaena* spp., contribute positively to the nutrient balance via nitrogen fixation. In samples taken in the Nyanza Gulf in 1989–1990, Gophen *et al.* (1995) also mentioned significant numbers of filaments of *Cylindrospermopsis*, another N-fixing genus. Some species, such as *Microcystis aeruginosa*, *M. wesenbergii* and *Anabaena flos-aquae*, produce toxins against zooplankton (Gilbert, 1994; Vasconcelos, 1994). The relatively large colonies and biomass of these species may not be effectively

utilized by zooplankton and other aquatic organisms, thereby affecting their recruitment. In grazing experiments on water samples from Lake Victoria, Lehman & Branstrator (1993) observed no significant effect of crustacean zooplankton abundance on phytoplankton biomass. The influence of grazing by microzooplankton and mesozooplankton on the present-day phytoplankton of the lake is insufficiently known and should be further investigated. An atyid prawn, *Caridina nilotica* (P. Roux), seems to play an increasing role as a phytoplanktivore, while the absence of large populations of phytoplanktivorous fish (Witte *et al.*, 1992) could contribute to the increases in overall algal biomass in Lake Victoria. Although planktonic blue-greens may be digested by fish, their mass occurrence may also be associated with fish kills. This was mentioned for Lake Victoria by Ochumba (1987, 1990), and recently, in a Brazilian lagoon by Azevedo & Carmouze (1994).

As previously mentioned, we observed substantial numbers of *Aulacoseira nyassensis* only at stations 1, 2 and 53, i.e. in the vicinity of river mouths. Other *Aulacoseira* spp. (i.e. *A. agassizii*, *A. ambigua* and *A. granulata*) were relatively scarce in the Nyanza Gulf. *Aulacoseira agassizii* was absent from deep water samples, contrary to observations made by Talling (1957b, 1966) in the 1950s and in 1960–1961, when this species dominated in the lower layers of the open lake. When compared with values of *Aulacoseira* mentioned by Talling (1957b, 1966), we see now that the numerically most important diatom in the open lake is *Nitzschia acicularis*.

The increased chlorophyll *a* concentration and higher abundance of the buoyant cyanobacteria have resulted in a decrease in transparency. While values of transparency were clearly lower than those measured in 1927, i.e. 7.3–7.9 m for offshore stations and 1.3–1.45 m in the Nyanza Gulf (Worthington, 1930), we observed an average transparency in the stations of the open lake an average transparency in the dry season of 1.1 m (chlorophyll *a* concentration = 11.4 mg m⁻¹), and in the rainy season, 1.38 m (chlorophyll *a* concentration = 6.3 mg m⁻³). In the Nyanza Gulf, the average transparency in the dry season was 0.68 m, the highest value being observed at station 4 (chlorophyll *a* = 14.8 mg m⁻³); the average in the rainy season was 0.58 m, with the highest value (1 m) also at station 4 (chlorophyll *a* = 11.2 mg m⁻³). In the 1990s, Mugidde (1993) and Gophen *et al.* (1995)

also recorded values of 1.3–3 m offshore near Bugaia Island in Uganda and 1.8 m offshore in the Kenyan waters of the lake, respectively, whereas Ochumba & Kibaara (1989) recorded a value of 0.2 m during an algal bloom offshore in the Kenyan waters.

Our results confirm the eutrophication of Lake Victoria which had already been initiated in the 1920s (Bootsma & Hecky, 1993; Hecky, 1993). Its apparent acceleration may be attributed to the rapidly increasing human population around the lake, and to the intensification of agriculture and industry in its catchment.

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