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Spatial and seasonal variation in the phytoplankton community of Lake Victoria's Mwanza Gulf, compared to northern parts of the lake

Theo H. Frank [a,b], Ilse J.M. Cornelissen [a,c], Jacobus Vijverberg [a], Leopold A.J. Nagelkerke [c,*]

[a] *Netherlands Institute of Ecology (NIOO-KNAW), Droevendaalsesteeg 10, 6708 PB Wageningen, the Netherlands*
[b] *Marwei 104, 8508RH Delfstrahuizen, the Netherlands*[1]
[c] *Aquaculture and Fisheries Group, Wageningen University & Research, P.O. Box 338, 6700 AH Wageningen, the Netherlands*

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ABSTRACT

We investigated the phytoplankton species composition and abundance in two seasons in Mwanza Gulf, Lake Victoria (Tanzania). Phytoplankton was sampled and chlorophyll *a* content was measured in the dry and wet seasons of 2010–2011 at three stations, from the southern land-inward end of the Gulf towards the open lake. Cyanobacteria, mostly small colonial and filamentous species (e.g., *Aphanocapsa* spp., *Planktolyngbya* spp., *Merismopedia* spp.) dominated at each station (76–95 %), followed by Chlorophyta (5–21 %), whereas the contribution of Bacillariophyceae was small (0–6 %). Phytoplankton densities were generally higher in the rainy season and strongly increased going land-inward from the open lake. Low abundance of N-fixing phytoplankton species suggests that N-fixation was low. The chlorophyll *a* content in the mouth of the Gulf was low (mean values 4–6 µg/L) compared to values reported previously. Also, chlorophyll *a* values (means 11–14 µg/L) at land-inward stations of Mwanza Gulf were much lower than those in the northern gulfs (Napoleon Gulf, Murchison Bay and Nyanza Gulf). Between 2002 and 2009 the phytoplankton composition of Mwanza Gulf changed from a community mostly dominated by Bacillariophyceae into a community dominated by Cyanobacteria. In the open water of Lake Victoria, Bacillariophyceae and Cyanobacteria were both abundant. Cyanobacteria dominated both in the three northern gulfs and Mwanza Gulf, but all four showed substantial differences in species and genus compositions. Phytoplankton composition and abundance in Mwanza Gulf differs in many respects from the open water of Lake Victoria and its three northern gulfs.

Introduction

Lake Victoria endured multiple stresses over the past century including human population growth, increased cultivation of land, meteorological variability, resource extraction, intensive fishing, introduction of exotic species, and, more recently, climate warming (Hecky et al., 2010). A profound shift in its phytoplankton community from Bacillariophyceae through much of the year (Talling, 1966) to near-continuous dominance by filamentous and colonial Cyanobacteria (Kling et al., 2001) has occurred as a result of the enrichment in dissolved phosphorus (P) and nitrogen (N), and depletion of silica (Si). Transition to a novel ecosystem state with a transformed food web and a highly productive algal community may have been triggered by a period of low wind stress followed by regional warming, especially since the 1980s (Hulme et al., 2001; Vollmer et al., 2005). Increasing physical stability and shallower mixing depths (Hecky, 1993) would have contributed to the extensive anoxic and hypoxic conditions that occurred then (Hecky et al., 1994). More recently, increased wind stress (Kolding et al., 2008; van Rijssel, 2014) resulted in deeper mixing and decreased stratification, which improved visibility and oxygen conditions to levels of before 1987, and to reduced chlorophyll *a* concentrations (Cornelissen, 2015; Sitoki et al., 2010).

Until now most algological studies were carried out in the Ugandan and the Kenyan waters of Lake Victoria (e.g., Cózar et al., 2012; Guildford et al., 2003; Haande et al., 2011; Lung'ayia et al., 2000; Mugidde, 2001; North et al., 2008; Okello et al., 2010; Silsbe et al., 2006; Talling, 1987, 1966), whereas the Tanzanian waters represent 35,088 km^2 corresponding to ca. 51 % of the total lake surface area. Studies on the abundance and distribution of phytoplankton taxa at the Tanzanian side of the lake are especially scarce. The studies of Akiyama et al. (1977), Mbonde et al.

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* Corresponding author.
E-mail address: Leo.Nagelkerke@wur.nl (L.A.J. Nagelkerke).
[1] Present address.

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(2015, 2004), Sekadende et al. (2005), and Ngupula et al. (2011) are notable exceptions. The studies of Mbonde et al. (2015, 2004) are limited to the phytoplankton of the nearshore waters of Lake Victoria, whereas Ngupula et al. (2011) also included offshore and far offshore sites. In Tanzanian waters Bacillariophyceae were found to dominate in abundance and were uniformly distributed in all waters (Ngupula et al., 2011). The next most abundant group was Cyanobacteria, with decreasing abundances towards the more offshore locations. Chlorophyta were on average the least abundant of the three main taxa but increased in relative abundance towards the more offshore locations. At the far offshore sites Chlorophyta showed similar densities as Cyanobacteria (Ngupula et al., 2011).

Despite the ongoing nutrient loading into the lake, phytoplankton biomass has not increased since the 1990s (Haande et al., 2011; Silsbe et al., 2006; Sitoki et al., 2010) and is now supposedly light-limited in Lake Victoria and its highly eutrophic gulfs in the north (e.g., Cózar et al., 2012; Silsbe et al., 2006). However, chlorophyll *a* concentrations observed in Mwanza Gulf (Cornelissen et al. 2014; Shayo et al. 2011) were in general two- to threefold lower than in highly eutrophic gulfs in Uganda, such as Napoleon and Murchison Bay (Cózar et al., 2007; Haande et al., 2011; Lehman and Branstrator, 1993; Mugidde, 2001; North et al., 2008; Okello et al., 2010; Silsbe et al., 2006; Yasindi and Taylor, 2003). A difference in seasonal cooling cycles between northern and southern Lake Victoria may explain the general lower chlorophyll *a* concentrations in Southern Lake Victoria (Cózar et al., 2012). Furthermore, Cornelissen et al. (2014) showed that besides light, nutrients can be limiting photosynthesis in Mwanza Gulf. Therefore, a further increase in nutrient loadings and climate change affecting monsoon cycles, could lead to higher chlorophyll *a* concentrations, higher primary production and shifts in phytoplankton species composition in Mwanza Gulf.

The phytoplankton community of Mwanza Gulf was only studied twice before: by Akiyama et al. (1977) during 1973–1975 and by Sekadende et al. (2005) in May to August 2002. Akiyama et al. (1977) studied the seasonal variation of the fourteen main phytoplankton genera at one station in the middle of the Gulf, close to the Tanzania Fisheries Research Institute. At that time Bacillariophyceae such as *Aulacoseira* and *Nitzschia* dominated the phytoplankton whereas the Cyanobacteria *Dolichospermum* sp. (formerly named *Anabaena*) showed high densities during the rainy season particularly in the surface layers. Sekadende et al. (2005) studied the variation of the biovolume of the four main taxa from May to August (mostly dry season) at two stations, one inshore, close to Mwanza city in 3 m deep water and one offshore in Luchiri Bay close to Kome Island. The phytoplankton community was, in terms of biovolume, dominated by Bacillariophyceae: mainly *Nitzschia acicularis* and unidentified centric diatoms. The Cyanobacteria *Planktolyngbya* spp. and *Aphanocapsa* sp. contributed substantially to the biovolume of total phytoplankton, whereas *Dolichospermum* sp. and *Microcystis* spp. were low in abundance. No significant differences were found in phytoplankton composition between the offshore and inshore stations and no accumulation of Cyanobacteria in the surface layers was reported, as was reported earlier by Akiyama et al. (1977).

A more detailed analysis of the spatial and temporal patterns in phytoplankton composition and abundance in Mwanza Gulf is still lacking, but urgently needed, especially at this time when the environment of Lake Victoria is rapidly changing. Therefore, the aim of this study is to provide a detailed baseline report on the composition and abundance of phytoplankton in the Mwanza Gulf of Lake Victoria, and to assess how these vary along an inshore – offshore gradient and between seasons. The results are discussed in the context of recorded historical changes in Lake Victoria and of differences between the northern and southern parts of the lake.

Methods

Study area

Samples were collected at 3 stations in Mwanza Gulf (Fig. 1). Mwanza Gulf is located in south-east Lake Victoria in Tanzania and is about 60 km long, 2.5–11 km wide, 3–25 m in depth, and covers a surface area of approximately 500 km^2 (Witte and van Densen, 1995). Mwanza City is located near the entrance of the Gulf at its northern edge (Fig. 1) where the shoreline is completely urbanized. Outside the city range, the littoral zone is characterized by a mixed vegetation of papyrus, *Cyperus papyrus* L.), reeds (e.g., *Phragmites australis* (Cav.) Trin. Ex Steud.) and water hyacinth (*Eichhornia crassipes*, (Martius) Solms-Laubach), and by rock formations. The bottom of Mwanza Gulf consists of soft, fine-grained sediment. The south of the Gulf at station 1 is shallow with a depth of <5 m (Fig. 1). This area can be considered as a littoral habitat with benthic and terrestrial influences. Station 3 is located in the open lake outside the Gulf with a depth of 25–28 m (Fig. 1). This area can be considered as a pelagic habitat. Station 2 has an intermediate depth range of 6–8 m with both littoral and pelagic habitat characteristics (Fig. 1).

Climate

The climate in Lake Victoria is characterized by three seasons, based on the yearly monsoon cycles. During the cooler dry season, from June to August, strong southerly winds and low precipitation keep the water well-mixed, isothermal, and oxygenated (Akiyama et al., 1977; Talling, 1966). During the short rainy season, from September to December, winds decline and rainfall and temperature increase, warming up the surface layer of the water column, which becomes gradually stratified. During the long rainy season, from January to May, precipitation is high, and stratification of the water column becomes strong (Talling, 1966).

Sampling

Seston was sampled between 10:00 h and 14:00 h during five days in the period 31 August–7 September 2010 (towards the end of the dry season, with ca. 6 mm rainfall in September), and on four days in the period 2–10 April 2011 (during the wet season, with ca. 130 mm rainfall in April) at each of the three stations (Fig. 1), resulting in a total of 27 samples. Each of these samples consisted of subsamples taken at three separate locations per station, each ca. 500 m apart. Each subsample was taken with a volume sampler (Offenberg) at three different depths: just below the surface, at the euphotic depth and at intermediate depth. Because stations had different depths sampling depths also differed. Water from all depths and locations per station were pooled. Immediately after return to the laboratory the chlorophyll *a* content was measured with a Hydrolab DS5 multiprobe (OTT Messtechnik GmbH and Co, Kempten, Germany). For the analysis of phytoplankton composition, the pooled samples from each station, taken on 4 April and 1 September were used (total of six pooled samples).

Phytoplankton analysis

For phytoplankton analysis, a well-mixed, 1-litre subsample of lake water was taken from each of the abovementioned six pooled samples. Each subsample was placed in a glass bottle and fixed with 5 mL Lugol's iodine solution. After 1 week the upper layer was siphoned off with a pipette, the lower layer (ca. 200 mL) containing the sedimented algae was stirred and transferred to a

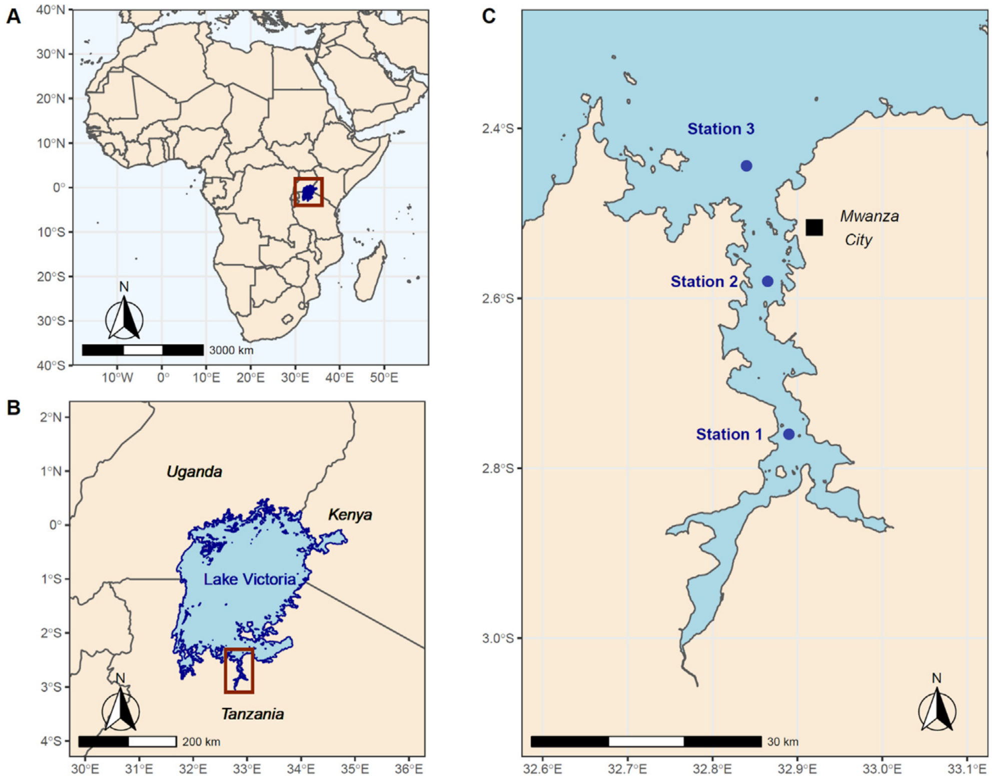

Fig. 1. Locations of the three sampling stations (stations 1, 2 and 3) in the Mwanza Gulf. Station 1 has a depth range of < 5 m, station 2 a depth range of 6–8 m and station 3 a depth range of 25–28 m.

250 mL bottle. After 1 week the upper layer was again siphoned off and the lower layer (ca. 45 mL) with the sedimented algae was then transferred to a 50 mL polyethylene tube and preserved with 2.3 mL 40 %-formaldehyde solution. Finally, distilled water was added to a volume of exactly 50 mL. Samples were stored in a refrigerator or cool box until microscopic analysis.

A fixed volume of concentrated sample was used for microscopic identification, counting, and measuring of phytoplankton individuals. After careful homogenization, one drop (0.05336 mL) of the sample was transferred to a microscope slide and covered by a standard cover slip with a surface area of 400 mm^2. To prevent evaporation, the edges of the cover slip were sealed with nail polish. After drying, the prepared mount was observed top-down with an inverted microscope (Leitz diavert) at 400-times magnification. The surface area in which the phytoplankton individuals were counted was measured with an ocular square grid, which was divided in 100 squares of (0.02935 mm)^2. A total of 210–305 individuals were counted in different grids.

Phytoplankton species were identified using the species descriptions of Huber-Pestalozzi (1938), Komárek and Kling (1991), Komárek and Anagnostidis (1999), Komárek et al. (2002), Komárek and Anagnostidis (2005), and Komárek (2013) for Cyanobacteria, those of Huber-Pestalozzi (1942), Krammer and Lange-Bertalot (1986), Krammer and Lange-Bertalot (1988) and Krammer and Lange-Bertalot (1991) for Bacillariophyceae, and those of Coesel and Meesters (2007) and Komárek and Fott (1983) for Chlorophyta. In addition, the keys of Prescott (1962) as well as Talling (1987) on Lake Victoria were consulted. Nomenclatural authorities and abbreviations for species are given in Table 1. Higher taxa were checked in AlgaeBase (Guiry and Guiry, 2022).

Phytoplankton species densities (individuals mL^{-1}) were estimated by counting all individuals, whether these were single cells, colonies, or filaments. We defined colonies as individuals consisting of two or more cells. Thus, also Chlorococcales species, such as *Scenedesmus*, where individuals mostly contain only a few cells, were categorized as colonies. Spherical, elliptical, and short cylindrical unicellular individuals (<4.5 μm) were counted from diameter 2 μm, and elongated unicellular or filamentous individuals from a length of 4.5 μm, even with diameters < 2 μm. Colonial individuals were always counted, even if the diameter of their composing cells was < 2 μm.

Within Cyanobacteria and Chlorophyta, we distinguished five morpho-functional groups (MFG), an approach based on morphological and structural traits (Salmaso and Padisák, 2007). These MFG’s were: 1) colonies without mucus; 2) colonies with mucus; 3) filaments without heterocytes; 4) filaments of taxa which generally developed heterocytes; and 5) single cells.

We also characterised the whole phytoplankton community at the three stations in the two seasons by their size structure. Size was estimated by the largest dimension of phytoplankton individuals.

Statistics

Effects of station and season on chlorophyll *a* contents were analysed through ANOVA, followed by testing for pairwise comparisons with Tukey’s range test. Normality and homoscedasticity of residuals were checked through visual inspection of Q-Q plots. The effects of station and season on size distributions of phytoplankton were analysed through pairwise Chi-square tests with the Holm–Bonferroni method to control for multiple comparisons. All statistical analyses were performed in R, version 4.1.0 (R Core Team, 2021). All data can be found in Frank et al. (2023).

Results

Mean phytoplankton biomass was measured as μg L^{-1} chlorophyll *a* content (Fig. 2). There was a statistically significant spatial

Table 1
List of phytoplankton species recorded in August/September 2010 (dry season) and April 2011 (rainy season) in stations 1, 2 and 3: (+) present and (–) absent.

Species	Dry season			Rainy season		
	St. 1	St. 2	St. 3	St. 1	St. 2	St. 3
Cyanobacteria						
Anabaenopsis arnoldii Apt	–	–	–	–	–	+
Aphanizomenon cf. *gracile* (Lemm.) Lemm.	+	+	–	–	–	–
Aphanocapsa delicatissima W. et G.S. West	+	+	+	+	+	+
Aphanocapsa elachista W. et G.S. West	+	+	+	+	+	+
Aphanocapsa koordersii Ström	+	+	+	+	+	–
Aphanocapsa nubilum Kom. et Kling	+	+	+	+	+	+
Aphanocapsa stagnalis sensu Kom. et Anagn. in Kom. and Anagn. 1999	–	–	–	–	–	+
Aphanothece cf. *smithii* Kom.-Legn. et Cronberg	–	+	+	+	+	+
Aphanothece clathrata W. et G.S. West	+	+	+	+	+	–
Aphanothece comasii Kom.-Legn. et Tavera	+	–	–	–	–	–
Aphanothece stagnina (Spreng.) A. Br.	–	+	–	+	+	–
Borzia sp.	–	–	–	–	+	–
Chroococcus dispersus (Keissl.) Lemm.	+	+	–	+	+	–
Chroococcus distans (G.M. Smith) Kom.-Legn. et Cronberg	+	+	+	–	+	–
Chroococcus minimus (Keissl.) Lemm.	–	–	–	+	+	+
Chroococcus sp.	–	+	–	–	–	–
Coelomoron pusillum (van Goor) Kom.	–	–	–	–	–	+
Coelosphaerium kuetzingianum Näg.	+	–	–	–	+	–
Coelosphaerium cf. *punctiferum* Kom. et Kom.-Legn.	–	–	–	–	–	+
Cyanodictyon cf. *endophyticum* Pascher	–	–	+	–	–	–
Cyanodictyon cf. *filiforme* Kom.-Legn. et Cronberg	+	–	–	–	–	–
Cyanodictyon imperfectum Cronberg et Weibull	+	+	–	+	–	–
Cyanodictyon cf. *planctonicum* Meyer	–	–	–	+	+	+
Cyanodictyon cf. *reticulatum* (Lemm.) Geitl.	+	+	–	+	+	+
Cylindrospermopsis africana Kom. et Kling	+	+	–	+	–	–
Cylindrospermopsis cuspis Kom. et Kling	–	–	–	+	–	–
Cylindrospermopsis helicoidea Cronberg et Kom.	+	–	–	–	+	–
Cylindrospermopsis cf. *philippinensis* (Taylor) Kom.	–	–	–	+	+	–
Cylindrospermopsis cf. *raciborskii* (Wolosz.) Seenayya et Subba Raju	–	–	–	+	–	–
Dolichospermum flos-aquae (Bréb. ex Born. et Fl.) Wacklin et al	–	–	–	–	–	+
Lemmermanniella pallida (Lemm.) Geitl.	–	+	–	–	–	–
Leptolyngbya lagerheimii (Gom.) Anagn. et Kom.	–	–	–	–	–	+
Merismopedia punctata Meyen	+	+	+	+	+	–
Merismopedia tenuissima Lemm.	+	+	+	+	+	+
Merismopedia sp.	+	–	+	–	–	–
Microcystis cf. *firma* (Kütz.) Schmidle	–	–	–	–	+	–
Microcystis panniformis Kom. et al.	+	+	+	+	+	+
Microcystis sp.	+	–	+	–	+	–
Pannus cf. *planus* Hind.	–	+	–	–	–	–
Pannus cf. *spumosus* Hickel	–	–	–	–	–	+
Planktolyngbya circumcreta (G.S. West) Anagn. et Kom.	+	+	+	+	+	+
Planktolyngbya contorta (Lemm.) Anagn. et Kom.	+	+	+	+	+	+
Planktolyngbya limnetica (Lemm.) Kom.-Legn. et Cronberg	+	+	+	+	+	+
Planktolyngbya cf. *microspora* Kom. et Cronberg	–	–	–	–	+	–
Planktolyngbya cf. *minor* (Geitl.) Kom. et Cronberg	–	–	+	–	–	–
Planktolyngbya undulata Kom. et Kling	–	+	–	–	–	–
Pseudanabaena cf. *catenata* Lauterborn	–	–	–	–	+	–
Pseudanabaena mucicola (Naum. et Hub.-Pest.) Schwabe	–	–	+	–	+	+
Pseudanabaena cf. *raphidioides* (Geitl.) Anagn. et Kom.	–	–	–	–	–	+
Rhabdoderma lineare Schmidle et Lauterborn	–	–	+	+	–	+
Romeria cf. *elegans* Wolosz. et Koczw. ex Geitl.	–	–	–	+	+	+
Romeria victoriae Kom. et Cronberg	–	–	–	–	–	+
Romeria sp.	–	–	+	–	–	–
Spirulina abbreviata f. *minor* sensu Hortob. in Kom. et Anagn. 2005	–	–	–	+	–	–
Spirulina laxissima G.S. West	+	+	–	+	+	–
Chlorophyta						
Ankistrodesmus falcatus (Corda) Ralfs	–	–	–	–	–	+
Choricystis cf. *guttula* Hind.	–	+	–	–	–	–
Closterium acutum var. *variabile* (Lemm.) Willi Krieg.	–	–	+	–	–	–
Coelastrum pulchrum Schmidle var. *Pulchrum*	–	–	+	–	–	–
Coelastrum reticulatum (Dang.) Senn	+	–	–	–	–	–
Crucigeniella apiculata (Lemm.) Kom.	+	–	–	–	–	–
Dictyosphaerium subsolitarium van Goor	+	+	+	–	–	–
Dictyosphaerium cf. *tetrachotomum* Printz	–	–	–	–	–	+
Eutetramorus sp.	–	–	+	–	–	–
Kirchneriella mayori (G.S. West) Kom.-Legn.	+	–	–	–	–	+
Kirchneriella cf. *obesa* var. *pygmaea* W. et G.S. West	+	–	–	–	–	–
Kirchneriella subcapitata Korš.	+	+	–	–	–	–
Kirchneriella sp.	–	–	+	–	–	–
Lagerheimia genevensis (Chod.) Chod.	+	–	–	–	–	–
Monoraphidium arcuatum (Korš.) Hind.	+	+	–	–	+	+

Table 1 (*continued*)

Species	**Dry season**			**Rainy season**		
	St. 1	St. 2	St. 3	St. 1	St. 2	St. 3
Monoraphidium caribeum Hind.	–	–	+	–	+	–
Monoraphidium (cf.) *contortum* (Thur.) Kom.-Legn.	+	+	+	+	–	+
Monoraphidium griffithii (Berk.) Kom.-Legn.	+	+	+	–	–	–
Monoraphidium komarkovae Nyg.	–	+	–	–	–	+
Monoraphidium mirabile (W. et G.S. West) Pankow	–	–	+	–	–	+
Monoraphidium pseudobraunii (Belch. et Swale) Heynig	+	–	–	–	–	–
Monoraphidium tortile (W. et G.S. West) Kom.-Legn.	+	–	–	–	–	–
cf. *Nephrocytium* sp. Näg.	+	+	+	–	+	+
Oocystis lacustris Chod.	–	–	–	–	+	–
Oocystis cf. *parva* W. et G.S. West	+	–	–	–	–	–
Oocystis sp.	–	–	+	+	–	–
Pediastrum simplex Meyen var. *simplex*	+	–	–	–	–	–
Pediastrum tetras (Ehrenb.) Ralfs	–	–	+	–	–	–
Scenedesmus acuminatus (Lagerh.) Chod.	+	–	–	–	–	–
Scenedesmus acuminatus var. *elongatus* G.M. Smith sensu Hortob. 1969	–	–	–	+	–	–
Scenedesmus ecornis (Ehrenb.) Chod.	+	–	–	–	–	+
Scenedesmus (*Desmodesmus* sensu stricto) sp.	+	–	–	–	–	–
Schroederia nitzschioides (G.S. West) Korš.	–	–	–	–	+	–
Schroederia setigera (Schröd.) Lemm.	–	–	–	–	–	+
Selenastrum capricornutum Printz	–	–	+	–	–	–
Staurastrum gracile var. *nyansae* G.S. West	–	–	–	–	+	–
Teilingia sp.	+	–	–	+	–	–
Tetrachlorella alternans (G.M. Smith) Korš.	–	+	–	–	–	–
Tetraedron minimum (A. Br.) Hansg.	–	–	–	+	+	–
Bacillariophyceae						
Aulacoseira ambigua (Grun.) Sim.	–	–	–	–	+	–
Aulacoseira granulata (Ehrenb.) var. *angustissima* (O. Müll.) Sim.	–	–	–	–	+	–
Fragilaria sp.	–	–	–	–	+	–
Navicula cf. *rhynchocephala* Kütz.	+	+	–	+	–	–
Nitzschia acicularis (Kütz.) W. Smith	+	+	+	–	+	+
Nitzschia fonticola var. *pelagica* Hust.	+	+	–	–	+	–
Nitzschia cf. *paleacea* (Grun.) Grun.	–	–	–	–	+	+
Nitzschia lacustris Hust.	–	–	+	–	+	+
Rhizosolenia eriensis H.L. Smith	–	–	–	–	+	–
Rhizosolenia sp.	–	–	+	–	–	–
Synedra (*Fragilaria*) *cunningtonii* G.S. West	–	–	+	+	+	+

effect of station on chlorophyll-content (ANOVA: $F_{2,\ 21}$ = 130.4, p < 0.0001), with the highest values at the land-inward side of the gulf (station 1) and lowest values at the lakeside mouth of the gulf (station 3). There was no significant effect of season ($F_{1,\ 21}$ = 0.032, p = 0.86) per se, but the interaction between station and season was significant ($F_{2,\ 21}$ = 6.11, p = 0.008), which was apparent from station 1 having a statistically significant higher chlorophyll *a* concentration than station 2 in the dry season, but not in the rainy season (Fig. 2).

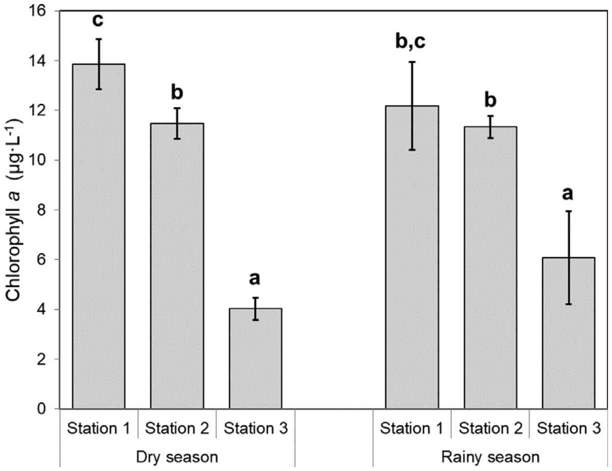

Fig. 2. Mean chlorophyll *a* content (mean ± SD, µg/L) in Mwanza Gulf at sampling stations 1, 2 and 3 in August/September 2010 (dry season) and April 2011 (rainy season). Different letter markers indicate statistically significant differences (P < 0.05).

More than 92 % of all planktonic organisms could be identified to at least genus level, and more than 99 % to the main phytoplankton groups. A total of at least 105 phytoplankton species were identified during the study (Table 1). There were 55 Cyanobacteria species, 39 Chlorophyta species, and 11 Bacillariophyceae species. Euglenophyceae, Dinophyceae, or Chrysophyceae species were not found. We observed clear patterns of spatial and temporal variation in species presence/absence. Species numbers varied between 31 and 44 per station per season, with 8 species being shared by all stations in every season and between 4 and 12 species being unique for a season-station combination (Table 1).

The six most abundant genera belonged to the Cyanobacteria: *Aphanocapsa* spp. (20–44 %), *Planktolyngbya* spp. (5–26 %), *Merismopedia* spp. (5–14 %), *Aphanothece* spp. (0.6–14 %), *Cyanodictyon* (0.2–6 %), and *Chroococcus* (0.1–5 %) (Table 2). Only the seventh most abundant genus was a *Nephrocytium*-like green alga (0–9 %). Fifteen genera represented > 87 % of the observed individuals (overall mean of all stations in both seasons). Of these genera, eleven were Cyanobacteria, three were Chlorophyta, and only one belonged to the Bacillariophyceae (Table 2).

Each station was dominated by Cyanobacteria (76–95 %), followed by relative low numbers of Chlorophyta (5–21 %), while the contribution of the Bacillariophyceae was insignificant (0.3–6 %) (Fig. 3). In both seasons we observed relatively high total phytoplankton values at the land-inward side of the Gulf (station 1), relatively low values at the mouth of the Gulf (station 3) and intermediate values half-way (station 2). In the rainy season

Table 2
Relative densities (individuals, %) in sequence of decreasing abundance of the twelve most abundant genera (together > 80 % of individuals observed) of phytoplankton in the Mwanza Gulf of Lake Victoria during August/September 2010 (dry season) and April 2011 (rainy season) in stations 1, 2 and 3.

Genus	**Group**	**Dry season**			**Rainy season**			**Overall percentage**
		St. 1	St. 2	St. 3	St. 1	St. 2	St. 3	
Aphanocapsa	Cyanobacteria	44.3	38.5	32.0	19.6	35.7	23.3	30.4
Planktolyngbya	Cyanobacteria	15.8	14.1	9.7	26.1	10.9	4.8	18.1
Merismopedia	Cyanobacteria	12.4	9.5	10.4	13.8	10.5	4.8	11.9
Aphanothece	Cyanobacteria	0.6	3.9	5.1	12.5	13.9	5.3	9.0
Cyanodictyon	Cyanobacteria	3.4	2.3	0.2	5.6	0.7	3.0	3.5
Chroococcus	Cyanobacteria	0.6	1.1	0.1	3.5	4.7	1.7	2.8
cf. Nephrocytium	Chlorophyta	4.7	8.9	2.0	0.0	3.9	2.5	2.8
Monoraphidium	Chlorophyta	3.8	3.7	2.2	0.3	0.5	3.8	1.6
Microcystis	Cyanobacteria	2.3	0.3	10.9	0.9	0.6	2.5	1.4
Spirulina	Cyanobacteria	0.9	0.5	0.0	2.7	0.3	0.0	1.4
Cylindrospermopsis	Cyanobacteria	1.0	0.2	0.0	2.5	0.3	0.0	1.3
Tetraedron	Chlorophyta	0.0	0.0	0.0	1.8	1.0	0.0	1.0
Nitzschia	Bacillariophyta	0.1	0.4	1.8	0.0	2.2	5.9	0.9
Pseudanabaena	Cyanobacteria	0.0	0.0	1.0	0.0	1.5	6.7	0.7
Romeria	Cyanobacteria	0.0	0.0	0.3	0.3	2.0	2.3	0.7
Unidentified genera		3.9	10.2	13.9	7.5	9.1	17.3	7.9
Sum		93.8	93.8	89.5	97.0	97.8	83.8	95.4

densities of total phytoplankton at all sites were clearly higher than in the dry season.

Twelve phytoplankton species with mean densities higher than 1,000 individuals mL^{-1}, represented together more than 78 % of the total densities of taxa. Eleven of these abundant species belonged to the Cyanobacteria, one to the Chlorophyta and none to the Bacillariophyceae (Table 3). Of these twelve species, ten were forming colonies, nine Cyanobacteria and one green alga. Remarkably, all these ten colonial species consist of cells of picophytoplankton size (i.e., diameter of cells < 3 μm). Their cells were mostly spherical, elliptical, short rounded and rod-shaped, or short fusiform and surrounded by much mucus. The mean contribution of these ten colonies was 62 % and 54 % of the total individuals in the dry- and rainy season respectively.

Densities of the twelve most abundant species were generally higher in the rainy season. This was particularly the case at stations 1 and 2 where densities were approximately twice as high as in the dry season (Table 3). Most of them decreased strongly in both seasons from the land-inward end of the Gulf towards the lake. *Aphanocapsa elachista*, *A. nubilum*, *Aphanothece* cf. *smithii*, *A. clathrata*, *Chroococcus minimus*, *Cyanodictyon imperfectum*, *Merismopedia punctata*, *Planktolyngbya contorta*, and *P. limnetica* all showed their strongest decrease from station 1 towards station 3 in the rainy season (from 88 to 100 %). In contrast, *Aphanocapsa delicatissima*, *Merismopedia tenuissima*, and cf. *Nephrocytium* sp. showed their strongest decrease in the dry season (from 95 to 97 %). The only species increasing from the land-inward end of the Gulf towards the lake was *Aphanothece* cf. *smithii* in the dry season, although with very low densities. *Aphanocapsa elachista* and cf. *Nephrocytium* sp. showed highest densities in the middle of the Gulf (station 2), in the dry and rainy seasons respectively.

The mean numerical abundances of the morpho-functional groups (MFG) show the same tendencies in both seasons (Fig. 4): high abundances of colonies with mucus, moderate abundances of filaments without heterocytes (N-fixing cells) and individual cells, and low densities of colonies without mucus, and of filaments with heterocytes. Almost all groups, except for colonies without mucus and single cells in the dry season, were dominated by Cyanobacteria. Absolute densities were generally higher in the rainy season.

Eight cyanobacterial filamentous species, belonging to four genera of the Aphanizomenonaceae family, possessed heterocytes, but they were present at low densities and were not observed at each station (Table 4). The low abundances of Cyanobacteria with heterocytes in the Mwanza Gulf indicated that phytoplankton growth is not *N*-limited. *Cylindrospermopsis* spp. and *Aphanizomenon* cf. *gracile* showed higher densities at the land-inward side of the gulf (station 1). *Anabaenopsis arnoldii* and *Dolichospermum flos-aquae* were exclusively found at the lake side (station 3) and only observed in the rainy season (Table 4).

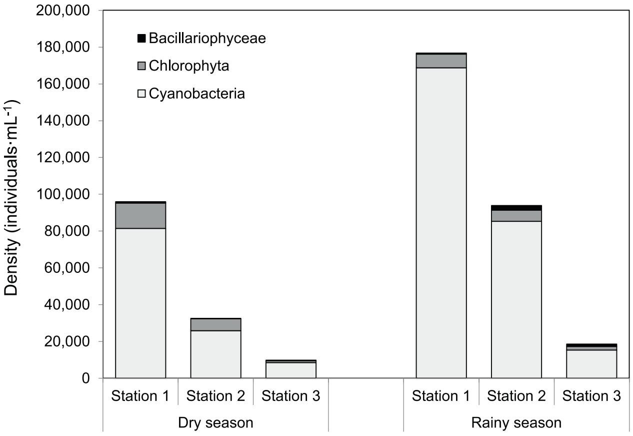

Fig. 3. Density (individuals mL^{-1}) of phytoplankton main taxa in Mwanza Gulf of Lake Victoria in August/September 2010 (dry season) and April 2011 (rainy season).

Lengths of phytoplankton individuals ranged from 2 to 914 μm. Small individuals (log$_2$ size classes 1–3, i.e., ranging from 2 to 11 μm) dominated the phytoplankton community in both seasons and at all three stations (43–62 % of all individuals). More than 95 % of all individuals belong to log$_2$ size classes 6 or smaller, i.e., <90μ. Differences between stations and seasons were statistically significant (χ^2 = 109.7, d.f. = 35, p = 0.0005), but small. The most land-inward station (station 1) was less dominated by small individuals (43 % in the rainy and 45 % in the dry season) than stations 2 and 3 (52–62 % and 58–60 % in the rainy and dry seasons respectively).

Discussion

The phytoplankton of Mwanza Gulf is not as well-studied as the plankton of the northern gulfs of Lake Victoria. We know only of two previous studies: one was carried out between 1973 and

Table 3
Absolute densities (individuals mL^{-1}) of the twelve most abundant species (average density ≥ 1,000 individuals mL^{-1}) of phytoplankton in the Mwanza Gulf of Lake Victoria during August/September 2010 (dry season) and (b) April 2011 (rainy season) in stations 1, 2 and 3. These species together represent > 75 % of the total density of all taxa.

Species	Group	Dry season			Rainy season			Mean density (numbers·mL^{-1})	Overall percentage
		St. 1	St. 2	St. 3	St. 1	St. 2	St. 3		
Aphanocapsa delicatissima	Cyanobacteria	16,751	7,074	826	9,202	28,007	4,139	11,000	15.2
Aphanocapsa nubilum	Cyanobacteria	26,628	4,905	1,818	23,906	3,036	694	10,165	14.1
Planktolyngbya limnetica	Cyanobacteria	12,230	2,997	203	30,851	7,267	414	8,994	12.4
Merismopedia tenuissima	Cyanobacteria	9,002	2,898	261	19,556	10,511	1,087	7,219	10.0
Aphanothece cf. smithii	Cyanobacteria	0	477	540	17,473	10,993	1,190	5,112	7.1
Planktolyngbya contorta	Cyanobacteria	3,019	1,897	534	14,794	3,517	595	4,059	5.6
Aphanocapsa elachista	Cyanobacteria	241	1,975	992	3,543	5,734	415	2,150	3.0
cf. Nephrocytium sp.	Chlorophyta	4,738	3,243	227	0	4,072	560	2,140	3.0
Merismopedia punctata	Cyanobacteria	3,341	550	818	6,727	337	0	1,962	2.7
Cyanodictyon imperfectum	Cyanobacteria	2,843	548	0	7,330	0	0	1,787	2.5
Aphanothece clathrata	Cyanobacteria	96	808	38	4,216	2,367	0	1,254	1.7
Chroococcus minimus	Cyanobacteria	0	0	0	3,318	2,367	378	1,011	1.4
Sum		78,889	27,372	6,257	140,916	78,208	9,472	56,852	78.6

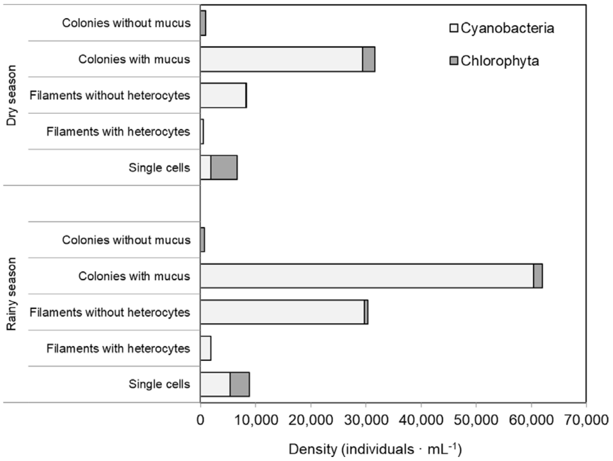

Fig. 4. Density (individuals mL^{-1}) of morpho-functional groups (MFG) for Cyanobacteria and Chlorophyta in Mwanza Gulf of Lake Victoria in August/September 2010 (dry season) and April 2011 (rainy season).

1975 (Akiyama et al., 1977), another in 2002 (Sekadende et al., 2005). Therefore, the primary aim of this study was to bridge that gap and provide a detailed baseline report on the composition and abundance of the phytoplankton community in Mwanza Gulf. To that end we applied a sampling strategy focused on two contrasting seasons, and along a stable and large-scale (>30 km) inshore – offshore gradient. As we also sampled the whole water column at three locations per station, we are confident that our aggregated samples give a reliable representation of phytoplankton composition and abundances, and of the variation between stations and seasons. We acknowledge however, that the limited extent of the sampling programme does not allow for detailed analysis of spatial and temporal dynamics of phytoplankton in Mwanza Gulf.

The two aforementioned studies from Mwanza Gulf generally showed a dominance of Bacillariophyceae, although the findings of Akiyama et al. (1977) are not comparable to our results, as their samples were filtrated through a 110-μm plankton net after collection, which resulted in under-representation of small algae, which, at the time of our study, were the most dominant algae in Mwanza Gulf (Fig. 5). Sekadende et al. (2005) also reported that Bacillariophyceae, mainly represented by *Nitzschia acicularis* and unidentified centric diatoms, were generally dominating the phytoplankton community. This strongly contrasts with our present study, which indicates a numerical dominance of Cyanobacteria in both seasons and all three stations (Fig. 3). The latter is supported by another study carried out between 2009 and 2011 (Cornelissen et al. 2014). It appears that between 2002 and 2009 the relative abundances of the major phytoplankton phyla changed drastically from a community dominated by Bacillariophyceae into a community dominated by Cyanobacteria.

Besides the dominance of Bacillariophyceae, Sekadende et al. (2005) found that, similar to our findings, *Planktolyngbya* spp. and *Aphanocapsa* spp. were the most abundant Cyanobacteria, while *Dolichospermum* (formerly named *Anabaena* spp.) and *Microcystis* spp. were relatively scarce. In our study diatoms were scarce, with *Nitzschia* spp., especially *N. fonticola* var. *pelagica* and *N. acicularis*, being the most common, next to small unidentified centric diatoms, which also agrees with Sekadende et al. (2005). The contribution of Chlorophyta to total phytoplankton in our study was higher than in the study of Sekadende et al. (2005), who did not even explicitly mention any of the Chlorophyta species. Thus, although the relative densities of the main groups changed

Table 4
Absolute densities (individuals mL^{-1}) of the species of Cyanobacteria which may possess heterocytes (N-fixing cells) in the Mwanza Gulf of Lake Victoria, Tanzania in the dry season (August/September 2010) and the rainy season (April 2011) at stations 1, 2 and 3.

Species	Dry season			Rainy season			Mean density (numbers·mL^{-1})	Overall percentage
	St. 1	St. 2	St. 3	St. 1	St. 2	St. 3		
Anabaenopsis arnoldii	0	0	0	0	0	200	33	0.04
Aphanizomenon cf. gracile	193	79	0	0	0	0	45	0.06
Cylindrospermopsis africana	482	79	0	519	0	0	180	0.23
Cylindrospermopsis cuspis	0	0	0	2,653	169	0	470	0.61
Cylindrospermopsis helicoidea	0	0	0	519	0	0	87	0.11
Cylindrospermopsis cf. philippinensis	0	0	0	1,039	0	0	173	0.22
Cylindrospermopsis cf. raciborskii	474	0	0	0	169	0	107	0.14
Dolichospermum flos-aquae	0	0	0	0	0	898	150	0.19
Sum	1,149	158	0	4,730	338	1,098	1,245	1.61

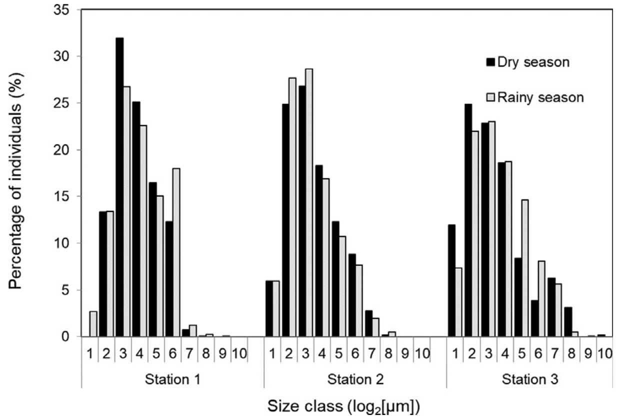

Fig. 5. Size structure (%) of the phytoplankton community in Mwanza Gulf of Lake Victoria in August/September 2010 (dry season) and April 2011 (rainy season) at sampling stations 1, 2 and 3. Size classes are indicated as a log$_2$-scale.

between 2002 and 2009, the taxonomic composition of Cyanobacteria and Bacillariophyceae remained similar.

An important question is how the phytoplankton biomass and taxonomic composition of Mwanza Gulf compares to the open water of Lake Victoria and to other gulfs in the north of Lake Victoria: Napoleon Gulf and Murchison Bay in Uganda, and Nyanza Gulf in Kenya.

First, phytoplankton biomass (expressed as concentrations of chlorophyll *a*) is considered. Before 1980 chlorophyll *a* concentrations in Lake Victoria were low (3.0–4.6 µg·L^{-1}) in both offshore and inshore waters, but from 1980 onwards these values rapidly rose to an average of 40 and 60 µg·L^{-1} in offshore and inshore waters respectively (Sitoki et al., 2010). A more recent series of lake-wide surveys revealed that the concentrations of chlorophyll *a* in the surface layer of the lake were much lower than in the 1980s and remained constant between 2000 and 2001 (mean of 9.7 µg·L^{-1}) and between 2005 and 2009 (mean of 10.6 µg·L^{-1}) (Sitoki et al., 2010). During both periods the concentrations of chlorophyll *a* were somewhat higher in inshore waters (mean 12–15 µg·L^{-1}) than in offshore waters (mean of 6–7 µg·L^{-1}). The values of 4–6 µg·L^{-1} we found in the mouth of the Mwanza Gulf were slightly lower (Fig. 2: station 3).

The algal biomass is distinctly lower in the open water of L. Victoria than in all three northern gulfs and southern Mwanza Gulf (Akiyama et al., 1977; Cornelissen et al., 2014; Cózar et al., 2007; Haande et al., 2011; Lehman and Branstrator, 1993; Lung'ayia et al., 2000; Mugidde, 2001; North et al., 2008; Okello et al., 2010; Shayo et al., 2011; Silsbe et al., 2006; Yasindi and Taylor, 2003). However, the chlorophyll *a* concentrations observed in Mwanza Gulf (Cornelissen et al., 2014; Shayo et al., 2011; present study) were (much) lower than in the highly eutrophic northern gulfs in Uganda and Kenya. Napoleon Gulf is the least eutrophic northern Gulf with mean chlorophyll *a* concentrations of 10–24 µg·L^{-1} in most recent studies (Silsbe et al., 2006; Okello et al., 2010), although earlier studies reported higher levels of 48–71 µg·L^{-1} (Lehman and Branstrator, 1993, Mugidde, 2001). In Murchison Bay, chlorophyll *a* varied between 15–60 µg·L^{-1} (Haande et al., 2011) and Lung'ayia et al. (2000) reported concentrations of 9–71 µg·L^{-1} for Nyanza Gulf, whereas we measured 11–14 µg·L^{-1} in Mwanza Gulf (Fig. 2: stations 1 and 2).

Secondly, when evaluating the taxonomic composition on the phytoplankton community in Lake Victoria, previous studies showed that Bacillariophyceae (especially *Nitzschia acicularis*, but in the 1960′s also *Aulacoseira* spp. and *Cyclostephanos* spp.) and Cyanobacteria (especially *Cylindrospermopsis* spp., *Dolichospermum* spp., *Microcystis* spp., and *Planktolyngbya* spp.) dominated (Kling et al., 2001; Lung'ayia et al., 2000; Mbonde et al., 2004; Ngupula et al., 2011). In most of the above-mentioned studies Bacillariophyceae were either as abundant as Cyanobacteria, or even dominant, with the exception of Kling et al. (2001), who reported that close to Jinja, Uganda, diatoms became of secondary importance after Cyanobacteria in the mid-1990′s. Also, Mbonde et al. (2004), reported a dominance of Cyanobacteria in the Tanzanian parts of the lake during the rainy season of 2002. However, Ngupula et al. (2011) reported a dominance of Bacillariophyceae again at 51 stations in the Tanzanian parts of the lake in the years 2005–2007. These historical species compositions and relative densities are contrasting with those of Mwanza Gulf (present study) and the northern gulfs.

The phytoplankton compositions in the three northern gulfs were different from each other. Okello et al. (2010) found that in 2004 in Napoleon Gulf Cyanobacteria dominated, Chlorophyta were subdominant, and Bacillariophyceae were of minor importance. Of the Cyanobacteria, *Aphanocapsa* spp. and the large colony-forming *Dolichospermum* spp. were the most abundant taxa, followed by *Microcystis* spp. In 2017–2018 Cyanobacteria also dominated, with *Dolichospermum circinale* and *Planktolyngbya circumcreta* as most abundant species. As in 2004, also *Aphanocapsa* spp. and *Microcystis* spp. were abundant (Olokotum et al., 2021).

For Murchison Bay, Okello et al. (2010) reported a similar phytoplankton community composition as for Napoleon Gulf, with a dominance of Cyanobacteria, a lower biovolume of Chlorophyta, and almost no Bacillariophyceae. Also, here *Aphanocapsa* spp., *Dolichospermum* spp., and *Microcystis* were the dominant Cyanobacteria. Haande et al. (2011), in a study in 2003–2004, also found Cyanobacteria to be dominant (62–64 % of total biovolume), with *Dolichospermum* spp. and *Microcystis* spp. as most abundant taxa, but in contrast with Okello et al. (2010), they found Bacillariophyceae to be subdominant (23–31 %) with *Nitzschia acicularis* as most abundant species. 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 in Murchison Bay (Haande et al., 2011). Finally, Olokotum et al. (2021) found that in 2017–2018 Cyanobacteria dominated Murchison Bay, also with *Dolichospermum circinale* and *Planktolyngbya circumcreta* as abundant species, besides *Microcystis flos-aquae* and *M. aeruginosa*.

In Nyanza Gulf Cyanobacteria were abundant and also taxonomically diverse, while Bacillariophyceae and/or Chlorophyta were subdominant. During 1994–2009, Nyanza Gulf was strongly dominated by Cyanobacteria (*Microcystis* spp., *Dolichospermum* sp., *Anabaenopsis* sp. and *Chroococcus* spp.), whereas *Aulacoseira nyassensis* was the most important diatom species (Lung'ayia et al., 2000; Sitoki et al., 2012).

Although Cyanobacteria dominated in all three northern gulfs as well as in Mwanza Gulf, they all showed different phytoplankton compositions. In Napoleon Gulf and Mwanza Gulf Chlorophyta were subdominant, whereas in Murchison Bay and Nyanza Gulf Bacillariophyceae and /or Chlorophyta were subdominant. On the genus and species level there were differences too. For instance, the Cyanobacteria *Dolichospermum* spp. (formerly named *Anabaena*) was rare or absent in Mwanza Gulf, while it was abundant in Napoleon Gulf, Murchison Bay, and Nyanza Gulf. Also, *Gomphosphaeria aponina*, another Cyanobacterium, was found in Murchison Bay and Nyanza Gulf, but absent from Mwanza Gulf. Furthermore, high abundances were found of the diatoms *Aulacoseira granulata* in Murchison Bay and *A. nyassensis* in Nyanza Gulf, whereas they were insignificant in Mwanza Gulf and Napoleon Gulf.

Conclusions

In Mwanza Gulf each station was dominated by Cyanobacteria (76–95 %), followed by relative low numbers of Chlorophyta, whereas the contribution of the Bacillariophyceae was mostly very low. The phytoplankton was dominated by small colonial (with cells of picoplankton size, i.e., < 3 μm), and filamentous Cyanobacteria species. Densities of most species were generally higher in the rainy season and decreased strongly from the land-inward end of the Gulf towards the Lake.

The present study of phytoplankton from Mwanza Gulf showed several substantial differences with previous studies. The chlorophyll *a* content of the water in the mouth of the Gulf was low (mean values 4–6 μg/L) compared to values reported in the literature for inshore stations in the Lake. Also, the chlorophyll *a* values in Mwanza Gulf (mean values 11–14 μg/L) were generally much lower than those measured in the northern Gulfs. Comparison with literature revealed that in 2002 the phytoplankton composition of Mwanza Gulf was dominated by Bacillariophyceae instead of Cyanobacteria.

In the open water of Lake Victoria Bacillariophyceae were, in almost all cases, either as abundant as Cyanobacteria or dominant. In contrast with Mwanza Gulf, *Nitzschia acicularis* was much more numerous there, whereas *Planktolyngbya circumcreta* and *Microcystis* spp. dominated the Cyanobacteria community. Cyanobacteria dominated both in the three northern gulfs and in Mwanza Gulf, but all four showed substantial differences in species and genera compositions. Therefore, we conclude that the phytoplankton composition and abundance in Mwanza Gulf differs in many respects from the open water of Lake Victoria and its three northern gulfs.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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