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Phytoplankton dynamics and cyanobacterial dominance in Murchison Bay of Lake Victoria (Uganda) in relation to environmental conditions

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ABSTRACT

Murchison Bay is a shallow embayment in the north-western part of Lake Victoria, strongly influenced by urban pollution from the Ugandan capital Kampala. Two stations, representing the semi-enclosed innermost part of the bay and the wider outer part of the bay, were sampled in the period from April 2003 to March 2004, in order to assess the phytoplankton community and the nutrient status in the bay. Murchison Bay was highly eutrophic with average concentrations ($n=25$) of total phosphorous $>90\,\mu g\,L^{-1}$ and total nitrogen $>1100\,\mu g\,L^{-1}$ in the inner part of the bay. The phytoplankton community was dominated by a variety of cyanobacterial species and diatoms. Cyanobacteria were dominant in the whole bay, whereas diatoms were more abundant in the outer part of the bay. Moreover, the proportion of N-fixing species like *Anabaena* sp. was higher in the outer part of the bay, whereas species like *Microcystis* sp. were more abundant in the inner part of the bay. The phytoplankton community, especially in the outer part of the bay, may be influenced by light limitation. Low NO_3–N concentrations in the bay may also indicate a possible N-limitation, thus favouring growth of N-fixing cyanobacteria. The open bay is, however, a complex system, and additional environmental factors and loss processes most likely affect the phytoplankton community.

Introduction

The Lake Victoria ecosystem has undergone substantial changes over the last five decades, including introduction of exotic species, severe eutrophication and climate change (e.g. Hecky, 1993; Verschuren et al., 2002). Expanding urban, agricultural and industrial development has caused historically high nutrient loadings into the lake (Hecky and Bugenyi, 1992; Lipiatou et al., 1996; Verschuren et al., 2002). The overall phytoplankton biomass has increased (e.g. Ochumba and Kibaara, 1989; Ochumba, 1990; Mugidde, 1993; Lung'ayia et al., 2000, 2001), with a fourfold and eightfold increase in the Chlorophyll *a* (Chl-*a*) concentrations in the offshore and inshore areas, respectively, and a notable decrease in water transparency both offshore and inshore (Mugidde, 1993). Whereas rates of primary production have increased near the lake surface, the rates of decomposition have depressed dissolved oxygen concentration to $\leq 1\,mg\,L^{-1}$ in the deepest one-third of the water column (Hecky et al., 1994). Lake Victoria is regarded as highly eutrophic and blooms of cyanobacteria have now become common (Ochumba and Kibaara, 1989; Lung'ayia et al., 2000; Kling et al., 2001). Probably the most known ecological change is the introduction and successful establishment of Nile perch (*Lates niloticus*) which dramatically has altered the indigenous fauna in Lake Victoria (for a review see Goudswaard et al., 2008). The large scale invasion of water hyacinth (*Eichhornia crassipes*) has been another threat by an introduced species to the Lake Victoria ecosystem (Twongo, 1991; Albright et al., 2004). The lake supports one of the largest commercial freshwater fisheries in the world (Simonit and Perrings, 2005), but largely due to failures in controlling the fishing effort, the fish stocks are currently considered overexploited (Simonit and Perrings, 2005). There has been a massive focus on fish and fisheries in Lake Victoria, and the dramatic ecosystem alterations have to a large extent been explained by foodweb changes caused by "top-down" predation by the introduced Nile perch and by overfishing (Goudswaard et al., 2008). It is however, evident that the increased nutrient loading results in a "bottom-up" effect and changes the phytoplankton productivity (Mugidde, 1993) and community structure (Kling et al., 2001), and there is a recent increasing awareness that the ongoing eutrophication is as much a threat to the Lake Victoria ecosystem.

Lake Victoria has attracted scientific interest ever since the late 19th century. The first reported phytoplankton investigation in the lake was accomplished by Schmidle (1902), and since then

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several studies on phytoplankton taxonomy and ecology have been conducted (for a review see Talling, 1987). The phytoplankton community in Lake Victoria before antropogenic eutrophication (1960s) was dominated by diatoms, cyanobacteria and chlorophytes (Talling, 1987). The present composition of the phytoplankton community has to a large extent changed after the significant increase in nutrient loading into Lake Victoria and there is now a strong dominance of cyanobacteria and the diatom *Nitzschia* (Kling et al., 2001). Cyanobacterial blooms in Lake Victoria were reported already at the beginning of the 20th century (Ostenfeld, 1908) and more recent records from Lake Victoria focus on the increasing mass occurrences of cyanobacteria, especially in near shore areas of the lake (e.g. Ochumba and Kibaara, 1989; Hecky and Bugenyi, 1992; Hecky, 1993; Gophen et al., 1995; Lung'ayia et al., 2000; Kling et al., 2001; Krienitz et al., 2002; Sekadende et al., 2005; Okello et al., 2009). Worthington (1930) differentiated two main types of environments within Lake Victoria; the shallow semi-enclosed gulfs and bays that are not deep enough to be persistently stratified, and the open lake waters with stratification and clear seasonality; thus, the physico-chemical environment changes from inshore to offshore waters. Accordingly, there is a differential distribution and abundance of phytoplankton species between the inshore and offshore areas of the lake (Talling, 1987; Lung'ayia et al., 2000; Kling et al., 2001). In tropical areas, where there are only small temperature variations throughout the year, light and nutrient levels may be the main environmental factors influencing the phytoplankton biomass and species composition. In Lake Victoria, changing nutrient conditions, silicon depletion and nitrogen limitation, light limitation, influence of dry and wet season, and food-web changes have been proposed as main factors regulating the phytoplankton populations (Mugidde, 1993; Lung'ayia et al., 2000; Kling et al., 2001; Gikuma-Njurua and Hecky, 2005; Silsbe et al., 2006).

Whereas several studies on phytoplankton have been carried out in other large bays and gulfs of Lake Victoria, there are few reports on phytoplankton biology and ecology from Murchison Bay in the north western part of Lake Victoria. The inner part of Murchison Bay serves as a drinking water supply for Kampala, the capital of Uganda, and is also a recipient of both industrial and municipal wastes, sewage effluents and surface runoff from the city and is shown to be highly eutrophic with a dominance of cyanobacteria (Källqvist et al., 1996; Schröder et al., 1998). The development of cyanobacterial blooms in drinking water supplies calls for special attention due to the ability of many cyanobacterial species to produce toxic compounds (cyanotoxins) which can cause considerable hazards to animal and human health (Krienitz et al., 2003; Bell and Codd, 1994; Kuiper-Goodman et al., 1999). Thus, it is of great importance to understand phytoplankton dynamics and the factors influencing cyanobacterial growth and distribution in water bodies used for drinking water purposes. The aim of this study was therefore to (a) investigate the diversity of the phytoplankton community in Murchison Bay, in particular the cyanobacterial population, and (b) to assess the influence of environmental factors.

Material and methods

Study site

Murchison Bay is an extension of Lake Victoria to the north towards Kampala, and is divided in a semi-enclosed inner part and a wider outer part by narrows about 5 km from the inner shores (Fig. 1). The shallow embayment is 30 km long and the bottom has a gentle slope from the outlet of the Nakivubo channel to about 11 m depth at the Gaba narrows and to about 12 m at the outer part of the bay. The Inner Murchison Bay (mean depth 3.2 m) covers an area of about 18 km^2 and has a catchment area of 282 km^2, both comprising wetland areas and parts of the urban areas of Kampala (>1 million inhabitants). The most significant drainage of the catchment area is the Nakivubo channel, going through Kampala and the wetland areas surrounding the bay, entering the inner part of the bay from the north. In the past, the Nakivubo channel ended in the outer part of the wetland areas, allowing the water to be drained in the papyrus swamps before entering the bay. In 2001–2003, the Nakivubo channel was enlarged to remove storm water more efficiently from the urban areas. It was widened to about 20 m and stretched through the wetland ending only a couple of hundred meters before Murchison Bay. The water in the channel is a mixture of secondary effluents from the Bugolobi sewage treatment works and heavily polluted untreated wastewater from the city. Moreover, the predominant papyrus wetland has been drained and turned into agricultural areas or developed for commercial, industrial or residential purposes (Kansiime et al., 2005). Due to these major changes in the wetland areas, the retention of nutrients and other pollutants is now moderate to absent, increasing the concerns for the water quality in the bay (Kansiime et al., 2005).

The Lake Victoria region has an equatorial climate with small variations in solar radiation over the year. The lake is situated at an altitude of 1135 m and the mean annual temperatures in areas close to Murchison Bay range from 21.5 to 22.5 °C. As a rule, there are two rainy seasons, the long rains from March to May with a peak in April and the short rains from October to November. There are, however geographical and annual variations.

Sampling

Sampling ($n=25$) of physical, chemical and biological parameters was done at two stations in Murchison Bay every second week in the period April 2003 to March 2004. There had been established four stations in a longitudinal transect from the inner to the outer bay (Haande, 2008), and we have used two of these sampling stations in this study (Fig. 1). Station 2 (St. 2) was in the inner part of the bay (00°15.727′N 32° 38.749′E, max depth 5 m) and station 4 (St. 4) was in the outer part of the bay (00°08.715′N 32° 37.580′E, max depth 11 m). The proximity of Murchison Bay to Kampala allowed the samples to be immediately transported to Makerere University for preservation and analysis. The sampling was carried out between 9 am and 3 pm, starting at station St. 4 and ending at station St. 2. A number of vertical temperature measurements taken at several different sites in Murchison Bay, both fortnightly daytime measurements during the whole sampling period (see Fig. 2) and some day/night samplings (every 6 h), showed that there was no constant thermal stratification in the bay and that the water column was well mixed. Therefore, water samples were taken with a 1 m tube sampler (5 L) of the Van Dorn type (Modified Ramberg Sampler, Norwegian University of Science and Technology, Trondheim, Norway) at the surface (0–1 m) and regarded as representative for the whole water column.

Physical measurements and nutrient analysis

Vertical profiles of water temperature, dissolved oxygen and electrical conductivity were measured with a model 85 oxygen meter (YSI, Yellow Springs, OH, USA) on each sampling date. Data on daily precipitation were from the Makerere Hill in Kampala and were assumed to be representative for the watershed.

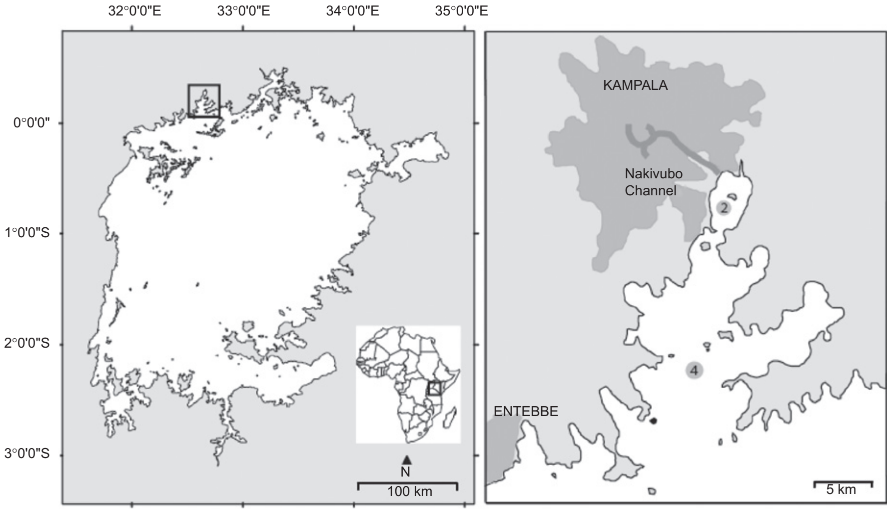


Fig. 1. Geographic situation of Murchison Bay of Lake Victoria and location of sampling stations.

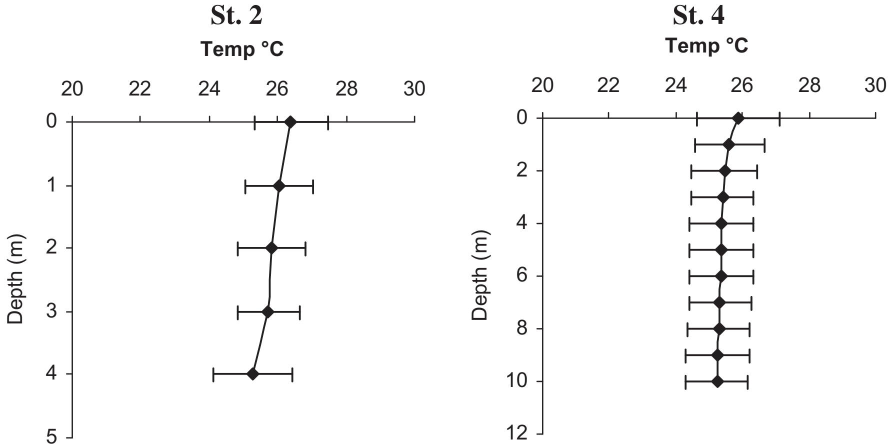


Fig. 2. Vertical temperature profiles showing mean temperatures (±SD) at the two stations in Murchison Bay of Lake Victoria for the period from April 2003 to March 2004.

Water transparency (Secchi disc depth, SDD) was measured with a white Secchi disc (Ø25 cm). Euphotic depth (Z_{eu}), defined as 1% of surface light, was determined by using the measured SDDs and estimates of the light attenuation coefficient. The estimated coefficient was defined as $k=1.25/\mathrm{SDD}$ derived from the regression equations for $\mathrm{Chl}_{Z_{eu}}$ versus k_{PAR} and SDD based on measurements in Murchison Bay presented by Silsbe et al. (2006). The value of Z_{eu} was defined according to Kirk (1983) as $Z_{eu}=4.6/k$.

Water for analysis of nutrients was collected in 500 m L^{-1} polyethylene bottles and preserved with 1 m L^{-1} 5 M sulphuric acid until the analyses were performed in Norway. Nutrients were analysed using scalar autoanalyser according to Norwegian- and ISO-standard methods; total phosphorous (TP, NS 4725), orthophosphate (PO_4^{2-}, NS 4724), total nitrogen (TN, NS 4743), nitrate (NO_3^-, NS-EN ISO 10304-1). Total organic carbon (TOC) was analysed on a Phoenix 8000 TOC-TC analysator (NS-ISO 8245). Silicon (Si) was analysed by Perkin Elmer Optima 4300 DV ICP-AES Spectrometer (ISO 11885/NS4770).

Phytoplankton analysis

Samples for identification and counting of phytoplankton were collected in 100 mL glass bottles and fixed immediately with Lugol's iodine solution. 10 mL of each sample was sedimented for the inverted microscope technique according to Olrik et al. (1998). The following references were used for identification and taxonomic classification of the phytoplankton: Süsswasserflora von Mitteleuropa, vol. 1–19 (Büdel et al., 1985–2005; Talling, 1987; Komárek and Kling, 1991; Cronberg and Komárek, 2004).

For chlorophyll-*a* analysis, 100–200 m L^{-1} of water were filtered through Whatman GF/C glass–fiber filters onboard and the filters were kept in a cool ice box during transportation to the laboratory. The samples were stored at −20 °C and transported frozen to Norway for analysis. The filters were extracted in 5 mL 90% acetone, processed by ultrasound and incubated at room temperature for 2.5 h and clarified by centrifugation. Chl-*a* concentrations were analysed by using high-pressure liquid chromatography (HPLC, Walters 2695 separations module), with diode array detection system (Walters 2996 Photodiode array detector) following the method described in Jeffrey et al. (1997) using detection by absorbance at 440 nm.

Statistical analysis

Species distribution was analysed by canonical correspondence analysis (CCA; Legendre and Legendre, 1998), using the square-root transformed biovolumes of the single species and genera. Environmental factors were selected based on having <0.05 likelihood of being randomly associated based on a permutation test. Goodness of fit for the single species was assessed by the proportion of a species' variation explained by the constrained axes. (CCA and CCA-permutation test were performed using the *vegan* package in R; R Development Core Team 2007).

Results

Physico-chemical conditions

It rained every month in the study period, but on average, the minimum precipitation was found in September 2003 and March 2004 and the maximum was found in April, August and December (data not showed). The rain often came as heavy rain showers resulting in very variable runoff in the channel leading into Murchison Bay. In 2003 and 2004, the annual precipitation was 1415 and 1456 mm, respectively (Meteorology Department, Makerere University). The water temperature in Murchison Bay was high throughout the survey, always exceeding 23 °C throughout the entire water column (Fig. 2). The mean surface water temperature (0–1 m) in the inner part of the bay was 26.2 (± 1.0) °C (mean value, SD, $n=25$) (St. 2) and 25.7 (± 1.1) °C in the outer part of the bay (St. 4), and there was no constant thermal stratification at any time during this study. The water column in the bay was well oxygenated at all times (data not shown). The water transparency (SDD) was on average 0.8 m at St. 2 and 1.1 m at St. 4. Fig. 3 shows that the transparency was higher during the first 5 months (April–August 2003) of the study compared to the last 7 months (September 2003–March 2004) at both stations. Accordingly, the estimated euphotic depth Z_{eu} was deeper in the first part of the studied period than in the last part at both stations (Fig. 3). The euphotic depth was on average 3.0 m at St. 2 and 4.0 m at St. 4.

The seasonal development of the total and the dissolved inorganic fractions of the macronutrients P and N at the two stations in Murchison Bay are shown in Fig. 4a and b. The concentration of TP was high at both stations, with a mean concentration of $91 \pm 27.8\ \mu g\ L^{-1}$ (mean value ± SD, $n=25$) at St. 2 and $65 \pm 22.5\ \mu g\ L^{-1}$ at St. 4. The mean concentration of PO_4–P was $33.5 \pm 19.8\ \mu g\ L^{-1}$ at St. 2 and $19.6 \pm 12.6\ \mu g\ L^{-1}$ at St. 4. The lowest detected value was $10\ \mu g\ L^{-1}$ at St. 2 and $6.5\ \mu g\ L^{-1}$ at St. 4, and these values indicate that P may not be a limiting factor in the system. The TN concentrations were high both in the inner and outer part of the bay, and the mean concentration was $1127 \pm 253\ \mu g\ L^{-1}$ at St. 2 and $806 \pm 194\ \mu g\ L^{-1}$ at St. 4. There was a marked increase in the TP, PO_4–P and TN concentration from September to March at both stations. There were generally very low concentrations of NO_3–N in Murchison Bay in the studied period ($<10\ \mu g\ L^{-1}$), with the exception of a peak at St. 2 in June and July. The average concentration was $39 \pm 75\ \mu g\ L^{-1}$ at St. 2 and $8.6 \pm 9.0\ \mu g\ L^{-1}$ at St. 4. The mean concentration of silicon (Si) was $0.9 \pm 0.6\ mg\ L^{-1}$ at St. 2 and $0.3 \pm 0.3\ mg\ L^{-1}$ at St. 4 and there was also a marked increase of Si concentration in the last part of the study period (Fig. 4c). The nutrient concentrations were generally higher in the inner than the outer part of Murchison Bay, indicating a dilution outwards in the bay.

Phytoplankton community

Fig. 5 shows the seasonal variation in concentration of Chl-*a* at the two stations in Murchison Bay. The mean concentration of Chl-*a* was $31.1 \pm 9.8\ \mu g\ L^{-1}$ at St. 2 and $20.9 \pm 5.9\ \mu g\ L^{-1}$ at St. 4. At St. 2, the Chl-*a* concentration was ranging from 20 to $40\ \mu g\ L^{-1}$ in April 2003–January 2004, and increased to $40–60\ \mu g\ L^{-1}$ in February and March 2004. At St. 4, the Chl-*a* concentration was ranging between 15 and $25\ \mu g\ L^{-1}$ in April 2003–January 2004, and increased slightly during the last 2 months of the study period to $20–30\ \mu g\ L^{-1}$.

The phytoplankton community consisted of more than 80 taxa belonging to 56 genera within nine classes and six phyla: Cyanophyta (Cyanobacteria), Chlorophyta (Chlorophyceae, Trebouxiophyceae, Zygnemophyceae), Heterokontophyta (Chrysophyceae, Bacillariophyceae), Cryptophyta, Dinophyta and Euglenophyta (For a full list of phytoplankton species and genera see Supplementary data, Table S1).

Cyanobacteria and Bacillariophyceae were the most abundant groups in Murchison Bay (Fig. 6). At St. 2, the proportions of cyanobacteria and diatoms were 64% and 23%, respectively. At St. 4, the proportion of cyanobacteria was about the same as in the inner part of the bay (62%), whereas the diatoms were more abundant (31%). The Chlorophyta comprised the most diverse phylum with respect to number of genera and species, but they only accounted for about 2% of the total biovolume at both St. 2 and St. 4. Species of Chlorophyta and Cryptophyta were present throughout the year, but never at high abundances. Species of Chrysophyceae, Dinophyta and Euglenophyta were found in smaller proportions and not at all times of the year. In addition, there were several different picoplankters (cell diameter 0.2–2 μm) at both stations. The average total phytoplankton biovolume was $1.7 \pm 1.0\ mm^3\ L^{-1}$ (mean value SD, $n=24$) at St. 2 and $2.6 \pm 1.0\ mm^3\ L^{-1}$ at St. 4. The biovolume of the total phytoplankton ranged from 0.7 to $4.7\ mm^3\ L^{-1}$ at St. 2 and from 0.9 to $5.3\ mm^3\ L^{-1}$ at St. 4. The most abundant species at

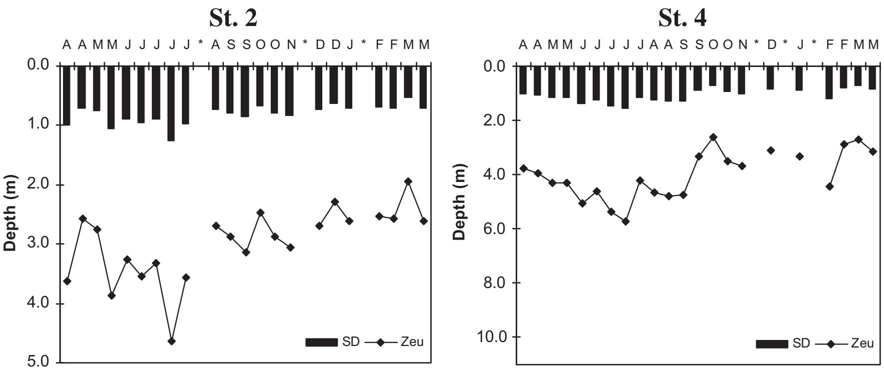


Fig. 3. Water transparency (Secchi disc depth) and estimated euphotic depth (Z_{eu}) at the two stations in Murchison Bay of Lake Victoria from April 2003 to March 2004. (*No data.)

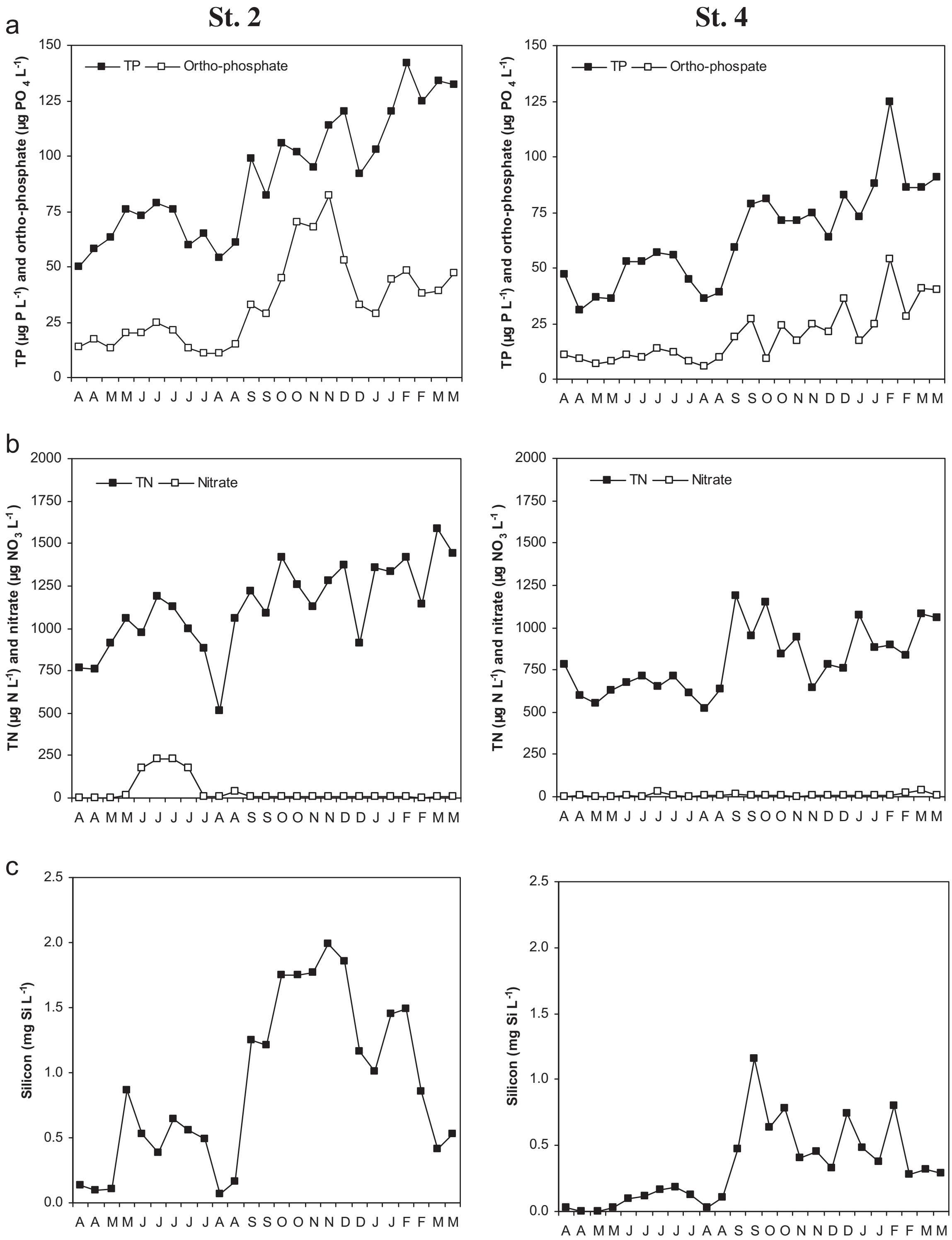


Fig. 4. Concentrations of soluble nutrients at the two stations in Murchison Bay of Lake Victoria from April 2003 to March 2004: (a) total phosphorous (TP) and ortho-phosphate, (b) total nitrogen (TN) and nitrate, and (c) silicon.

St. 2 were the diatom *Aulacoseira granulata* (15.4%) and the cyanobacteria *Anabaena* sp. (12.4%), *Microcystis wesenbergii* (11.6%), *Gomphosphaeria aponina* (8.6%) and *Microcystis aeruginosa* (8.5%). At St. 4, the most abundant species were the diatom *Nitzschia acicularis* (28.2%) and the cyanobacteria *Anabaena* sp. (25.3%), *Planktolyngbya circumcreta* (6.7%), *M. wesenbergii* (5.8%) and *G. aponina* (5.5%). About 20 species of cyanobacteria were found in Murchison Bay (Fig. 7). The average total biovolume of cyanobacteria was 1.0 ± 0.7 mm^3 L^{-1} (mean value SD, $n=24$) at St. 2 and 1.6 ± 0.7 mm^3 L^{-1} at St. 4. The genus *Anabaena* contributed the largest proportion of the cyanobacteria at both stations, on average 20% at St. 2 and 40% at St. 4. At St. 4, the cyanobacterial biovolume was higher than at St. 2, mainly because of a higher proportion of members of the genus *Anabaena*.

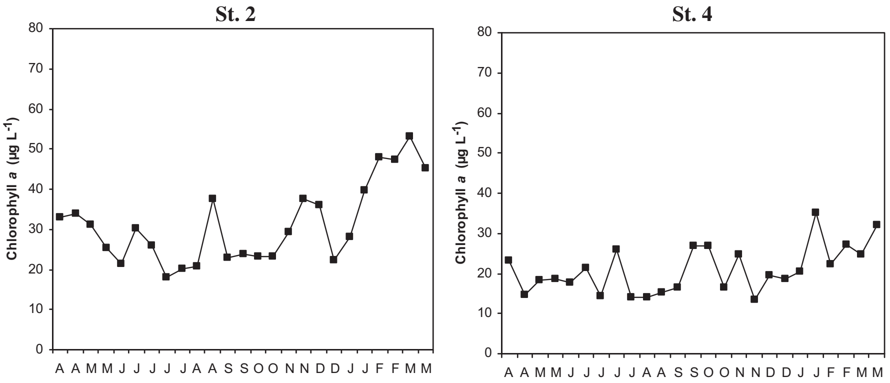
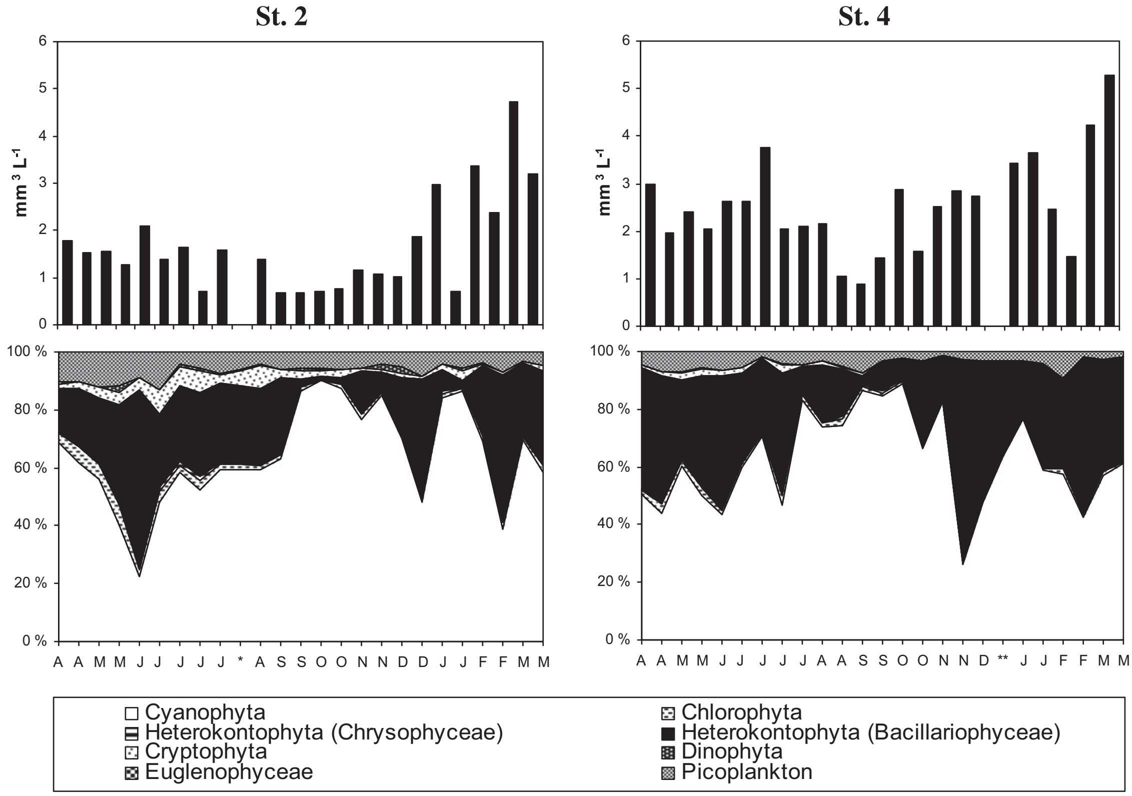


Fig. 5. Concentration of Chrorophyll-*a* at the two stations in Murchison Bay of Lake Victoria from April 2003 to March 2004.



* Missing data 14.08.2003
** Missing data 20.12.2003

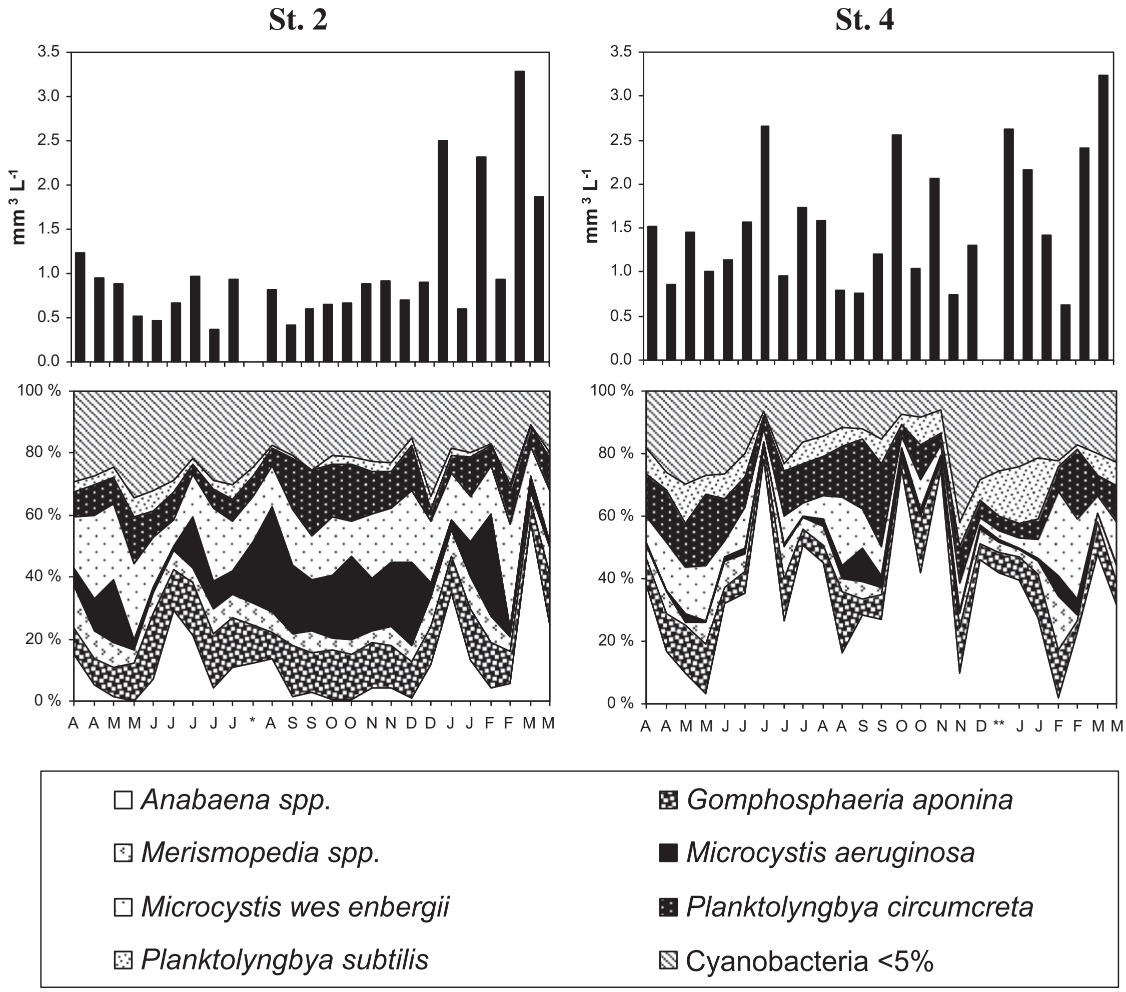
Fig. 6. Total phytoplankton concentration (upper panel) and the relative abundance of phytoplankton classes (lower panel) at the two stations in Murchison Bay of Lake Victoria from April 2003 to March 2004.

Relating phytoplankton species to environmental factors

Species dynamics were analysed in a constrained correspondence analysis (CCA), where all data of a given station were pooled in one analysis. The analyses revealed several autocorrelations in the dataset, and it was not possible to appoint any environmental factor as a significant driver explaining the phytoplankton dynamics (data not shown).

Discussion

The results presented in this study clearly show that Murchison Bay was highly eutrophic and that the phytoplankton community was dominated by a variety of cyanobacterial species. Two surveys in the inner part of the Murchison Bay conducted in the 1990s concluded that there had been a major increase in nutrient loading to the bay since the 1960s (Källqvist et al., 1996; Schröder et al., 1998). Källqvist et al. (1996) detected values of TP $<50\,\mu g\,L^{-1}$ and TN $<500\,\mu g\,L^{-1}$ at Gaba, close to St. 2 used in this study, whereas we found mean concentrations of TP $>90\,\mu g\,L^{-1}$ and TN $>1100\,\mu g\,L^{-1}$ in the inner part of the bay. Interestingly, the phytoplankton biovolume did not change accordingly. Källqvist et al. (1996) collected a phytoplankton sample close to the Gaba narrows in the inner part of the bay, and calculated that the biovolume was $2.4\,mm^3\,L^{-1}$. We found that the total biovolume at St. 2 in the inner part of the bay was ranging from 0.7 to $4.7\,mm^3\,L^{-1}$ in 2003–2004. Although compared to a single sample from 1995, the



* Missing data 14.08.2003
** Missing data 20.12.2003

Fig. 7. Total biovolume of cyanobacteria (upper panel) and the relative abundance of the most abundant cyanobacterial species (lower panel) at the two stations in Murchison Bay of Lake Victoria from April 2003 to March 2004. Species of cyanobacteria accounting for less than 5% of the total cyanobacterial biovolume are shown as one group.

phytoplankton biovolume we detected seems to be within the same order of magnitude/range. Despite the increase in nutrient loading to the bay, the phytoplankton biovolume remains comparably low, and it is likely that there are factors limiting the phytoplankton growth in Murchison Bay or enhancing phytoplankton loss.

In general, cyanobacteria have higher temperature optima for growth than other algal groups, and hence elevated temperatures are found to favour abundance of cyanobacteria (e.g. Robarts and Zohary, 1987; Dokulil and Teubner, 2000). The water temperatures measured in Murchison Bay were high throughout the whole year (23.3–27.8 °C); however, rainy seasons were slightly warmer than the dry seasons. These tropical conditions most likely constituted a good environment for cyanobacterial growth. The relative proportion of cyanobacteria and diatoms changed from rainy to dry seasons at both stations, with a higher proportion of cyanobacteria in the dry seasons and a higher proportion of diatoms in the periods of rainy seasons. There was however no correlation between the amount of phytoplankton biovolume and wet/rainy seasons. Lung'ayia et al. (2000) found higher biomasses of phytoplankton during rainy season in Nyanza Gulf in the Kenyan part of Lake Victoria and also a higher proportion of diatoms in rainy seasons compared to dry seasons when cyanobacteria were dominating. Earlier investigations have also found higher biomass of phytoplankton during rainy seasons in Lake Victoria (Talling, 1966, 1987). The increase of phytoplankton biomass and higher abundance of diatoms during rainy seasons may also be due to higher input of P, N and Si (Lung'ayia et al., 2000).

Light limitation has been proposed for the phytoplankton production in the offshore areas of Lake Victoria, as the mixed water column exceeds the depth of the euphotic zone (Figs. 2 and 3; Mugidde, 1993; Hecky, 1993; Kling et al., 2001). Mugidde (1993) suggested that the phytoplankton populations in the shallow parts of the lake were usually self-shaded due to high-chlorophyll standing crops. Measurements of global photosynthetic active radiation (PAR) at the Physic Department of Makerere University (Kampala) over a 5 year period (2003–2007) show that there is an annual average light intensity of 1500–2500 μmol m^{-2} s^{-1} in the area of Murchison Bay, indicating a high surface irradiance level. In the outer part of the bay, with a depth of 12 m, we estimated the euphotic depth to be about 4 m and in the inner part of the bay, where the depth is about 5 m, we estimated a euphotic depth of about 3 m. The regular vertical mixing of the water column in Murchison Bay cause a frequent movement of the phytoplankton well below the euphotic zone; thus, leading to possible light limitation in periods of the day, especially in the outer part of the bay.

Nutrient dynamics can impact phytoplankton assemblages by limiting rates of growth and by affecting species composition and dominance patterns. The TN:TP ratio is often used as an indicator for determining the potential limiting nutrient (Smith, 1983). Based on studies from several lakes, amongst them the tropical Lakes Victoria and Malawi, Guildford and Hecky (2000) have suggested that there will be P-deficiency if the TN:TP ratio >50 (atomic ratio) and a N-deficiency if the TN:TP ratio <20 (atomic ratio), and that intermediate TN:TP ratios, either N or P can become a limiting factor. In Murchison Bay, the atomic TN:TP ratios were 29 at St. 2 and 30 at St. 4; thus, giving no clear indication of nutrient limitation. The concentrations of dissolved inorganic PO_4–P in the water remained $>10\,\mu g\,L^{-1}$ at both stations throughout the study period, and it is therefore likely that the phytoplankton growth was not limited by P. Most cyanobacterial species can have maximal growth with PO_4–P concentrations $>10\,\mu g\,L^{-1}$, and in addition, most cyanobacterial species have a capacity to store P (Istvánovics et al., 2000). Lehman and Branstrator (1994) concluded that the Lake Victoria phytoplankton rarely, if ever experienced P limitation. As for N, limitation can be suspected, since low NO_3–N values ($<10\,\mu g\,L^{-1}$) were detected at both stations at most times during the study period. There was, however, a period when higher NO_3–N concentrations were detected at St. 2 in June–July (about $250\,\mu g\,L^{-1}$) without any detectable effect in the phytoplankton biovolume. N-limitation has been proposed to be a limiting factor to the offshore phytoplankton as nitrate was nearly always undetectable (Talling, 1966; Hecky, 1993), favouring growth of N-fixing cyanobacteria (Mugidde et al., 2003). The cyanobacterial community in Murchison Bay consisted of more than 20 species belonging to the orders Chroococcales, Oscillatoriales and Nostocales. Species of the order Nostocales have the ability to produce specialised cells; heterocysts, which can fix molecular nitrogen and thereby offset nitrogen demand under conditions of nitrogen deficiency. Mugidde et al. (2003) found that the rate of N-fixation in Lake Victoria was high. Interestingly, the composition of the cyanobacterial community was clearly different from St. 2 to St. 4. At St. 2 the cyanobacterial community was made up of 65% Chroococcales, 15% Oscillatoriales and 20% Nostocales species and at St. 4 it was 30% Chroococcales, 22% Oscillatoriales and 48% Nostocales species. The N-fixing species *Anabaena* sp. was the most dominating cyanobacterial species at both sites in Murchison Bay, but it was more abundant in the outer part of the bay, suggesting an effect of nitrogen on the cyanobacterial composition. In the inner part of the bay, species like *Microcystis wesenbergii* and *Microcystis aeruginosa* were more abundant. This differentiated species distribution is in accordance to other studies in Lake Victoria (Lung'ayia et al., 2000; Kling et al., 2001).

Despite the dominance of cyanobacteria in the phytoplankton community, the diatom *Nitzschia acicularis* was the single most abundant species in Murchison Bay and comprised about 28% of the total biovolume at St. 4. At St. 2, this species was less dominant (5% of total biovolume), but here the diatom *Aulacoseira granulata* was the more abundant species and constituted about 15% of the total biovolume. This species was nearly absent at St. 4 (0.5% of total biovolume). The more oligotrophic typical *Aulacoseira agassizii* was only found in low abundances at both stations. This distribution pattern of diatom species in the inshore and near-shore areas confirm other findings from Lake Victoria (Lung'ayia et al., 2000; Kling et al., 2001). The concentration of Si was higher in the inner part of the bay and decreased to lower concentrations at St. 4 in the outer part of the bay. Dissolved Si has been depleted in Lake Victoria since the 1960s (Kilham et al., 1986; Hecky, 1993) as a result of an increased diatom biomass. *Aulacoseira* was earlier the most abundant diatom in the offshore areas of Lake Victoria, but is now excluded by the continuously low Si concentrations (Hecky, 1993; Kling et al., 2001) and can only be abundant in near-shore areas where there is input of Si from the catchment area. The smaller and faster growing *Nitzschia acicularis* is less Si dependent (Kilham et al., 1986) and is now the most dominant diatom species in the offshore waters of Lake Victoria (Hecky, 1993; Kling et al., 2001). The nutrient concentrations significantly increased in the later part of the study period (September–March), probably due to the expansion work on the Nakivubo channel in the wetland areas. There was, however, no immediate increase in the phytoplankton biovolume in Murchison Bay. We found that the total biovolume was higher in the outer part of the bay, whereas the Chl-*a* concentration was higher in the inner part of the bay. This may be due to the different composition of the phytoplankton community in the different parts of the bay with very high proportion of the diatom *Nitzschia acicularis* in the outer part of the bay having a lower Chl-a/unit biovolume. Also the light climate might affect the Chl-a/unit biovolume. A possible stronger effect of N limitation in the outer part of the bay may be the reason for the higher abundance of *Anabaena* sp. and may explain the overall higher biovolume of phytoplankton at St. 4.

The statistical analyses did not reveal any significant indications on the possible effects of environmental factors on the phytoplankton dynamics in Murchison Bay. Murchison Bay is a complex system and a range of additional environmental factors and loss processes most likely affect the phytoplankton population. The inshore areas of Lake Victoria are dynamic systems connected to the main lake, and not separate water bodies. There were excessive amounts of nutrients entering the Murchison Bay during this study, but data showed that there was a rapid decrease in conductivity and nutrient concentrations from the innermost part of the bay towards St. 4 in the outer part of the bay (Haande, 2008). Schröder et al. (1998) found a similar gradient of decreasing nutrient concentrations with increasing distance from the Nakivubo Swamp. Larsson et al. (2009) provide evidence of dilution in nutrients from the inner bay to the outer bay and attribute this to surface seiches which cause considerable daily water exchange in the Murchison Bay. Kansiime and Nalubega (1999) also pointed out that water exchange between the inner and outer parts of the bay may be responsible for the dilution of pollutants from the Inner Murchison Bay. Both horizontal and vertical water movements will lead to water turbulences that may strongly affect the development of phytoplankton in the bay. Another significant loss factor could be grazing by phytoplanktivorous fish. A study in Murchison Bay on regular fishing and diet analyses of the phytoplanktivorous Nile Tilapia (*Oreochromis niloticus*) showed that cyanobacteria accounted for more than 80% of the ingested phytoplankton, indicating that *O. niloticus* may be an important grazer of the cyanobacterial population in Murchison Bay (Semyalo, 2009). Similar studies have also shown that cyanobacteria account for a significant part of the diet of adult *O. niloticus* (McDonald, 1987), and other studies have shown that this species may significantly cause reduction of cyanobacteria in eutrophic water bodies (Miura, 1990; Datta and Jana, 1998).

This study has shown that there is a dominance of the potentially toxin producing cyanobacteria *Microcystis aeruginosa* and *Anabaena* spp. in Murchison Bay. The bay is not only the drinking water supply for Kampala; the lake water is also used directly by the people living at the shores of Murchison Bay, and there is a risk for lake users to be exposed to cyanobacterial toxins. Studies of isolated strains of cyanobacteria from Murchison Bay revealed no toxin production (Haande et al., 2007, 2008), however, data from regular sampling in Murchison Bay (2003–2004) showed that the microcystin concentration in the water at times was higher than $1\,\mu g\,L^{-1}$ (Haande, 2008). Although several factors influence the phytoplankton community in the bay, the high nutrient load from the catchment area probably enhances the cyanobacterial dominance. It is therefore important to sustainably manage the land use and human activities in the wetland areas surrounding Murchison Bay and to improve the management of waste disposal from the city of Kampala.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.limno.2010.03.016.

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