PHYTOPLANKTON AND NUTRIENTS STUDIES IN MAGU BAY, SPEKE GULF, LAKE VICTORIA, (TANZANIA) FOLLOWING THE 2001 PRINCIPAL RAIN SEASON

JF Machiwa¹, C Lugomela¹ & ANN Muzuka.²

¹Faculty of Aquatic Sciences and Technology, University of Dar es Salaam,
P.O. Box 35064 Dar es Salaam, Tanzania.

²Institute of Marine Sciences, University of Dar es Salaam,
P.O. Box 668 Zanzibar, Tanzania.

Accepted 27 January 2004

ABSTRACT

Phytoplankton abundance and species composition in relation to some physico-chemical parameters were studied in Magu Bay, Lake Victoria, in May 2001. Investigations on the influence of Simiyu River on the biological and physical characteristics of the Bay were carried out. Surface and bottom currents flowed in the northeast direction close to the river mouth but were completely reversed after about 1.5 km from the river mouth. Most suspended particles brought in by the river were deposited within 0.5 km after entering the lake. Nutrient concentrations were generally high towards the eastern part of the bay as compared to the rest of the bay area probably due to the reversal in the direction of current flow. Phytoplankton were generally dominated by the cyanobacteria Microcystis and Anabaena species though the diatoms Nitzschia and Melosira species were more abundant in some sampling stations. Phytoplankton abundance ranged from 500 cells ml¹ at stations LV36 and LV37 to 1440000 cells ml¹ at station LV1. The high abundance encountered at stations LV1, LV2, and LV3 is assumed to be due to formation of surface scum of the gas vacuolated Microcystis cells as a result of wind action. Phytoplankton production was possibly light limited in areas with simultaneously high nutrient concentrations and high turbidity. More data are required to corroborate the current study and to have a full picture of the influence of the river during different seasons.

INTRODUCTION

Lake Victoria is believed to have evolved about one million years ago and may have experienced desiccation several times with the last one being around 12 ka ago (Johnson et al. 1996). Drainage occurs via an outlet for the Nile River at the northern end of the lake, but also as much as 90% of the water loss from the basin is removed by evapo-transpiration (Kendall 1969). Thus, the hydrology of the lake is strongly dominated by the ratio of precipitation to evaporation over the lakes surface. The lake is considered to be eutrophic with productivity being higher inshore than in the offshore waters (Talling 1966).

It has been reported that the lake is generally facing environmental problems with some of the endemic vertebrate faunas such as haplochromine cichlid species facing extinction (Witte et al. 1992). The introduced Nile perch decimated endemic fish populations; thermal stratification has grown more persistent while N:P ratios and silica concentrations decreased; the overall diatom abundance declined, and *Nitzschia* spp. and cyanobacteria replaced *Aulacoseira* spp. in the plankton (Ochumba and Kiabara 1989; Hecky 1993). Seasonal changes of phytoplankton have been reported for Lake Victoria with cyanophytes

like Anabaenopsis tanganyikae and Anabaena flos-aquae dominating the epilimnion during stratified periods, while diatoms species like Melosira nvassensis var. victoriae. Nitzschia spp. Stephanodiscus spp., Surirella spp. replace most other forms of algae in the water column during wind driven mixing in July-August, January and March (Talling 1966; 1987). Also, the phytoplankton biomass and productivity has increased dramatically compared to how it was in 1960's leading to a two-fold decline in water transparency (Hecky 1993, Mugidde 1993). The rapid population growth and its associated primitive subsistence agriculture, intense animal husbandry occupancy of the riparian shorelines for access to fish and water, eutrophication, over-fishing, and technological development have been mentioned to be among the factors that led to the observed environmental degradation with impact to Lake Victoria (Hecky 1993).

The purpose of the present study was to investigate the influence of Simiyu River on physicochemical characteristics of Lake Victoria and their consequence on the phytoplankton abundance and composition.

MATERIALS AND METHODS Study area

Speke Gulf is the second largest gulf of Lake Victoria, located on the southeastern part of the lake and has a surface area of approximately 2425 km². Magu Bay (Fig. 1) is located in Speke Gulf, with a surface area of approximately 80 km² and it is one of the most lucrative fishing grounds in the Tanzanian waters of the lake. Magu Bay is renowned for its fishery of *Lates niloticus* and *Oreochromis niloticus*. Most of the species that have disappeared in the lake, e.g. *Labeo victoriamus*, *Schilbe intermedius* etc. are still found in Magu Bay though in small numbers Benno (2003). Magu Bay is shallow

with depth ranging between 0.5 m (in areas very close to shore) and 15 m (approx. 15 km from Simiyu River mouth). In the shallow area close to the shore, most of the lake bottom is soft, laden with detritus and large quantities of dead mollusk shells. At the mouth of the river and all along the river stretch the bottom is typically muddy or silty. Sandy areas appear at some points only occasionally. Most of the shoreline along the bay and particularly at Simiyu river mouth, is fringed by dense reeds/sedges, especially *Cyperus papyrus* although *Pistia niloticus*, *Phragmites*, *Vossia* and *Typha* species and the water hyacinth (*Eichhornia crassipes*) are common in some areas of the bay.

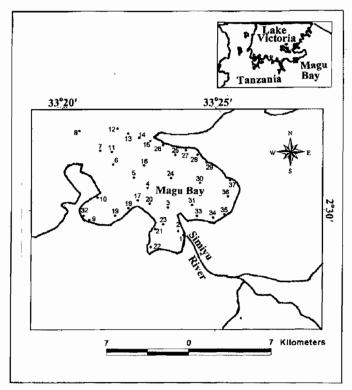


Figure 1: Map of Magu bay showing sampling stations

Physico-chemical parameters

The study was conducted from 8-12 May 2001 in Magu Bay, following the principal rain season in the area. During the sampling period, River Simiyu, a seasonal river that dries out during the dry season, was still vigorously discharging into the bay. Samples were collected onboard an eight-meter long wooden boat fitted with an

outboard engine. A total of 37 sampling stations were covered (Fig. 1). Depth was measured using a potable echo sounder. Water temperature was determined by using a self-recording current meter; model 9 (Aanderaa Instruments, Norway) attached with a temperature sensor. Suspended sediments (SS) were determined by filtering water through GF/C filters.

Water samples for nutrient analysis were collected using a one-liter sampling bottle; filtered onboard using Whatman GF/C filters. Filtered samples were placed in an icebox while on transit and stored frozen in the laboratory until they were analysed within two weeks. nutrient fluxes were determined Benthic following the chamber method described by Johnstone et al. (1988), Johnstone and Olafsson (1995) and Mohammed and Mgaya (2001). Water samples from chambers were collected at intervals of 1 h and 30 min. However, due to limited visibility in Magu Bay during the sampling period sampling using benthic chambers was conducted at only two shallow water stations, i.e. station LV9 & LV32.

Analysis of nutrients (nitrate, ammonia, reactive phosphate and soluble rective silica) was basically in accordance with standard methods, APHA (1992). Where necessary, the analytical protocol was checked against suggested protocol by Crul et al. (1993). UV-Vis Spectrophotometer (Shimadzu UV-1601) was used to measure absorbance.

Phytoplankton identification

Samples were collected by towing 20 _m-mesh size plankton net at a low speed for about 5 minutes. Collected samples were immediately fixed using 2% formaldehyde and stored in plastic bottles. Samples were observed using a light microscope and identification was done according to Prescott (1964). A checklist given by Cocquyt et al. (1993) was also consulted.

Benthic microalgae identification

Sediment samples for benthic microalgae identification were collected using a box corer. After retrieval, the top 1 cm sediment layer was collected by using a 2 cm diameter corer and stored in plastic vials. The collected sediment samples were preserved using 2% formaldehyde in plastic vials. In the laboratory the samples were analyzed using a light microscope and identification was performed as described above.

Phytoplankton biomass

At each station, a sampler was used to collect water at the surface and mid depth. Samples were stored in 50 ml glass vials containing 0.5 ml of Lugol's solution. Phytoplankton cells were counted using a Sedgewick-Rafter cell (Woelkerling et al. 1976) instead of Utermöhl method (Utermöhl 1931) because of high-suspended particles.

Student's t-test was used to check differences in phytoplankton abundance in surface and midwater depth water samples. Pearson correlation was performed between phytoplankton abundance and some physico-chemical variables.

RESULTS

Physico-chemical parameters

The depth at the various stations ranged from 0.8 to 15.0 m with the minimum depth recorded at station 2 and the maximum depth at station 8. Surface water temperature ranged from 26 °C (Station LV23) to 28 °C (station LV2) while bottom water temperature ranged from 24 °C to 26 °C (Fig. 2). The concentration of SS was as high as 1573 mg/l at the river mouth, progressively decreasing along the plume axis, at a distance of 0.5 km from the river mouth towards offshore the concentration of SS was 533 mg/l (Fig. 2).

Nutrient concentrations (Fig. 3) did not show any clear pattern of variability between stations though there was a general tendency of increasing nutrient concentration towards the eastern side of the bay (i.e. stations LV31, LV35, LV36 & LV37). Nitrate concentration ranged from 2.3 (station LV4) to 38.6 µg NO₃-N/1 (station LV31). Soluble reactive phosphate ranged from 41.5 (station LV5 and LV22) to 335.5 µg PO₄ -P/l (station LV36) while ammonia ranged from 22.5 (station LV15) to 121.4 μg NH₄-N/I (station LV37) and Si ranged from 59.1 (station LV5) to 596.2 µg-at Si/l (station LV29). The results of benthic nutrient fluxes revealed that nitrate/nitrite and ammonia had upward fluxes of 12.8 μ g NO₃-N Γ^{1} h⁻¹ and 6.0 μ g NH₄⁺-N Γ^{1} h⁻¹, respectively while soluble reactive Phosphorus and Silica did not show any net change with time.

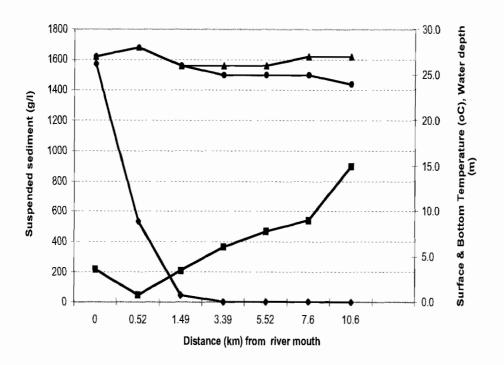


Figure 2: Variations of the concentration of suspended particles (diamonds), surface water temperature (triangles), bottom water temperature (cycles) and water depths (squares) with distance from the river mouth.

Phytoplankton species composition and abundance

A total of 39 phytoplankton species were identified from the 23 different stations sampled for plankton analysis in Magu Bay. Cyanobacteria were most common, comprising 31% of all the species identified followed by Bacillariophyceae, 23%, Chlorophyceae, 23%, Dinophyceae, 15%, Chrysophyceae, 5%, and Euglenophyceae, 3% (Fig. 4). Table 1 shows a list of species identified at the sampled stations.

Sixteen genera were identified from sediments out of which fifteen were diatoms, while only one genus was a cyanobacterium. Most of the identified from sediments were pinnate These were Amphiprora diatoms. *Amphipleura* **Amphiprora** sp., sp., Anomoeoneis sp., Bacillaria sp., Cymbella sp., Diatomella sp., Navicula sp., Pinuralia sp., Stauroneis sp. and Surirella sp. Centric diatoms were Coscinodiscus sp., Melosira sp. and Rhizosolenia cylindrus. Schizothrix sp. was the only cyanobacteria encountered in sediment samples.

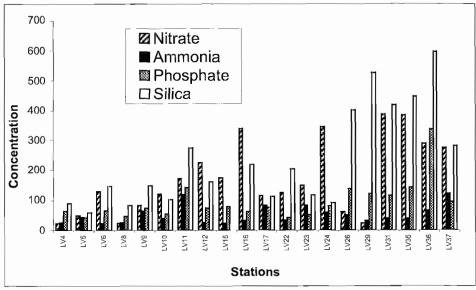


Figure 3: Concentrations of nitrate-N (x 10⁻¹ μg/l), ammonia-N (μg/l), phosphate-P (μg/l) and silica (μg-at Si/l) in Magu Bay during the sampling period

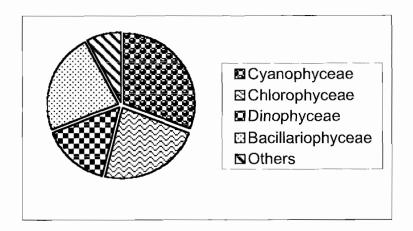


Figure 4: Percentage number of phytoplankton species identified in Magu Bay during the sampling period

Table 1: List of phytoplankton species identified from various stations in Magu bay during the study period

Species	Stations 1 2 3 4 5 6 8 9 10 11 12 15 16 17 23 24 26 29 31 35 36																					
	1	2	3	4	5	6	8	9	10	11	12	15	16	17	23	24	26	29	31	35	36	37
Cyanobacteria																						
Anabaena spiroides var. crassa Lemm.		\mathbf{x}	\mathbf{x}	\mathbf{x}	x	X	X	x	X	x	x	x	\mathbf{x}	X	x	X	x	\mathbf{x}	X	x		
Anabaena sp.				x	X		X								X							
Anabaenopsis elenkinni Miller			Х		\mathbf{x}	X																
Aphanocapsa sp.						X	X		X	X			X	х	X	X	X	x	X			
Chroococcus sp.							X							X	X			x				
Coelosphaerium kuetzingianum Näg.															\mathbf{x}		X					
Gloeocapsa sp.																						X
Merismopedia elegans var. major G.M. Smith						Х							x	х				х				
Merismopedia glauca (Ehr.) Näg.				X																		
Microcystis aeruginosa (Kutz) Elenkin Microcystis flos-aquae (Wittr.) Kirch.	X	X	x	X	X	x	X	X		x	X	X	x	X	X	X	X	X	X	x	X	X
Nostoc sp.				x																х		
Chlorophyceae				Λ																Λ		
Ankistrodesmus braunii (Näg.) Brunn										x		х							х	x	x	
Ankistrodesmus convolutus Corda										1		"							Α.	x	**	
Ankistrodesmus falcatus (Corda) Ralfs							x													25		
Draparnaldia sp.	x																					
Golenkinnia radiata (Chod.) Wille																		x		x		
Kirchneriella lunalis (Kirch.) Moebius																				x		
Pectyodctiyon cubicum Taft	х																					
Pediastrum biradiatum vax. emarginatum								х														
Scenedesmus quadricaudata (Turp.) Breb					х																	
Euglenophyceae																						
Phacus curvicauda Swir.													X									
Chrysophyceae																						
Merimgosphaera spinosa Presc.																				X		
Phyllosiphon arisari Kuhn.	X					\mathbf{x}									X			\mathbf{x}				X
Dinophyceae																						
Amphidinium sp.						X							X									
Exuviella sp.	X		х											\mathbf{x}								
Glenodinium kulezynski (Wolsz.)										\mathbf{x}												
Gonyaulax sp.							X	X					X			X						
Gymnodinium palustre Schilling			X		X					X		x	x		X	X			X	х		
Gymnodinium fuscum (Ehr.) Stein Bacillariophyceae					X																	
Amphipleura sp.											x											
Attheya zachariasi Brun.									x							x						
Bacillaria paradoxa Gmel		X	х		x	x	x	х		х	х	x	x	x		x	x		х			х
Coscinodiscus sp.		x				x			x					х								
Melosira sp.		x	х		x	x	х	x	x	x	x	x	x	X	x	x	x	x	х	x	x	X
Navicula sp.		x	x	x	x	x	X	x	x	x	x	x	x	x	х	x	x	x	x	x		Х
Rhizosolenia ariensis H.L. Smith								x	x	X						x	x					
Rhizosolenia cylindrus									\mathbf{x}	x	x	\mathbf{x}	\mathbf{x}		x		\mathbf{x}		x	x		x
Stauroneis parvula var. Prominula Grun.																x						

Phytoplankton abundance was high stations LV1, LV2, & LV3, reaching cell concentrations of 14,200,000; 636,000 and 210,000 cell ml⁻¹, respectively, as opposed to the rest of the stations where cell densities did not exceed 15.000 cells ml⁻¹. Apart from stations LV1, LV2 and LV3 phytoplankton abundance increased towards the open waters. Student's t-test showed no significant difference (p 1.0)phytoplankton concentration between surface and at mid-depth water samples. At stations LV1, LV2 & LV3 the phytoplankton abundance was dominated by the unicellular colony forming cyanobacteriun of the Genus Microcystis. The eastern part of the bay had lowest phytoplankton abundance, but it generally tended to increase towards the open waters. A strong positive correlation observed between phytoplankton abundance and turbidity (r = 0.98, n = 8). However, there was a weak correlation between phytoplankton biomass and the concentration of nitrate, ammonia, reactive phosphate and silicate, r = -0.11, n = 20; r = - 0.20, n = 19; r = - 0.31, n = 20 and r =- 0.45, n = 20, respectively.

DISCUSSION

It appears that the high concentrations of nutrients towards the eastern part of the bay is a result of the reversal in the direction of the current flow from the northeast direction at the mouth of the river to southerly direction after about 1.5 km from the mouth (Machiwa et al. 2003). This could result in less mixing of water in the eastern part of the bay with water from the open lake. As a result, the water in the eastern part of the could possess more inshore characteristics such as elevated nutrient levels. The results also show lack of net phosphorus fluxes in the benthic chambers suggesting that adsorption and de-sorption of soluble reactive phosphorus at the sediment surface proceeded at almost equal rates. It has been observed that PO₄³ adsorbs strongly on CaCO3 rich sediment (De Kanel and Morse 1978), this is likely to be the case at stations LV9 and LV 32 where

benthic chambers were placed. The sediments at these two stations are rich in mollusk shells. If benthic chamber experiments were placed in deeper waters with fine grained/muddy deposits, away from the shore, probably a different scenario would have been observed.

Phytoplankton species composition was generally dominated by the cyanobacterium Microcystis spp. at stations LV1, LV2 and LV3. At the rest of the stations Microcystis was still commonly found though dominating phytoplankton species were cyanobacterium Anabaena spiroides var. crassa or the diatoms Nitzschia spp. and/or Melosira spp. The reason for this variation dominance of species composition between stations is not clear. In general cyanobacteria such as Microcystis spp. and Anabaena spiroides var. crassa were most common at stations that were more turbid probably due to the ability of many cyanobacterial species to tolerate low light intensities (e.g. Tandeau de Marsac and Houmard 1993).

It appears that during sampling a localized Microcystis surface bloom/scum at stations LV1, LV2 and LV3 was encountered. Microcystis, as is the case to many other cyanobacteria, forms gas vacuoles composed of hollow proteinaceous vesicles filled with air. These facilitate buoyancy regulation enabling access to both near surface light energy and the more nutrient-rich deeper waters (Walsby 1978; 1994). Gas vesicles may be the reason why cyanobacteria often form scum, which results from wind action on the shore regions of a lake. Theoretically, the number of cyanobacterial cells in the open water need not be high to form scum on the shore. As few as 10^3 cells ml⁻¹ are enough to form a significant scum near the shore if moved horizontally and accumulated by wind over a larger distance from the open water to the shore (Walsby 1994). The lack of significant differences cell. concentration between surface and mid-water

collected samples suggests a well-mixed water column.

Apart from the higher biomass dominated by Microcystis spp. at stations LV1, LV2 and LV3. phytoplankton numerical abundance at the rest of the stations was comparable to a study by Lung'ayia et al. (2000) carried out in Nyanza Gulf, in the Kenyan waters of Lake Victoria. Generally the phytoplankton cell density was low at the stations close to the river mouth and in the eastern part of the bay that had higher nutrient concentrations. This anomaly could be explained by the fact that turbidity at the stations close to the river mouth and to the eastern part of the bay was high probably limiting phytoplankton production. Indeed, phytoplankton production has been observed to be low close to river mouths in estuaries despite the high nutrient concentrations in those areas, with production peaking a few nautical miles offshore as turbidity decreases (Levinton 1995). The positive correlation that was seen between phytoplankton cell number and SS may be an artifact resulted from the Microcystis spp. accumulation at stations 1, 2 and 3 as a result of wind action (as postulated above). In addition, due to technical difficulties determination of SS was terminated after station LV9, therefore, this relationship does not represent the whole bay area.

The cyanobacteria that comprised 31% of the phytoplankton species identified during this study were also often numerically the most dominant taxa at the various stations. Some of these taxa such as the Anabaena sp. are known to be diazotrophic (e.g. Bergman et al. 1997) and can influence the nitrogen budget of the bay through nitrogen fixation. This observation tallies with the finding by Hecky (1993) who reported that nitrogenfixing cyanobacteria now dominate in inshore and open lake areas relative to the 1960s. The dominance of cyanobacteria in the bay may have other consequences to the health of people surrounding the bay and to the fishery, as some cyanobacterial species

are associated with toxic bloom formation. *Microcystis*, for example, that dominated the plankton samples at stations LV1, LV2 and LV3 is related to hepatotoxic poisoning (e.g. Sivonen 1996).

In conclusion, the study showed that nutrient concentrations were generally high towards the eastern part of the bay as compared to the rest of the bay area. Much of the suspended particles are deposited within the first 0.5 km from the river Phytoplankton production mouth. possibly light limited in areas simultaneously high nutrient concentrations and high turbidity. It will be interesting to conduct a similar study but during the dry season when River Simiyu is dry in order to have a better picture of the influence of the river on the nutrient and phytoplankton dynamics in the bay. This study provides basic information from which future studies may be compared.

ACKNOWLEDGEMENT

This study was supported by funds from Lake Victoria Environmental Management Project. Mohammed Suleiman, Shelard Mukama and Amos Lugata assisted in field or laboratory work. The anonymous reviewers are thanked for their invaluable comments.

REFERENCES

- APHA 1992 Standard Methods for the Examination of Water and Wastewater. American Public Health Association 18th Edition, Washington DC.
- Benno B 2003 The movement, habitat use, fishery and trophic status of Labeo victorianus of Lake Victoria, Tanzania. PhD thesis, University of Waterloo, Canada.
- Bergman B, Gallon JR, Rrai AN and Stal LJ 1997 N₂ fixation by nonheterocystous cyanobacteria. - FEMS Microbiol. Rev. 19: 139-185.
- Cocquyt C, Vyverman W and Compere P 1993 A Check-list of algal flora of

- the Eastern African Great Lakes (Malawi, Tanganyika and Victoria). National Botanical Garden of Belgium, Meise, Belgium, Universa Wetteren, 55 pp.
- Crul RCM, Silvestre GT, Postma DJ van Oijen MJP, Acere TO and Bongers G 1993 Monographs of the African Great Lakes: Limnology and Hydrology of Lake Victoria. UNESCO/IHP-IV Project M-5.1, Paris.
- De Kanel J and Morse JW 1978 The chemistry of orthophosphate uptake from seawater on calcite and aragonite. *Geochimica et Cosmochimica Acta* **42**: 1335-1340.
- Hecky RE 1993 The eutrophication of Lake Victoria. Verh. Internat. Verein. Limmnol. 25: 39-48.
- Levinton JS 1995 Marine biology: function, biodiversity, ecology. Oxford University Press, Oxford, 201 pp.
- Johonson TC, Scholz CA, Talbot MR, Kelts K, Ricketts RD, Ngobi G, Beuning K, Ssemanda I and McGill J W 1996 Late Pleistocene desiccation of Lake Victoria and rapid evolution of cichlid fishes. Science 273: 1091-1093.
- Johnstone R, Koop K and Larkum WD 1988 Fluxes of inorganic nutrients between sediments and water in a coral reef lagoon. *Proceedings of Linnean Society of New South Wales*, 110: 219-227
- Johnstone R and Olafsson E 1995 Some environmental aspects of open water algal cultivation: Zanzibar, Tanzania. *Ambio*, **24**: 465-469.
- Kendall RL 1969 An ecological history of the Lake Victoria basin. *Ecol. Monogr.* **39**:121-176.
- Lung'ayia HBO, M'harzi A, Tackx M, Gichuki J and Symoens J 2000 Phytoplankton community structure and environment in the Kenyan waters of Lake Victoria. Freshwater Biol. 43: 529-543.

- Machiwa JF, Muzuka ANN, Dubi AM,
 Ndaro SGM and Lugomela C 2003
 Sedimentation studies at the Simiyu
 River Mouth (Magu Bay, Speke Gulf),
 Lake Victoria, Tanzania. A report
 submitted to Lake Victoria
 Environmental Management Project,
 Vice Presidents Office, The United
 Republic of Tanzania. 97 pp.
- Mohammed MS and Mgaya YD 2001

 Nutrient levels and their dynamics in the coral reefs off Zanzibar town.

 In:Richmond and Francis J (eds.)

 Marine Science development in Tanzania and Eastern Africa. 1: 171-183.
- Mugidde R 1993 The increase in phytoplankton primary productivity and biomass in Lake Victoria (Uganda). Verh. Internat. Verein. Limmnol. 25: 846-849.
- Ochumba PBO and Kibaara DI 1989 Observations on blue-green algal blooms in the open waters of Lake Victoria, Kenya. *African J. Ecol.* 27: 23-34
- Prescott GW 1964 How to know the freshwater algae. 3rd Edition. Wm, C. Brown Company Publishers, Dubuque, Iowa, USA. 293 pp
- Sivonen K 1996 Cyanobacterial toxins and toxin production. *Phycologia* **35**(6): 12-24
- Talling JF 1966 The annual cycle of stratification and phytoplankton growth in Lake Victoria (East Africa). *Intern. Rev. ges. Hydrobiol.* **51**: 545-621
- Talling JF 1987 The phytoplankton of lake Victoria (East Africa) Arch Hydrobiol. Beih. Ergebn. Limnol. 25: 229-256
- Tandeau de Marsac N and Houmard J 1993
 Adaptation of cyanobacteria to environmental stimuli: new steps towards molecular mechanisms.

 FEMS Microbiol. Rev. 104: 119-190
- Utermöhl H 1931 Nue Wege in der quantitaiven Erfassung des Planktos. Verh. Int. Ver. Limnol. 5

- Walsby AE 1978 Properties and buoyance providing role of gas vacuoles in *Trichodesmium* Ehrenberg. *Br. Phycol. J.* **13**: 103-116
- Walsby AE 1994 Gas vesicles. *Microbiol.* Rev. **58**: 94-144
- Witte F and van Oijen MJP 1992 Species extinction and concomitant ecological
- changes in Lake Victoria. *Netherlands J. Zool.* **42**: 214-232.
- Woelkerling WJ, Kowal RR and Gough SB 1976 Sedgewick-Rafter cell counts: a procedural analysis. *Hydrobiologia* 48: 95-107.