



High nutrient loading and climatic parameters influence the dominance and dissimilarity of toxigenic cyanobacteria in northern bays of Lake Victoria

Mark Olokotum^{a,b}, Marc Troussellier^c, Arthur Escalas^c, Sahima Hamlaoui^d, William Okello^b, Ronald Semyalo^a, Jean-François Humbert^e, Cécile Bernard^{d,*}

^a Department of Zoology, Entomology and Fisheries Sciences, Makerere University, Kampala, Uganda

^b National Fisheries Resources Research Institute (NaFIRRI), Jinja, Uganda

^c MARBEC, CNRS-Univ Montpellier-IFREMER-IRD, Montpellier, France

^d UMR 7245 Molécules de Communication et Adaptations des Microorganismes (MCAM), CNRS-MNHN, Muséum National d'Histoire Naturelle, Paris, France

^e INRAE-Institute of Ecology and Environmental Sciences of Paris (iEES), Sorbonne University, Paris, France

ARTICLE INFO

Article history:

Received 25 November 2020

Accepted 20 April 2021

Available online 18 May 2021

Communicated by R. Michael McKay

Keywords:

Eutrophication

Lake Victoria

Cyanobacteria

Phytoplankton

Diversity

Bays and gulfs

ABSTRACT

Eutrophication of Lake Victoria led to changes in its phytoplankton communities. However, different levels of eutrophication exist in the open lake and the bays, and between embayments. This study utilized spatial and temporal sampling of Napoleon Gulf and Murchison Bay, exhibiting different trophic conditions. Over one year, we investigated phytoplankton biomass, richness, diversity and dissimilarity, and related the dynamics of the dominant species to the limnological and climatic conditions. The results confirmed that Napoleon Gulf and Murchison Bay showed large differences in eutrophication status, with lower nutrient concentrations in Napoleon Gulf than in Murchison Bay, where a strong gradient was observed from inshore to offshore areas. These nutrient dynamics resulted in a 4 to 10 fold higher chlorophyll-a in Murchison Bay than in Napoleon Gulf. From the embayments, 135 phytoplankton taxa were recorded with no significant differences in alpha diversity. However, high dissimilarity in community structure was observed in beta diversity, mostly due to a turnover among the dominant toxigenic species. Thus, from a similar species pool, there was a shift in the dominant toxigenic cyanobacteria from *Microcystis flos-aquae* and *M. aeruginosa* in Murchison Bay, *Dolichospermum circinale* and *Planktolyngbya circumcreta* in Napoleon Gulf to *D. circinale* in the offshore stations. These cyanobacteria are toxigenic taxa with known health hazards. Using partial least square models, we showed that both climatic variables (e.g. wind, solar radiation) and levels of inorganic dissolved nutrients (e.g. SRP, NO₃, and NH₄⁺) are the main drivers of differences and dominance in cyanobacteria communities in northern Lake Victoria.

© 2021 The Author(s). Published by Elsevier B.V. on behalf of International Association for Great Lakes Research. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>).

Introduction

After years of anthropogenic pressures, Lake Victoria is now considered to be persistently eutrophicated and polluted (Downing et al., 2012; Juma et al., 2014; Mbonde et al., 2015; Nassali et al., 2020; Olokotum et al., 2020). One well-known consequence of eutrophication is the significant modification of the phytoplankton community, which is the cornerstone supporting the productivity of all aquatic ecosystems (Boynton et al., 1983). How-

ever, anthropogenic pressures are not uniformly distributed, and bays and gulfs appear more affected by eutrophication than the open lake (Ngupula et al., 2012; Olokotum et al., 2020). In addition, the trophic status of the bays and gulfs varies greatly across the lake especially for the constricted and open bays (Mbonde et al., 2015). Beyond the ecosystem services identified for the whole lake (Sterner et al., 2020), these bays and gulfs provide crucial services for the riparian populations that are likely to be impaired by eutrophication. Most of these embayments are shallow and increasingly susceptible to point source pollution and, consequently, experience changes in phytoplankton diversity and increased biomass. These planktonic communities may experience extreme increases in biomass and drastic composition shifts, which

* Corresponding author.

E-mail address: cecile.bernard@mnhn.fr (C. Bernard).

often result in harmful algal blooms (HABs). These HABs impair the ecological functioning of these ecosystems and have both direct and indirect consequences for the local population. While many studies have separately investigated the biomass and taxonomic composition of phytoplankton community from different bays and gulfs (Olokotum et al., 2020), understanding the drivers of phytoplankton community modifications under different eutrophication pressures in Lake Victoria is still required. For that, we need to characterize not only phytoplankton communities' biomass, but also their diversity, both alpha (number of species within a community sample) and beta (extent of species replacement along environmental gradient) diversity (Whittaker, 1972; Wilson and Shmida, 1984). Alpha and beta diversity have been used to provide insight into habitat integrity and comparative changes along environmental gradients (Wilson and Shmida, 1984; Whittaker et al., 2001). Although phytoplankton alpha diversity is driven by local environmental conditions, beta diversity may be highly dependent on dispersal mechanisms and differences among environmental conditions of study sites (Moresco et al., 2017) which could be different between the bays and gulfs of Lake Victoria. These differences are known to be due to species replacement (turnover) and species loss or gain from one site to another (Baselga and Orme, 2012). This component of beta diversity is crucial towards understanding ecological status of bays and gulfs of Lake Victoria.

Noticeable differences between these bays and gulfs, and the open lake were observed as early as the 1920s (Worthington 1930), while evidence of an increase in phytoplankton biomass, as chlorophyll *a* (Chl-*a*) concentration, was recorded from the 1960s. The Kenyan part of the lake has experienced an increase in Chl-*a* concentration from 3–5 µg/L to 40–60 µg/L between the 1960s and the 2000s, with an extreme value of 650 µg/L in the Nyanza Gulf (Sitoki et al., 2012). In the northern part of Lake Victoria (Uganda), several bays and gulfs showed the same pattern. For instance, in Murchison Bay, Chl-*a* concentration increased from 20 µg/L to 60 µg/L between the 1990s and the early 2000s (Källqvist et al., 1996; Haande et al., 2011) and now exceeds 100 µg/L (Haande et al., 2011). Using paleolimnological data, Verschuren et al. (2002) showed that the increase of phytoplankton biomass since the 1930s mirrors the growth of human population and agricultural activities within the Lake Victoria watershed. There has also been, a shift in phytoplankton community composition from green algae and diatoms to cyanobacteria, especially toxin-producing ones (Olokotum et al., 2020). Eutrophic bays and gulfs such as Nyanza Gulf in Kenya (Onyango et al., 2020), Tanzanian bays (Mbonde et al., 2015) and Murchison Bay in Uganda (Okello and Kurmayer 2011), have cyanobacteria as the dominant taxonomic group. Cyanobacterial blooms in the bays and gulfs may have a direct impact on humans through the contamination of water and fish consumed by local populations (Onyango et al., 2020).

Investigations of phytoplankton distribution in the 1950s (Talling 1957) found associations with thermal stratification. By 2010 based on correlations, environmental factors such as sampling depth, light attenuation, and nutrients (SRP, NH₄⁺, TN and TP) were proposed to account for the changes in community structure from diatoms to cyanobacteria (Poste et al., 2013). In this context, it is important to identify the environmental variables which have significant effects on dominant cyanobacteria species to propose actions that can efficiently limit their impact. To identify these control factors, it is necessary to obtain data from sites with different degrees of eutrophication from the closed and open embayments of Lake Victoria.

At present state, there are significant contrasts between the constricted and open embayments and the open lake, especially regarding the dominance of Cyanobacteria (Mbonde et al., 2015; Olokotum et al., 2020). Although Haande et al. (2011), provided insights into the dynamics and factors influencing Cyanobacteria in Murchison Bay, modelling approaches were not attempted. Studies by Silsbe et al., (2006), reported how spatial and temporal environmental variations have affected primary productivity from the shallow to deep waters. We investigated the spatial and temporal changes of phytoplankton community biomass and diversity (alpha and beta) in two embayments in the northern part of Lake Victoria. Murchison Bay (MB), a constricted/closed bay and Napoleon Gulf (NG) an open bay, for which previous studies have reported different eutrophication status (Silsbe et al., 2006; Poste et al., 2013), and connection with the main lake provided suitable sites for a comparative study. In these two sites, the lake receives wastewater from and supplies drinking water for the two largest cities in Uganda (Kampala and Jinja) but is also consumed directly by people living on the shores who depend on it for fishing (Outa et al., 2020) and aquaculture (Musinguzi et al., 2019). In both bays, the phytoplankton community characteristics, climatic and limnological variables were measured monthly for one year along a transect from the inshore to the open lake.

Materials and methods

Study site and sampling procedures

The Napoleon Gulf and Murchison Bay are in the northern part of Lake Victoria (Uganda) and their characteristics are summarized in Table 1. Napoleon Gulf is surrounded by Jinja City, Buikwe and Buvuma districts. The gulf receives non-point source chemical pollutants (Oguttu et al., 2008), nutrients and wastewater across the wetland systems near the source of the Nile (major drainage outlet of Lake Victoria). Murchison Bay is surrounded by the Greater Kampala Metropolitan Area (KMA) which includes the districts of Kampala and Wakiso that are highly industrialized with large human populations. This bay receives a direct discharge of

Table 1
Major characteristics of the study sites and their catchment.

Characteristics	Napoleon Gulf	Murchison Bay
Location	33°15'11.64"E, 0°24'59.54"N	32°38'51.52"E, 0°15'25.03"N
Sampled depth (m) (Min -Max)	5.7 – 18.1	1.4–18.4
Size (km ²)	125	256 (137")
Catchment area (km ²)	187.92	593.92
Estimated population	900,000	5 million (Day) and 2 million (Night)
Major wetlands (km ²)	Kafunta (1.62) Kirinya (0.92), Masese (2.2) and Budumbuli (4.3)	Kinawataka (0.21), Nakivubo I and II (4.3 and 4.91) and Namanve (38.3)
Wastewater plant (connections)*	Kirinya (3,611)	Bugolobi (9,734)
Drinking water plant (connections)*	Walukuba (28,881)	Gaba I, II, & III (315,897)

*National Water and Sewerage Corporation (NWSC) annual report of 2019; water connections by NWSC doesn't necessarily equal the number of households since one connection might serve 4–7 households.

**Area if Inner Murchison Bay in parentheses.

wastewater mainly from the KMA through the Nakivubo channel and the adjacent wetland systems. Thus, point source pollution is more prominent in Murchison Bay than Napoleon Gulf. In addition, Murchison Bay is a more enclosed bay and has a much more populous watershed than Napoleon Gulf.

The sampling campaign was carried out monthly between November 2017 and October 2018. At each site, water samples were collected from four stations (NG1–4, MB1–4) along a transect from the inshore to the offshore station located 16 km outside the Murchison Bay and Napoleon Gulf area (Fig. 1).

Meteorological variables

Daily meteorological data (rainfall, air temperature, wind speed and solar radiation) were obtained from the Jinja and Kampala weather stations operated by the Uganda National Meteorological Authority (UNMA). To determine the influence of seasons, we used the rainfall data from UNMA to classify the months as wet (>60 mm total rainfall, $n = 6$ in Napoleon Gulf and $n = 7$ in Murchison Bay) and dry months (<60 mm total rainfall, $n = 6$ in Napoleon Gulf and $n = 5$ in Murchison Bay). In addition, climatic data for the previous 5 and 10 days before sampling (D5 & D10) and day of sampling (D0) (mean air temperature, mean wind speed D5, total rainfall D5 and mean solar radiation D10) were used for modelling the biovolume of dominant phytoplankton species.

Physical and chemical variables

For each sampling operation (site $\times$ month $\times$ station), we measured several limnological variables. Water depth was measured

using a portable depth sounder (Hondex PS-7), and water transparency using a Secchi disk (diameter = 20 cm). Water temperature, pH, electrical conductivity, dissolved oxygen, turbidity, and fluorescent dissolved organic matter (fDOM) were measured in-situ using the YSI Sonde EXO2 multiprobe meter (Sonde 16B102461). Water samples for chemical analysis were collected every meter of depth at each site using a 2-L horizontal van Dorn sampler as described by [Wetzel and Likens \(2000a\)](#). The samples were collected in a 20 L bucket as a composite sample. From the composite sample, 2 L were taken for chlorophyll-a (Chl-a) and nutrients analyses while 20 mL were used for phytoplankton analysis.

Samples for dissolved nutrient measurement were immediately filtered using Whatman GF/C filters ($\varnothing$ 47 mm). Soluble reactive phosphorus (SRP) was determined using the ammonium molybdate method ([Wetzel and Likens 2000b](#)), nitrate ($\text{NO}_3\text{-N}$) by the sodium salicylate method ([Müller and Wiedemann 1955](#)), ammonium ($\text{NH}_4\text{-N}$) using the indophenol blue method ([Krom 1980](#)), and soluble reactive silica (SRSi) using the yellow molybdate-silicic acid method ([Wetzel and Likens 2000b](#)). Raw water samples were also collected in acid-washed polyethylene containers for total phosphorus (TP) and nitrogen (TN) analysis using the persulphate digestion oxidation methods described in [Wetzel and Likens \(2000b\)](#).

Biological variables

Chlorophyll a (Chl-a) concentration

The Chl-a concentration was measured by filtering 100–500 mL of water (Whatman GF/C filters), followed by hot 90% ethanol

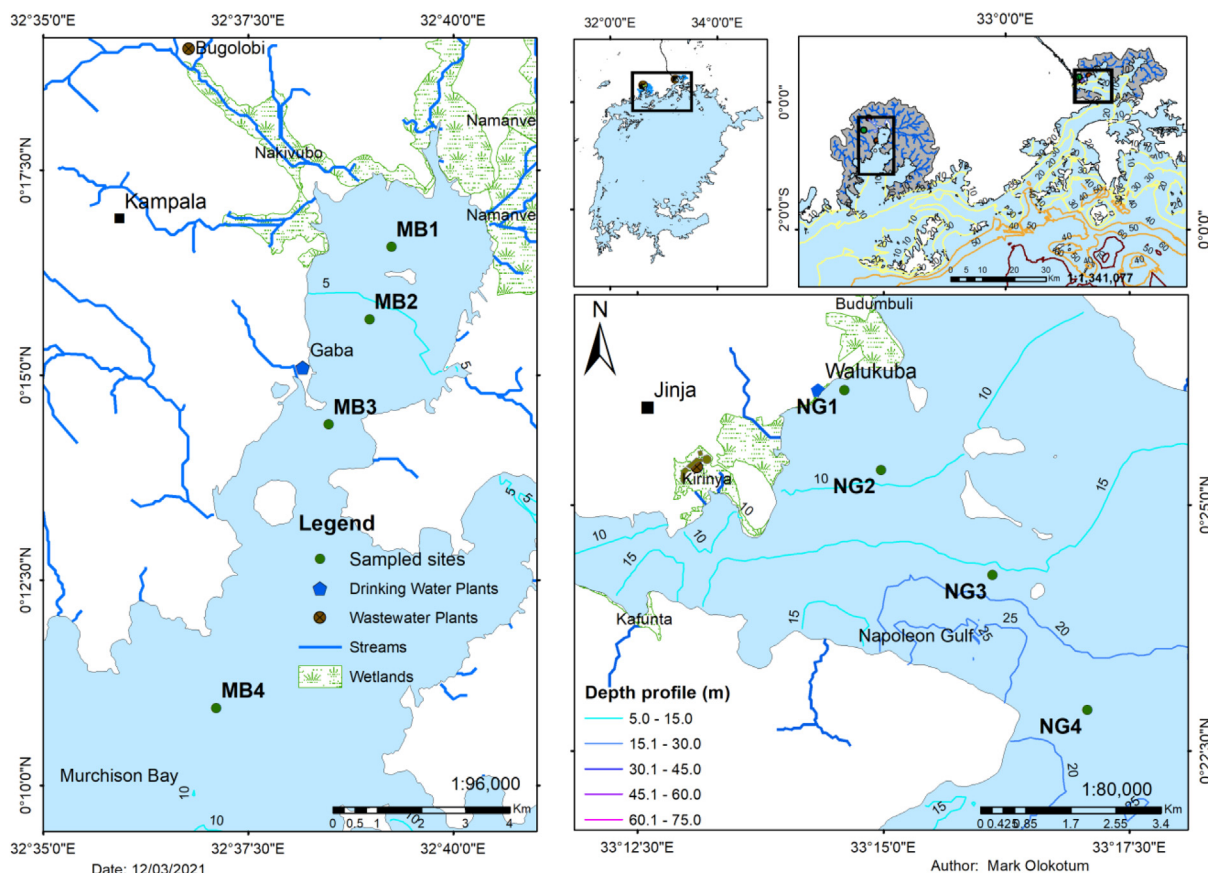


Fig. 1. Maps of Murchison Bay (MB) and Napoleon Gulf (NG) with the locations of sampling stations (MB1 to 4 and NG1 to 4) along the spatial transects. Inset are maps of northern Lake Victoria.

extraction (ISO-10260, 1992) of the filtered biomass and analysis with a Jenway 6505 UV/vis spectrophotometer. Briefly, 10 mL of 90% ethanol were added to filtered biomass and incubated in a water bath for 2 min at 78° and later sonicated for 15 min to accelerate pigments lysis. The extract was cooled in the dark and then filtered using the 0.2 µm mesh size membrane filter (Millex, GS). Absorbance measurement was done at 665 nm wavelength and corrected for turbidity by subtracting the absorbance measured at 750 nm wavelength. To the measured extract in the cuvette, 100 µL of 0.25 M hydrochloric acid was added, shaken and absorbance measured again at 665 nm and 750 nm.

Phytoplankton communities

Taxonomic identification, taxa abundance and biovolume estimation were performed following the procedure described by Catherine et al. (2017). The phytoplankton samples were fixed using Lugol's iodine solution and 2–5 mL of sample were sedimented for 6–12 h (Utermöhl, 1958). Chl-a concentration was determined in each sample. When Chl-a concentration was low (≤ 20 µg/L), 5 mL were sedimented. When it was high (≥ 20 µg/L), 2–3 mL were sedimented. The phytoplankton units were counted under a Nikon Eclipse TS-100 inverted microscope (400X) and identified using taxonomic guides and keys based on morphological characteristics as described in Talling (1987), and Cronberg and Annadotter (2006). At least 30 microscopic fields were counted in duplicate, and at least 400 phytoplankton units (cells, trichomes, and colonies) were counted to reduce errors to $< 10\%$ as described in Wetzel and Likens (2000a). *Microcystis* was first counted as colonies from which the number of cells per colony was estimated based on the size of the colony and cell size. Later samples containing *Microcystis* were re-counted using a Malassez counting chamber for counting *Microcystis* sp. The volume of each species was estimated using geometric shapes as described by Sun and Liu (2003).

Data analysis

Environmental characteristics

The environmental data were centred on a Euclidean distance matrix before performing principal component analysis (PCA) to condense multivariate information on limnological and climatic variables and reveal the dimensions and patterns of environmental variation between bays and stations. The PCAs were computed in 'FactoMinerR' package (Sébastien et al., 2008) and 'factoextra' package was used for visualization. Permutational multivariate analysis of variance (PERMANOVA) using the *adonis2* function of 'vegan' package (Oksanen et al., 2007) was used to test the differences in environmental conditions between bays, within stations and season (wet and dry). Pairwise differences between the bays and within stations were also compared using independent *t* tests and one-way ANOVA, respectively. Mann-Whitney and Kruskal-Wallis tests were performed where necessary in R software.

Phytoplankton communities

The list of phytoplankton taxa across sampling sites was tabulated, and we used Venn diagrams to interpret taxa richness relations between sites and stations along the gradient using the 'Limma' package in R software (Ritchie et al., 2015). Indices of α -diversity were calculated using Shannon-Weiner and Pielou evenness indices using the 'vegan' package (Oksanen et al., 2007). The biovolume for each taxon was summed and a rank-biovolume diagram created for the dominant taxa of each bay. Later, the changes

in the mean biovolume of the dominant taxa along the spatial transect were evaluated. Phytoplankton biovolume data were square root-transformed to increase the influence of rare taxa in the dissimilarity matrix. β -diversity based on the Bray-Curtis dissimilarity index was applied to the square root-transformed phytoplankton biovolume to characterize the differences in phytoplankton community between and within bays (tested using PERMANOVA). The same Bray-Curtis dissimilarity matrix was ordinated using non-metric dimensional scaling (nMDS). Further, the similarity percentage breakdown (SIMPER) analysis (Clarke, 1993) was used to assess the average contribution of individual phytoplankton taxa to biovolume-based Bray-Curtis dissimilarity between bays and within stations.

Influence of environmental variables on phytoplankton communities

Limnological and climate data, SRP, NO_3^- , NH_4^+ , SRSi, water temperature, mean wind speed (D5) and mean solar radiation (D10), were log-transformed to ensure normal distribution before fitting partial least square (PLS) regression models to the observed biovolume of dominant taxa (*M. flos-aquae*, *M. aeruginosa*, *D. circinalis* and *P. circumcreta*).

Results

Environmental characteristics of Napoleon Gulf and Murchison Bay

A total of 14 limnological and four climatic variables were used to characterize the environmental conditions experienced by phytoplankton communities in Napoleon Gulf and Murchison Bay (Table 2 and Electronic Supplementary Material (ESM) Table S1). The two bays differed in Secchi depth, turbidity, conductivity and fDOM (Mann-Whitney test, $p < 0.05$, ESM Table S1). Regarding limnological variables, the levels of turbidity, dissolved organic matter (fDOM), TP, SRP, NH_4^+ and TN were significantly higher in Murchison Bay than in Napoleon Gulf (6–10 times for fDOM, 10 times for NH_4^+ , Mann-Whitney test, $p < 0.001$, ESM Table S1). We also observed correlation between variables, for instance, negative correlation between fDOM, turbidity and ratio of N:P in Napoleon Gulf, while Secchi depth and NH_4^+ were negatively correlated in Murchison Bay (Fig. 2A). The physico-chemical conditions in the four stations of Napoleon Gulf are more homogeneous than those obtained in the Murchison Bay, with station 1 being different from stations 2 to 4. This was revealed by the lower overlap of ellipses from each station on the PCA (Fig. 2B).

Within each embayment, we observed significant differences among stations 1 to 4 (pseudo- $F = 12.9$, $P(\text{perm}) = 0.001$), and between dry and wet seasons (pseudo- $F = 2.2$, $P(\text{perm}) = 0.018$) for the following variables: conductivity, fDOM, SRP, NH_4^+ (Table 2). Particularly, the inshore Murchison Bay station (MB1) exhibited high conductivity and fDOM values but with low SRP compared to the offshore stations (MB 2 to 4). In Napoleon Gulf, conductivity, fDOM, nutrients, NO_3^- , NH_4^+ and SRSi, were significantly higher in the inshore (NG1) than the offshore areas (NG2 – 4), while the other variables (water temperature, pH, turbidity and Secchi depth) remained stable along the spatial transect (ESM Figure S1). Generally, there is a strong environmental gradient established in Murchison Bay inferred from the levels of dissolved oxygen, pH and conductivity with significantly high levels of nutrients into the bay unlike in Napoleon Gulf.

Spatial and temporal variations of phytoplankton biomass

Total phytoplankton biovolume was significantly and positively correlated with log-transformed Chl-a ($R^2 = 0.55$, $p < 0.0001$, ESM

Table 2

Summary statistics for the environmental and nutrient variables evaluated at the eight sites along the environmental gradients established in Murchison Bay (MB1– 4) and Napoleon Gulf (NG1– 4). Note: The negative values of fDOM means little or no fluorescence.

Parameters	MB1 Mean ± SD	Min	Max	MB2 Mean ± SD	Min	Max	MB3 Mean ± SD	Min	Max	MB4 Mean ± SD	Min	Max
Depth (m)	1.8 ± 0.3	1.4	2.5	5.4 ± 0.5	4.8	6.6	14.0 ± 2.3	9.4	18.4	12.7 ± 0.5	12	14
Secchi (m)	0.5 ± 0.1	0.3	0.7	0.6 ± 0.1	0.4	0.8	0.9 ± 0.2	0.7	1.3	1.2 ± 0.2	0.8	1.6
Temp (°C)	25.5 ± 0.7	24.2	26.4	25.3 ± 0.5	24.3	26	25.3 ± 0.6	24	25.9	25.2 ± 0.6	23.9	26.2
EC (µS/cm)	183.4 ± 45.4	124.4	251.5	126.4 ± 9.0	112.8	146.1	121.6 ± 8.2	105.6	132.3	106.1 ± 3.9	102	116
fDOM (QSU)	25.2 ± 10.6	15.7	45.8	20.9 ± 2.9	15.8	25.4	19.5 ± 3.8	12.6	27	11.8 ± 19.4	4.1	73.1
Turbidity (NTU)	78.9 ± 63.9	8.9	197.2	30.6 ± 18.7	9.7	73.7	14.0 ± 8.8	4.4	32.9	10.9 ± 8.6	2.1	30.9
DO (mg/L)	5.8 ± 2.4	2.7	9.6	7.2 ± 1.6	4.7	10.2	5.9 ± 1.2	4	7.7	7.2 ± 0.6	6.3	8.2
pH	8.2 ± 0.4	7.6	8.9	8.6 ± 0.5	8	9.4	8.3 ± 0.3	7.8	8.8	8.6 ± 0.3	8.1	9.1
TP (µg/L)	151.7 ± 150.8	18	521.9	80.3 ± 69.9	18.2	264.4	50.4 ± 37.1	14.4	139.3	59.2 ± 74.3	10.4	275.6
SRP (µg/L)	73.6 ± 107.8	7.1	380.3	7.3 ± 3.8	0.9	15.8	6.4 ± 2.9	3.4	13.3	7.1 ± 9.6	0.9	36.7
TN (µg/L)	3,008.6 ± 170.5	153.1	21,633.60	1,036.2 ± 877.9	170.5	3,294.60	1,020.0 ± 1104.0	162.6	3,955.60	950.4 ± 930.1	149.1	3,108.10
NO ₃ (µg/L)	88.4 ± 100.9	19	380.4	146.8 ± 258.4	8.5	940.1	84.1 ± 67.4	7.3	231.4	64.7 ± 55.1	9.7	170.1
NH ₄ ⁺ (µg/L)	337.1 ± 370.5	0.7	1,206.90	26.9 ± 37.7	0.5	133.4	32.5 ± 46.6	0.4	163.9	18.4 ± 27.6	0	81.4
SRSi (µg/L)	1,089.8 ± 922.7	282	3,081.90	483.0 ± 243.0	139.5	932.1	385.3 ± 185.7	112.4	685.6	235.9 ± 196.1	9	596.9
Parameters	NG1 Mean ± SD	Min	Max	NG2 Mean ± SD	Min	Max	NG3 Mean ± SD	Min	Max	NG4 Mean ± SD	Min	Max
Depth (m)	6.4 ± 0.5	5.7	7.2	9.2 ± 0.6	8	9.8	13.1 ± 1.2	11.4	15.8	18.1 ± 1.3	16.7	21.5
Secchi (m)	1.3 ± 0.3	0.9	1.8	1.3 ± 0.2	1	1.7	1.4 ± 0.2	1.1	1.7	1.6 ± 0.2	1.3	2
Temp (°C)	26.3 ± 0.6	25.4	27.3	26.0 ± 0.6	25.2	27	25.8 ± 0.5	24.9	26.7	25.7 ± 0.5	24.8	26.6
EC (µS/cm)	105.3 ± 4.7	99.8	115.7	102.8 ± 4.2	97.9	112.2	101.0 ± 2.8	97	106	100.5 ± 3.1	96	105.5
fDOM (QSU)	−0.2 ± 0.6	−1.3	1	−0.5 ± 0.5	−1.6	0.4	−0.6 ± 0.5	−1.6	−0.2	−0.8 ± 0.4	−1.5	0
Turbidity (NTU)	15.0 ± 15.9	0.7	58.1	12.7 ± 17.3	0.5	61.2	12.2 ± 13.9	0.2	40	6.9 ± 6.9	0	17.3
DO (mg/L)	7.3 ± 1.0	5.5	8.8	7.4 ± 0.8	6.4	8.8	7.1 ± 0.7	5.8	8.1	7.0 ± 0.8	4.9	7.9
pH	8.8 ± 0.3	8.4	9.4	8.8 ± 0.2	8.4	9.3	8.8 ± 0.3	8.2	9.3	8.7 ± 0.3	8	9.2
TP (µg/L)	37.9 ± 36.6	8.9	145.1	44.0 ± 24.9	8.2	168.4	40.6 ± 31.4	10.1	128.1	36.9 ± 22.8	8.6	94
SRP (µg/L)	4.5 ± 1.9	0.6	8	5.2 ± 2.3	0.7	9.5	6.4 ± 3.1	0.7	11	8.8 ± 5.3	0.7	18.2
TN (µg/L)	712.1 ± 474.7	129.7	1,664.70	380.8 ± 150.6	134.1	633.6	530.8 ± 321	148.5	1,210.20	570.3 ± 352.4	154.1	1,122.60
NO ₃ (µg/L)	28.6 ± 22.0	2.1	68.5	41.6 ± 43.5	1.9	153.9	50.4 ± 46.0	1.1	170.2	121.0 ± 262.2	2.1	947.4
NH ₄ ⁺ (µg/L)	6.9 ± 8.8	1.2	32.7	8.1 ± 10.4	0.6	31	7.8 ± 16.7	0.4	59.1	11.6 ± 21.1	0.5	76.4
SRSi (µg/L)	302.9 ± 194.2	99.9	635.4	308.2 ± 210.1	81.9	717.8	327.1 ± 194.5	80.2	629.9	368.8 ± 262.6	73.4	903.9

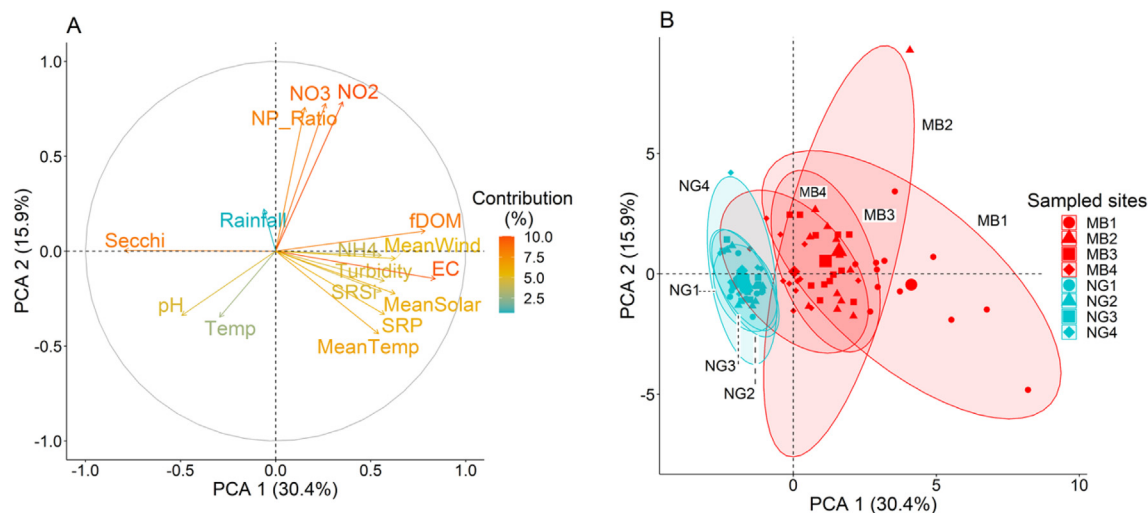


Fig. 2. Differentiation of Napoleon Gulf (NG) and Murchison Bay (MB) based on limnological and climatic variables. Principal Component Analysis (PCA) on Euclidean distance based on limnological and mean climatic variables. Plot A represents the circles of correlation between the first two PCs and explanatory variables. Plot B represents the distribution of monthly samples (November 2017 to October 2018) on the first two PCs. The first, second and third axes of the PCA accounted for 30.4%, 15.9% and 13.0% of the total variance respectively between Napoleon Gulf and Murchison Bay.

Figure S2), thus Chl-a was used as a proxy of total phytoplankton biomass. These Chl-a concentrations were higher (Mann-Whitney test, $p < 0.001$) in Murchison Bay (28.1 to 1087 µg/L) than in Napoleon Gulf (11.8 to 50.4 µg/L). No significant differences in Chl-a were found in the four sampling stations of Napoleon Gulf (Kruskal-Wallis test, $p = 0.476$) while in Murchison Bay mean

Chl-a decreased from the inshore (MB1) to offshore areas (MB4, Kruskal-Wallis test, $p < 0.001$, Fig. 3A). As shown by Fig. 3B, the temporal changes in Chl-a were stronger for Murchison Bay than Napoleon Gulf, notably for the two inshore stations (MB1, MB2). The highest Chl-a values were measured in December for Napoleon Gulf (50.4 µg/L) and September for Murchison Bay (1087.1 µg/L). In

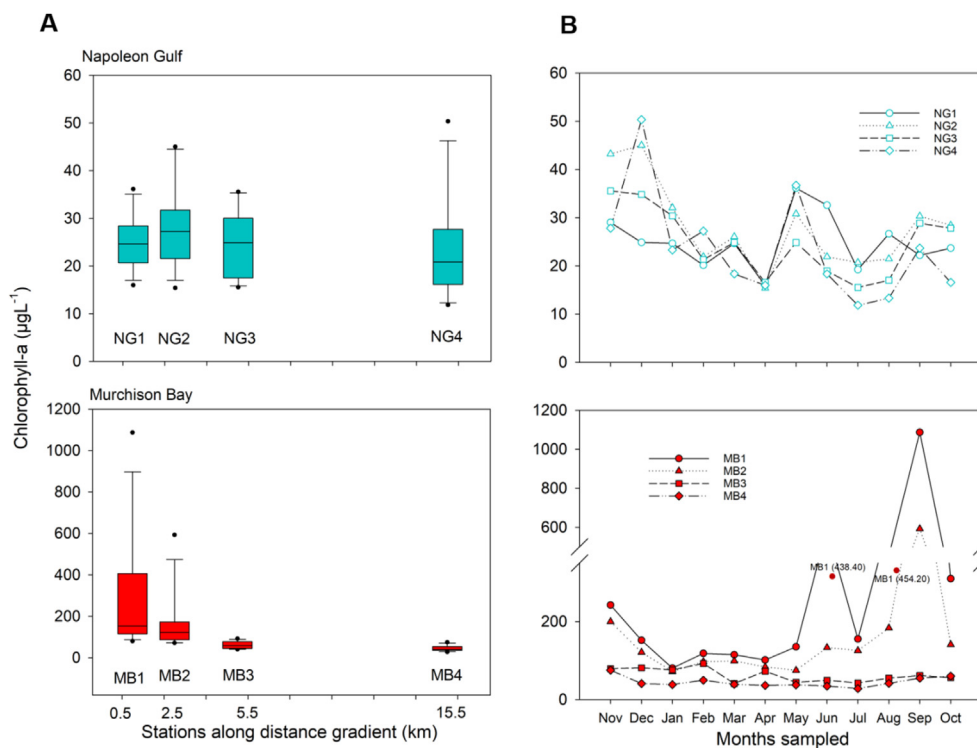


Fig. 3. Spatio-temporal variation in Chl-a between stations 1 to 4 in Napoleon Gulf (NG 1 to 4) and Murchison Bay (MB 1 to 4). Plot A: Spatial variation along the inshore-offshore distance gradient. Plot B: Temporal variation between November 2017 and October 2018.

summary, significantly high levels of phytoplankton biomass with seasonal difference were observed in Murchison Bay but not in Napoleon Gulf.

Diversity patterns and dynamics of phytoplankton communities

Phytoplankton richness and diversity

A total of 135 phytoplankton species belonging to 49 genera were identified during the sampling in both Napoleon Gulf and Murchison Bay (ESM Table S2). The Chlorophyta/Euglenophyta were the most diverse group with over 62 taxa from 21 genera, followed by cyanobacteria with 44 taxa from 13 genera, and then Bacillariophyta with 27 taxa from 11 genera. Dinophyta had two taxa from two genera, Cryptophyta two species from one genus and Chrysophyta one taxon from one genus. From these 135 taxa, 71 (53%) were found in both embayments while Napoleon Gulf and Murchison Bay exhibited 29 and 35 unique taxa respectively, leading to a total richness of 100 and 106 in Napoleon Gulf and Murchison Bay, respectively (Fig. 4A). The ranges of monthly phytoplankton richness were similar in both bays, 14–32 and 13–33 taxa in Napoleon Gulf and Murchison Bay, respectively. Similar numbers of taxa were shared across all stations in each embayment and the highest number of station-specific taxa was observed in the inshore stations, NG1 and MB1 (Fig. 4B).

Phytoplankton diversity was not significantly different between the two bays (Mann-Whitney test, $p = 0.091$, $H' = 2.12 \pm 0.26$ in Napoleon Gulf and 2.01 ± 0.28 in Murchison Bay). During the sampling, there was no significant difference in diversity between stations in Napoleon Gulf (min–max; 1.43–2.58, ANOVA test, $p = 0.944$) while significant differences were found in Murchison Bay (min–max; 1.29–2.54, ANOVA test, $p = 0.048$). The average

evenness was 0.672 ± 0.09 and 0.685 ± 0.07 in Murchison Bay and Napoleon Gulf, respectively.

The rank-biovolume distributions of phytoplankton taxa differed between the embayments (ESM Figure S3). Only two cyanobacterial taxa dominated the phytoplankton community in Napoleon Gulf (*Dolichospermum circinale* and *Planktolyngbya circumcreta*) while the biovolumes were more balanced in Murchison Bay between the top four taxa: *D. circinale*, *P. circumcreta*, *Microcystis flos-aquae* and *M. aeruginosa*. These dominant species were among the 71 shared species between the embayments and were present at all the sampled stations. Other phytoplankton taxa were rare and had very low biovolume. For instance, in Napoleon Gulf, *M. flos-aquae* contributed 4.8% while *Nitzschia acicularis* var. *acicularis* contributed 4.5%, *P. simplex* with 2.4% while the rest contributing between 0.008 and 1.5% to the total biovolume. On the other hand, in Murchison Bay, besides the co-dominance of *Microcystis* species, Chlorophyta *Pediastrum simplex* contributed 6.2%, *Selenastrum bibrainum* 1.9%, *Cosmarium habitat* 1.2% and Bacillariophyta *N. acicularis* var. *acicularis* 2.0% and the remaining taxa made up between 0.003 and 1.43%.

Dissimilarity between phytoplankton communities

The structure of phytoplankton community biovolume distributions differed significantly between Napoleon Gulf and Murchison Bay (PERMANOVA test, $p = 0.001$), with the two bays clustering separately on the nMDS ordination (Fig. 5A). There was a significant station effect in Napoleon Gulf and Murchison Bay (PERMANOVA test, $p = 0.002$); however, no effect of season on community structure was found (PERMANOVA test, $p = 0.086$). The estimated dissimilarity in the structure of the communities between Napoleon Gulf and Murchison Bay was 72.6% and mainly driven by 25 taxa (ESM Table S3). The average contribution of individual taxa to this dissimilarity was highly variable and mostly due

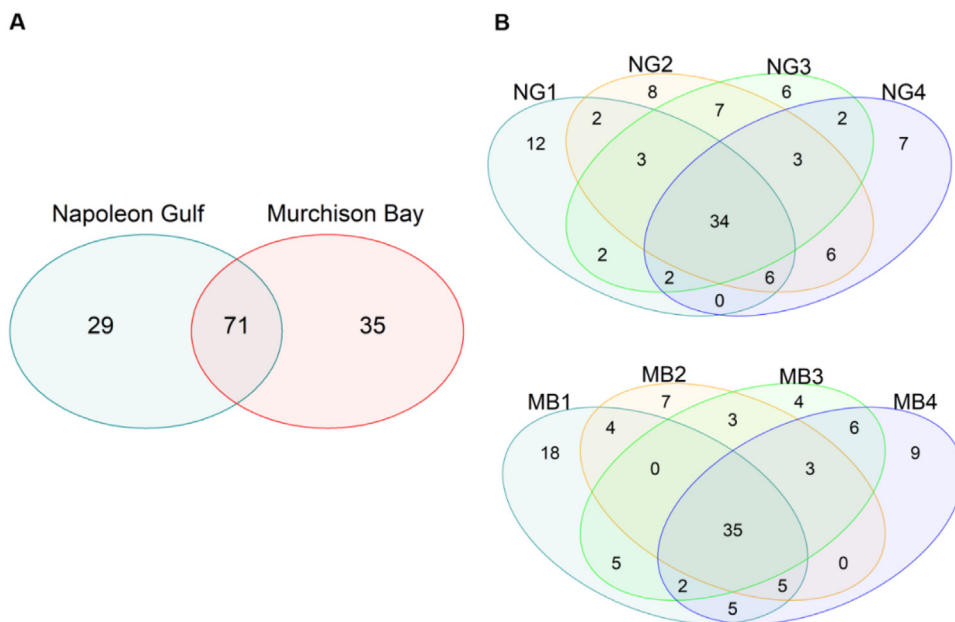


Fig. 4. Richness of phytoplankton communities in Napoleon Gulf and Murchison Bay. Plot A: Total phytoplankton richness within and between bays. Plot B: Station-specific richness and overlap among stations within Napoleon Gulf (NG 1 to 4) and Murchison Bay (MB 1 to 4).

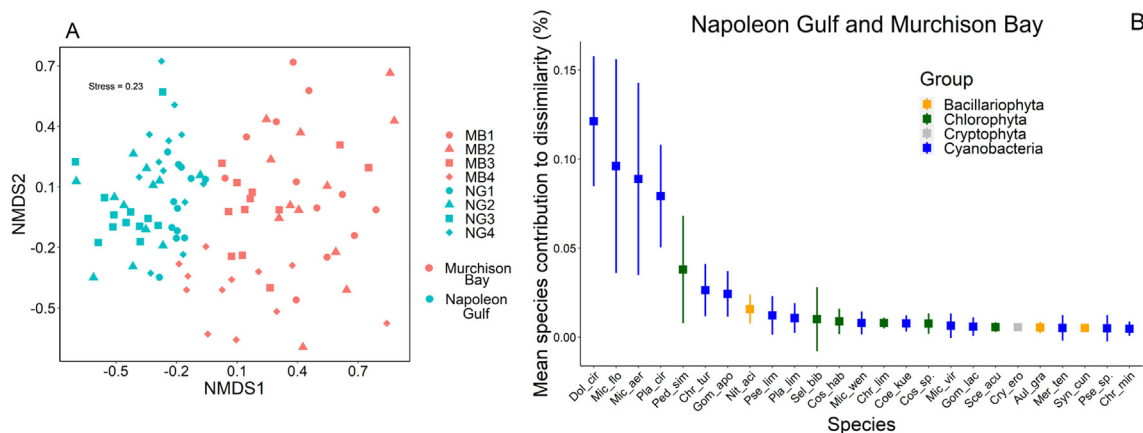


Fig. 5. Differences in structure of the phytoplankton communities and contributing taxa. Plot A: nMDS ordination of the communities performed on Bray-Curtis dissimilarities matrix using relative biovolume matrices (stress = 0.23). Plot B: Average taxa contribution to dissimilarity between phytoplankton communities from the two bays. The values are averaged across all pairs of communities. Note: Full names of the phytoplankton taxa are in ESM Table S3.

to 15 cyanobacterial taxa (Fig. 5B). The cyanobacteria *D. circinale*, *M. aeruginosa*, *M. flos-aquae* and *P. circumcreta* contributed the most to the dissimilarity between Napoleon Gulf and Murchison Bay communities, followed by the chlorophyte *Pediastrum simplex*, two cyanobacteria (*Chroococcus turgidus* and *Gomphosheria aponina*) and the bacillariophyte *Nitzschia acicularis*. The dissimilarity among stations of Napoleon Gulf, NG1 to NG4 (51.9–65.9%) was driven by the Cyanobacteria *D. circinale*, *M. flos-aquae* and *P. circumcreta* followed by the Bacillariophyta *N. acicularis* and the Cyanobacteria *Pseudanabaena* sp., *Merismopedia tenuissima* (ESM Table S4). In Murchison Bay, the dissimilarity among stations MB1 to MB4 (57.9–66.7%) was driven by *M. flos-aquae*, *M. aeruginosa*, *D. circinale*, and *C. turgidus* (ESM Table S3, Figure S4).

Spatio-temporal dynamics of the dominant taxa

During the study period, phytoplankton biovolume in Napoleon Gulf ($7.1 \times 10^6 \pm 3.1 \times 10^6 \mu\text{m}^3/\text{mL}$) was lower compared to Murchison Bay ($2.4 \times 10^7 \pm 1.3 \times 10^7 \mu\text{m}^3/\text{mL}$, Mann-Whitney test,

$p < 0.001$). Cyanobacteria contributed > 60% and > 90% of the total biovolume in Napoleon Gulf and Murchison Bay, respectively. The contribution of other groups (Chlorophyta/Euglenophyta, Bacillariophyta, and Dinophyta) was generally low with occasional dinoflagellates in the inshore areas of Napoleon Gulf (ESM Figure S5). Temporal variation in these groups was more prominent towards the offshore stations (ESM Figure S6). The relative phytoplankton species contribution was dominated by the cyanobacterium *D. circinale* (21.3%), followed by *P. circumcreta* (15.4%), *M. flos-aquae* (13.3%), *M. aeruginosa* (11.8%), the Chlorophyta *Pediastrum simplex* (5.3%) and the Bacillariophyta *Nitzschia acicularis*.var. *acicularis* (2.6%) in both Napoleon Gulf and Murchison Bay.

Only two taxa appeared co-dominant in the phytoplankton communities in Napoleon Gulf (*D. circinale* and *P. circumcreta*), followed by two taxa from the genus *Microcystis* (*M. flos-aquae* and *M. aeruginosa*). This was true in all the stations from Napoleon Gulf (Fig. 6). In Murchison Bay, these four taxa were co-dominant; while *D. circinale* and *P. circumcreta* exhibited an equivalent biovolume in all stations, the biovolume of *Microcystis* spp. decreased from the

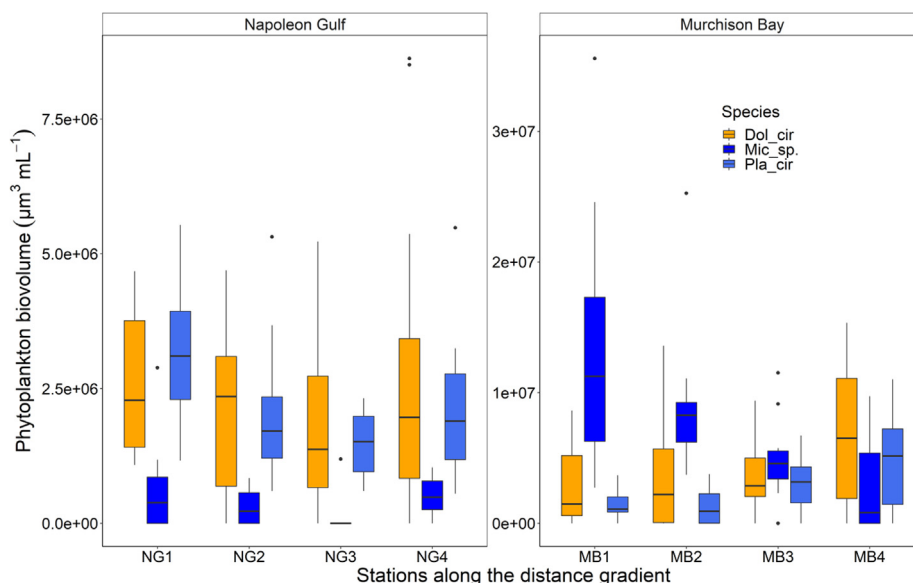


Fig. 6. Spatial changes in median biovolume of the dominant species along the distance gradient in Napoleon Gulf (Left panel) and Murchison Bay (Right panel) between November 2017 and October 2018. Note: Dol_cir = *Dolichospermum circinale*, Pla_cir = *Planktolyngbya circumcreta* and Mic_sp. = *Microcystis aeruginosa* + *Microcystis flos aquae*.

inshore to the open lake. Further, the balance between dominant taxa appeared similar in the offshore stations from both embayments (i.e., NG4 and MB4). Generally, and despite higher phytoplankton biovolumes in Murchison Bay than in Napoleon Gulf, the phytoplankton community in both sites were dominated by Cyanobacteria, contributing > 70% of the total phytoplankton biomass. Although the relative Cyanobacteria composition differed in the two embayments, they were similar in their offshore areas.

Factors influencing the dynamics of dominant taxa biovolumes

Environmental variables explained >64% of the variance (R^2) of PLS models for the three dominant taxa biovolume (*Microcystis* spp. (*M. flos-aquae* & *M. aeruginosa*; because of the coherence of the two species), *D. circinale* and *P. circumcreta*) (Table 3). Comparison of observed and predicted data revealed that the good performance of the models resulted from taking into account the pooled

Table 3

Standardized coefficients from the global Partial Least Square (PLS) Regression models for Chl-a biomass and biovolume of phytoplankton taxa in Napoleon Gulf and Murchison Bay. Note: Only significant explanatory variables are included (p value < 0.05), *Microcystis* spp. = *M. aeruginosa* + *M. flos-aquae*.

Variables	Log Chl-a	<i>Microcystis</i> spp.	<i>Dolichospermum circinale</i>	<i>Planktolyngbya circumcreta</i>
Log SRP	0.14	0.11		
Log NO ₃	0.11		0.13	0.09
Log NH ₄	0.23	0.18	0.18	0.16
Log SRSi	0.17	0.14		
Log water Temp		−0.12	−0.18	−0.19
Log MeanWind_D5	0.20	0.23	0.29	0.30
Mean Solar radiation_10		0.33		0.34
R ²	0.62	0.65	0.78	0.73

Table 4

Standardized parameter coefficients from the PLS models for Chl-a biomass and biovolume of phytoplankton taxa in the separate bays of Napoleon Gulf (NG1–4) and Murchison Bay (MB1–4). Note: statistical significance (p value < 0.05), *Microcystis* spp. = *M. aeruginosa* + *M. flos-aquae*.

Variables	Napoleon Gulf (NG)		Murchison Bay (MB)			
	Log Chl-a	<i>Dolichospermum circinale</i>	Log Chl-a	<i>Dolichospermum circinale</i>	<i>Planktolyngbya circumcreta</i>	<i>Microcystis</i> spp.
Log SRP	−0.14		0.24			0.18
Log NO ₃			0.30		−0.17	
Log NH ₄			0.30	−0.21	−0.20	0.24
Log SRSi			0.21			0.18
Log Water Temp	0.22	0.18				−0.19
Rainfall-5 days						
Log MeanWind_D5	−0.21	−0.19		0.29		
Mean Solar radiation_10	0.19	0.18				
R ²	0.44	0.30	0.54	0.36	0.37	0.38

data from the two contrasted embayments (ESM Figure S7; observed vs predicted biovolumes).

Climate variables (mean wind and solar radiation) were the major predictors for the biovolume of the three dominant species while nutrients (SRP, NO_3^- , NH_4^+ and SRSi) seemed to play a secondary role in the relative abundance of these species (Table 4). *D. circinale* and *P. circumcreta* biovolumes were explained by similar combinations of variables, with climatic variables such as solar radiation and wind appearing as the most important controlling factors, before dissolved inorganic forms of nitrogen (NO_3^- and NH_4^+). The *Microcystis* spp. model was slightly different, as SRP and NO_3^- were related to its biomass. NH_4^+ was the most important nutrient controlling the biovolumes of dominant taxa. Rainfall did not affect any response variables and the water temperature had a negative influence on the biovolume of the three dominant taxa. In summary, wind and solar radiation played a major role as nutrient conditions was secondary in the dynamics of the dominant taxa Napoleon Gulf and Murchison Bay.

Discussion

Limnological characteristics of Napoleon Gulf and Murchison Bay

This study assessed the spatio-temporal dynamics in phytoplanktonic communities in two embayments along a transect from inshore to open lake. Here we identified the most important predictors of the phytoplankton community structure of the dominant taxa in Napoleon Gulf and Murchison Bay.

As expected, large differences in limnological characteristics were observed between the two bays, especially regarding the concentration of inorganic nutrients which were much higher in Murchison Bay than in Napoleon Gulf. These higher concentrations in Murchison Bay originated from the newly expanded Nakivubo channel which collects part of the runoff and wastewater from Kampala (Luyiga et al., 2015; Akurut et al., 2017). The sampling station located near the channel showed the highest concentrations of nutrients, which decreased along the sampling transect. No such point source of wastewater was in Napoleon Gulf sampling area, where the Jinja city wastewater is discharged through wetlands outside of the gulf and near the source of the Nile. Consequently, we did not observe a concentration gradient from the inner to the outer part of the gulf in Napoleon Gulf. There are also various small-scale industries located near the shores of the two bays that discharge lower but highly contaminated flows in surface water of the bays (Oguttu et al., 2008).

According to Mbonde et al. (2015), Murchison Bay can be considered as a closed bay with only a low level of water exchange with the open lake relatively to its size, while Napoleon Gulf can be considered as an open bay with higher water renewal. As a consequence, the nutrient load in Napoleon Gulf from the watershed can be more efficiently diluted by open lake water than that discharged into Murchison Bay, especially as Napoleon Gulf is located at the outflow of Lake Victoria (Poste et al., 2013).

Previous studies such as Kabenge et al. (2016) have reported large increases in nutrient concentrations in the inner part of Murchison Bay during recent decades, rising as high 580 $\mu\text{g/L}$ in 2011 (Kabenge et al., 2016) and 380 $\mu\text{g/L}$ in 2017–2018 (this study). However, PO_4 being readily available, its concentration depends on the Chl-a biomass. TP is a better proxy of anthropogenic P input from population increases. The maximum TP in Murchison Bay increased from < 50 $\mu\text{g/L}$ in the early 1990 s (Källqvist et al., 1996) to 105–122 $\mu\text{g/L}$ in mid-2004 (Okello et al., 2010), 550 $\mu\text{g/L}$ by 2003 (Luyiga et al., 2015), and 550–1500 $\mu\text{g/L}$ ($91 \pm 27.8 \mu\text{g/L}$) by 2010 (Haande et al., 2011). According to Kabenge et al. (2016), this increase in TP results from population

growth in the Kampala urban and peri-urban areas, from 755,000 inhabitants in 1990 to 2,117,000 in 2011 and to 2,843,000 in 2017 (1,680,600 in the city) (Uganda Bureau of Statistics, 2017a).

On the contrary, PO_4^{3-} concentration did not increase as dramatically in Napoleon Gulf. Case in point, PO_4^{3-} was 0.08 μM (7.59 $\mu\text{g/L}$) (Lehman and Branstrator 1994), 54.8–68 $\mu\text{g/L}$ in between 2000 and 2002 (Gikuma-Njuru et al., 2005), 3–7 $\mu\text{g/L}$ (Okello et al. (2010); Poste et al. (2013) and 18.2 $\mu\text{g/L}$ (this study). We have also observed a mild increase in the TP within Napoleon Gulf over the years from $49.3 \pm 5.5 \mu\text{g/L}$ (Okello and Kurmayer, 2010), to $60 \pm 16.2 \mu\text{g/L}$ (Poste et al., 2013) and $190 \pm 2 \mu\text{g/L}$ (Egessa et al., 2018); but not in this study (39.8 ± 33.2 , max TP = 164 $\mu\text{g/L}$). Similarly, the number of inhabitants in the Jinja district increased at a lower rate than in Kampala: 289,476 in 1991, 387,573 in 2002, and 471,242 in 2014 (288,500 in Jinja city) (Uganda Bureau of Statistics, 2017b).

Maximum phytoplankton biomass (expressed as Chl-a) recorded in the two embayments also showed large differences as expected and was higher in Murchison Bay ($137.4 \pm 181.2 \mu\text{g Chl-a/L}$) than in Napoleon Gulf ($25.4 \pm 8.3 \mu\text{g Chl-a/L}$). Both spatial and temporal variations of Chl-a concentration were lower in Napoleon Gulf than in Murchison Bay where, in its inner part, Chl-a values ranged between 80 and 1000 $\mu\text{g/L}$. These shallow stations were subject to regular mixing that disrupts physical stratification and enhances nutrient availability but were also susceptible to the loading effect from Nakivubo channel during the rainy season.

Data from Uganda National Meteorological Authority (UNMA) indicated the increase in Chl-a in May was associated with the rainfall events of April (80 mm) and synchronised rainfall events of September (41.7 mm). Furthermore, the period between May and September was characterized by relatively high wind speed 4.9 – 8.1 m/s despite the solar radiation being within the same range throughout the study period. In a spatial context, previous studies showed that Chl-a within Murchison Bay has increased since the 1990 s (<20 $\mu\text{g/L}$, Källqvist et al., 1996), ranging from 20 to 60 $\mu\text{g/L}$ in the early 2000 s (Haande et al., 2011) and currently between 28 and 1087 $\mu\text{g/L}$ with a mean $\pm$ SD value of $137 \pm 181.2 \mu\text{g/L}$ (this study).

In Napoleon Gulf, the range of Chl-a values observed in this study (11.8–50.4, mean $\pm$ SD = $25.4 \pm 8.3 \mu\text{g/L}$) corresponds to the ones reported in the 2000–2010 period (10–55 $\mu\text{g/L}$) (Silsbe et al., 2006; North, 2008; Okello et al., 2010; Okello and Kurmayer, 2011). Therefore, using OECD (1982) classification, our TP and Chl-a data led to the classification of Murchison Bay as a hypereutrophic site while Napoleon Gulf is considered mesotrophic/eutrophic, as reported by Poste et al. (2013). The significantly greater increase in nutrient levels in Murchison Bay compared to Napoleon Gulf also suggests that the general pollution of Lake Victoria, which is directly associated with the population growth and activities of the major cities, seems to be increasingly stable.

Phytoplankton diversity and potential toxicity

Despite the large differences in limnological characteristics, no significant differences were observed between Napoleon Gulf and Murchison Bay in terms of phytoplankton richness and diversity. These richness values appeared as slightly higher than the one previously reported, with 80 taxa identified in Murchison Bay between 2003 and 2004 by Haande et al (2011). However, the sampling effort was lower in these previous studies than the one realized in the present study.

Consequently, we were unable to conclusively account for the increase in the number of phytoplanktonic taxa in these two bays, even in the hypereutrophic Murchison Bay. This implies that the

two bays contain enough environmental niches to maintain many species. Regarding the composition of the phytoplanktonic community, we found that around 53% of the taxa were shared by the two bays. This suggests that despite the large difference in the openness of these embayments to the lake, there is strong connectivity between the different bays and gulfs of Lake Victoria, allowing for colonization by similar planktonic communities (Borics et al., 2020). According to a study that modelled the currents in the lake (Nyamweya et al., 2016), the water flow alternates between gyres that favour water mixing in the open lake with a general northward flow. These patterns are expected to push the open lake waters in the direction of the northern shores towards our study sites, increasing the flow of planktonic organisms through their connectivity with other parts of the lakes.

In Murchison Bay and Napoleon Gulf, the dominant taxa are cyanobacteria, and this group represents one-third of all the taxa observed in this study. This dominance of cyanobacteria was already reported by many researchers about the embayments of Lake Victoria (Olokotum et al., 2020). Among these taxa, *Microcystis*, *Dolichospermum*, and *Planktolyngbya* were potentially able to produce toxins in Murchison Bay and Napoleon Gulf as earlier reported (Okello et al., 2010; Haande et al., 2011; Okello and Kurmayer, 2011) and were found in high abundance in this study. When potentially toxigenic cyanobacterial cells are present at > 100,000 cells/mL in drinking water, the World Health Organization (WHO) considers this the sanitary threshold beyond which serious health problems are likely (Mchau et al., 2019). The WHO also warns that recreational activities in waters with this level of potentially toxigenic cyanobacteria can cause short and long-term health problems (WHO, 2020). We applied these guidelines to our dataset and >20% of the samples (22/96) exceeded the WHO threshold especially in the wet season especially in particular, *Aphanocapsa* (22/96 with 15 samples during the wet season), *Dolichospermum* (4/96 with 3 samples in the wet season), and *Microcystis* (23/96, with 13 samples in the wet season). All of these samples were from Murchison Bay where fishers and locals living along the shores of the embayments directly drink the lake water. The WHO guideline for water is 1 µg/L of MC-LR, equivalent to ~ 5,000 cells/mL of cyanobacteria producing toxins (Chorus and Welker 2021). This suggests that fishers and the local population drinking relatively small amounts of water contaminated by toxigenic cyanobacteria could be harmed (Roegner et al., 2020). Thus, there is need for an in-depth study to assess the risks associated with cyanotoxins in these two bays and the exposure routes. In consequence of their substantial biomass and the toxins they can potentially produce, the dominant cyanobacteria may cause severe environmental and sanitary problems in the two embayments. To forecast and limit the development of these proliferations, it is necessary to identify the factors that trigger them (Rousso et al., 2020).

Multifactorial biomass modelling of dominant cyanobacteria taxa

Previous studies addressed the potential controlling factors of the spatiotemporal dynamics of phytoplankton communities in Lake Victoria (Poste et al., 2013; Mchau et al., 2019). However, to the best of our knowledge, none of them simultaneously modelled the limnological and climatic variables to assess their linkages with the dynamics of dominant taxa. Here, we applied the partial least squares (PLS) modelling approach to the biomass of each dominant taxon (*Microcystis* spp., *D. circinale*, and *P. circumcreta*) expressed in biovolumes. We benefited from the large range of environmental and phytoplankton variability evident in the two bays, which increased the accuracy of our statistical models. PLS modelling clearly predicted a large proportion of the variance (R^2) of the bio-

volume of the dominant cyanobacteria taxa: *Microcystis* spp. at 64.6% < *P. circumcreta* at 73.4% < *D. circinale* at 77.6%.

Nutrient concentration (SRP, NO_3^- , NH_4^+ and SRSi) and climatic variables (mean wind and solar radiation) had a significant positive influence on the biomass of the three dominant taxa, which validates the combining these two types of drivers. Among nutrients, NH_4^+ had the strongest influence on all dominant taxa, while SRP levels significantly affected *Microcystis* spp. biomass only. Thus, our results confirm that P and N concentrations are important drivers of cyanobacteria biomass and dynamics, as reported in an extensive review of models forecasting cyanobacterial blooms in freshwater lakes (Rousso et al., 2020). However, consistently detectable dissolved nutrients at all sampling stations, suggested that neither N nor P was a limiting factor in primary production of phytoplankton in the two bays, as reported by Poste et al. (2013). In Napoleon Gulf where nutrient concentration was the lowest, the two dominant taxa, *Dolichospermum* and *Planktolyngbya*, have developed physiological adaptations to cope with nitrogen limitation: heterocyst differentiation for *Dolichospermum* and high surface/volume ratio for *Planktolyngbya*.

Mean solar radiation positively influenced biovolume of the three dominant taxa, supporting the hypothesis that under conditions of very high biomass, light can become a limiting factor (Poste et al., 2013). An increase in solar radiation may temporarily suppress this limitation and allow a biomass increase of the taxa located in the upper part of the water column. If this is the case, those cyanobacteria taxa able to regulate their buoyancy such as *Microcystis* and *Dolichospermum* (Reynolds et al., 1987) would be favoured where they were dominant, *Microcystis* in Murchison Bay and *Dolichospermum* in Napoleon Gulf. Colony-forming genera such as *Microcystis* and filamentous genera such as *Dolichospermum* can use their intracellular aerotopes, to regulate their buoyancy and access light or nutrients resources in the upper water column (Bormans et al., 1999; Brookes et al., 1999). *Planktolyngbya* that lack gas vacuoles, forms thin filaments to compensate for sinking away from the nutrient-rich water column (Komárek 2003). Under laboratory conditions, isolated strains of *Planktolyngbya circumcreta* from Lake Victoria have shown chromatic adaption under red or green light (data not shown). It has also been reported that *Planktolyngbya* (Pseudanabaenaceae) is a shade-adapted genus (Reynolds 2002). We hypothesized that the coexistence *P. circumcreta* with *Dolichospermum* in Napoleon Gulf can be attributed to this cellular adaptation of the ability to synthesize phycoerythrin under certain light conditions (Kehoe 2010).

Among climatic variables, wind speed was significantly and positively related to phytoplankton biomass. There are several ways that wind could directly or indirectly influence the phytoplankton community. We suggest that wind increases water turbulence, and this might move phytoplankton from the bottom or intermediate depths to the surface of the water column. Such vertical movements would increase phytoplankton exposure to different light regimens that may provide the best compromise between light deficiency, light stress and the response to the dynamics of mixing (Bormans et al., 1999).

One intriguing result was the observation of a negative relationship with low variance between temperature and dominant taxa biomass. This is in direct contradiction to the literature which is full of examples of positive relationships between phytoplankton biomass and temperature, this latter being the most recurrent predictor in cyanobacteria models (Rousso et al., 2020). This unexpected negative relationship may arise from a non-causal covariation and also the very low variance in temperature between the embayments. In Murchison Bay, where the phytoplankton biomass is greater, self-shading due to high cell concentration may limit light penetration, including infra-red wavelengths. This

results in 'colder' water than in Napoleon Gulf where phytoplankton biomass is lower.

While the modelling approach used here provided interesting insights into the drivers of dominant taxa biomass in Lake Victoria, one could also consider predictive modelling using easily accessible variables. For instance, Silsbe et al. (2006) showed that in Lake Victoria, Secchi depth measurements were good predictors of Chl-a concentration. If one could correlate the Secchi depth to dominant taxa biomass, it would offer a very simple tool to get high-frequency monitoring of cyanobacterial blooms. Such an inexpensive and easy to use approach might be implemented by citizen science networks like the one reported by Mitroi et al. (2020) in a freshwater lagoon in Ivory Coast and would complement the monitoring of water agencies and the scientific community.

Conclusion

Napoleon Gulf and Murchison Bay exhibited different levels of eutrophication that influenced planktonic communities. The phytoplankton community comprises similar species, but the dynamics and dissimilarities in the phytoplankton assemblages of northern Lake Victoria are driven by the dominant cyanobacteria, *Microcystis flos-aquae* and *M. aeruginosa* in Murchison Bay and *Dolichospermum circinale* and *Planktolyngbya circumcreta* in Napoleon Gulf. Consequently, the water quality differences and phytoplankton functioning of the two bays makes Murchison Bay more susceptible to harmful cyanobacterial blooms with potential cyanotoxin production. The influence of climatic variables such as mean wind and solar radiation in combination with nutrients under increasing anthropogenic pressures might increase incidences of potential toxin production. This scenario requires future investigation into the dynamics of cyanotoxin production to assess specific health risks in the two embayments. In addition, it would be interesting to explore experimental approaches for nutrient limitation of phytoplankton growth, dynamics and functioning in the two bays.

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.

Acknowledgements

We thank, crews at Gaba KK beach and Rippon pier for the assistance during sampling and from the National Fisheries Resources Research Institute (NaFIRRI) analytical lab during sample preparation and analysis. We thank Uganda National Meteorological Authority (UNMA) for availing the climate data used during subsequent modelling and analyses. Research funding is supported by the French Facility for Global Environment (Fonds Français pour l'Environnement Mondial, FFEM) research program, Water Sources in Africa (WaSaf) for M. Olokotum PhD from Makerere University (2017–2020).

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jglr.2021.04.021>.

References

Akurut, M., Niwagaba, C.B., Willems, P., 2017. Long-term variations of water quality in the Inner Murchison Bay, Lake Victoria. *Environ. Monit. Assess.* 189.

- Baselga, A., Orme, C.D.L., 2012. *betapart*: an R package for the study of beta diversity. *Method. Ecol. Evol.* 3 (5), 808–812.
- Borics, G., Abonyi, A., Salmasso, N., Ptasnik, R., 2020. Freshwater phytoplankton diversity: models, drivers and implications for ecosystem properties. *Hydrobiologia*.
- Bormans, M., Sherman, B.S., Webster, I.T., 1999. Is buoyancy regulation in cyanobacteria an adaptation to exploit separation of light and nutrients? *Mar. Freshw. Res.* 50, 897–906.
- Boynton, W.R., Hall, C.A., Falkowski, P.G., Keefe, C.W., Kemp, W.M., 1983. Phytoplankton Productivity in Aquatic Ecosystems. In: Lange, O.L., Nobel, P.S., Osmond, C.B., Ziegler, H. (Eds.), *Physiological Plant Ecology IV: Ecosystem Processes: Mineral Cycling, Productivity and Man's Influence*. Springer, Berlin Heidelberg, Berlin, Heidelberg, pp. 305–327.
- Brookes, J.D., Ganf, G.G., Green, D., Whittington, J., 1999. The influence of light and nutrients on buoyancy, filament aggregation and flotation of *Anabaena circinalis*. *J. Plankton Res.* 21, 327–341.
- Catherine, A., Maloufi, S., Congestri, R., Viaggiu, E., Pilkaityte, R., 2017. Cyanobacterial samples: preservation, enumeration, and biovolume measurements. In: Meriluoto, J., Spoof, L., Codd, G.A. (Eds.), *Handbook of Cyanobacterial Monitoring and Cyanotoxin Analysis*. John Wiley & Sons Ltd, United Kingdom, pp. 313–330.
- Chorus, I., Welker, M. (Eds.), 2021. *Toxic Cyanobacteria in Water: A Guide to Their Public Health Consequences, Monitoring and Management*. 2nd Edition. CRC Press, London.
- Clarke, K.R., 1993. Non-parametric multivariate analyses of changes in community structure. *Aust. J. Ecol.* 18, 117–143.
- Cronberg, G., Annadotter, H., 2006. *Manual on aquatic cyanobacteria: A photo guide and a synopsis of their toxicology*. Intergovernmental Oceanographic Commission, UNESCO, Paris, France.
- Downing, A.S., Van Nes, E.H., Janse, J.H., Witte, F., Cornelissen, I.J., Scheffer, M., Mooij, W.M., 2012. Collapse and reorganization of a food web of Mwanza Gulf, Lake Victoria. *Ecol. Appl.* 22, 229–239.
- Egessa, R., Pabire, G.W., Ocaya, H., 2018. Benthic macroinvertebrate community structure in Napoleon Gulf, Lake Victoria: effects of cage aquaculture in eutrophic lake. *Environ. Monit. Assess.* 190, 112–122.
- Gikuma-Njuru, P., Rutagwema, D., Mugidde, R., Hecky, R., Mwebaza-Ndawula, L., Mwirigi, P., Abudha, J., Waya, R., Matovu, A., Kinobe, J., 2005. Eutrophication of the Lake Victoria Ecosystem. In: Muyodi, J.F., Hecky, R.E. (Eds.), *Lake Victoria Environment Management Project (LVEMP). Water Quality and Ecosystem Status, LVEMP, Entebbe, Uganda*, pp. 81–102.
- Haande, S., Rohrlack, T., Semyalo, R.P., Brettum, P., Edvardsen, B., Lyche-Solheim, A., Sørensen, K., Larsson, P., 2011. Phytoplankton dynamics and cyanobacterial dominance in Murchison Bay of Lake Victoria (Uganda) in relation to environmental conditions. *Limnol.- Ecol. Manage. Inland Waters* 41, 20–29.
- ISO-10260. 1992. Water quality - Measurement of biochemical parameters - Spectrometric determination of the chlorophyll-a concentration. Page 6. The International Organization for Standardization, Geneva, Switzerland.
- Juma, D.W., Wang, H., Li, F., 2014. Impacts of population growth and economic development on water quality of a lake: case study of Lake Victoria Kenya water. *Environ. Sci. Pollut. Res.* 21, 5737–5746.
- Kabenge, M., Wang, H., Li, F., 2016. Urban eutrophication and its spurring conditions in the Murchison Bay of Lake Victoria. *Environ. Sci. Pollut. Res.* 23, 234–241.
- Källqvist, T., Johansen, S., Löffler, H., 1996. Lake Victoria—limnological study of Murchison Bay and Napoleon Gulf, Uganda, with references to water supply and wastewater disposal at Kampala and Jinja, The World Bank. Norwegian Institute for Water Research, Department of Zoology, University of Vienna, Republic of Uganda.
- Komárek J. 2003. Planktic oscillatoriallean cyanoprokaryotes (short review according to combined phenotype and molecular aspects). In: Naselli-Flores L., Padišák J., Dokulil M.T. (eds) *Phytoplankton and Equilibrium Concept: The Ecology of Steady-State Assemblages*. Developments in Hydrobiology, vol 172. Pages 367–382. Springer, Dordrecht. https://doi.org/10.1007/978-94-017-2666-5_30
- Krom, M.D., 1980. Spectrophotometric determination of ammonia: a study of a modified Berthelot reaction using salicylate and dichloroisocyanurate. *Analyst* 105, 305–316.
- Lehman, J.T., Branstrator, D.K., 1994. Nutrient dynamics and turnover rates of phosphate and sulfate in Lake Victoria, East Africa. *Limnol. Oceanogr.* 39, 227–233.
- Luyiga, S., Haande, S., Semyalo, R.P., Kizito, Y.S., Miyingo-Kezimbira, A., Brettum, P., Solheim, A.L., Odong, R., Asio, S.M., Jensen, K.H., 2015. How water exchange and seasonality affect the eutrophication of Murchison Bay, Lake Victoria. *Limnol.-Ecol. Manage. Inland Waters* 53, 60–73.
- Mbonde, A.S., Sitoki, L., Kurmayer, R., 2015. Phytoplankton composition and microcystin concentrations in open and closed bays of Lake Victoria, Tanzania. *Aquat. Ecosyst. Health Manage.* 18, 212–220.
- Mchau, G.J., Makule, E., Machunda, R., Gong, Y.Y., Kimanya, M., 2019. Harmful algal bloom and associated health risks among users of Lake Victoria freshwater: Ukerewe Island, Tanzania. *J. Water Health* 17, 826–836.
- Mitroi, V., Ahi, K.C., Bulot, P.-Y., Tra, F., Deroubaix, J.-F., Ahoutou, M.K., Quiblier, C., Koné, M., Coulibaly Kalpy, J., Humbert, J.-F., 2020. Can participatory approaches strengthen the monitoring of cyanobacterial blooms in developing countries? Results from a pilot study conducted in the Lagoon Aghien (Ivory Coast). *PLoS ONE* 15, e0238832.
- Müller, R., Wiedemann, O., 1955. Die Bestimmung des Nitrations im Wasser. *Vom Wasser* 22, 247–271.

- Musinguzi, L., Lugya, J., Rwezawula, P., Kamya, A., Nuwahereza, C., Halafo, J., Kamondo, S., Njaya, F., Aura, C., Shoko, A.P., Osinde, R., Natugonza, V., Ogotu-Ohwayo, R., 2019. The extent of cage aquaculture, adherence to best practices and reflections for sustainable aquaculture on African inland waters. *J. Great Lakes Res.* 45, 1340–1347.
- Nassali J., Z. Yongji., and F. F. Fangninou. 2020. A Systematic Review of Threats to the Sustainable Utilization of Transboundary Fresh Water Lakes: A Case Study of Lake Victoria; International Journal of Scientific and Research Publications (IJSRP) 10(02) (ISSN: 2250-3153), Doi: 10.29322/IJSRP.10.02.2020.p9890
- Ngupula, G., Ezekiel, C., Kimirei, I., Mboni, E., Kashindye, B., 2012. Physical and chemical characteristics of the Tanzanian inshore and offshore waters of Lake Victoria in 2005–2008. *Afr. J. Aquat. Sci.* 37, 339–345.
- North, R.L., 2008. Phytoplankton dynamics in nearshore and offshore regions of the Great Lakes Erie, Malawi, Tanganyika, and Victoria PhD Thesis. University of Waterloo UWSpace.
- Nyamweya, C., Desjardins, C., Sigurdsson, S., Tomasson, T., Taabu-Munyaho, A., Sitoki, L., Stefansson, G., 2016. Simulation of Lake Victoria Circulation Patterns Using the Regional Ocean Modeling System (ROMS). *PLoS ONE* 11, e0151272.
- Moresco, G.A., Bortolini, J.C., Dias, J.D., Pineda, A., Jati, S., Rodrigues, L.C., 2017. Drivers of phytoplankton richness and diversity components in Neotropical floodplain lakes, from small to large spatial scales. *Hydrobiologia* 799 (1), 203–215.
- OECD. 1982. Eutrophication of waters. Monitoring, assessment, and control. pp. 147.
- Oguttu, H.W., Bugenyi, F.W., Leuenberger, H., Wolf, M., Bachofen, R., 2008. Pollution menacing Lake Victoria: quantification of point sources around Jinja Town, Uganda. *Water Sa* 34, 89–98.
- Okello, W., Kurmayer, R., 2011. Seasonal development of cyanobacteria and microcystin production in Ugandan freshwater lakes. *Lakes Reservoirs Res. Manage.* 16, 123–135.
- Okello, W., Portmann, C., Erhard, M., Gademann, K., Kurmayer, R., 2010. Occurrence of microcystin-producing cyanobacteria in Ugandan freshwater habitats. *Environ. Toxicol.* 25, 367–380.
- Oksanen, J., R. Kindt, P. Legendre, B. O'Hara, M. H. H. Stevens, M. J. Oksanen, and M. Suggests. 2007. The vegan package. *Community Ecology Package* 10:631–637.
- Olokotum, M., Mitroi, V., Troussellier, M., Semyalo, R., Bernard, C., Montuelle, B., Okello, W., Quiblier, C., Humbert, J.-F., 2020. A review of the socioecological causes and consequences of cyanobacterial blooms in Lake Victoria. *Harmful Algae* 96, 101829.
- Onyango, D. M., P. S. Orina, R. C. Ramkat, C. Kowenje, C. M. Githukia, D. Lusweti, and H. B. O. Lung'ayia. 2020. Review of current state of knowledge of microcystin and its impacts on fish in Lake Victoria. *Lakes & Reservoirs: Science, Policy and Management for Sustainable Use* 25:350–361.
- Outa, N. O., E. O. Yongo, J. L. A. Keyombe, E. O. Ogello, and D. Namwaya Wanjala. 2020. A review on the status of some major fish species in Lake Victoria and possible conservation strategies. *Lakes & Reservoirs: Science, Policy and Management for Sustainable Use* 25:105–111.
- Poste, A., Hecky, R., Guildford, S., 2013. Phosphorus enrichment and carbon depletion contribute to high *Microcystis* biomass and microcystin concentrations in Ugandan lakes. *Limnol. Oceanogr.* 58, 1075–1088.
- Reynolds, C.S., Oliver, R.L., Walsby, A.E., 1987. Cyanobacterial dominance: The role of buoyancy regulation in dynamic lake environments. *N. Z. J. Mar. Freshwater Res.* 21, 379–390.
- Reynolds, C.S., 2002. Ecological pattern and ecosystem theory. *Ecol. Model.* 158, 181–200.
- Ritchie, M.E., Phipson, B., Wu, D., Hu, Y., Law, C.W., Shi, W., Smyth, G.K., 2015. limma powers differential expression analyses for RNA-sequencing and microarray studies. *Nucleic Acids Res.* 43., <https://doi.org/10.1093/nar/gkv007> e47.
- Roegner, A., L. Sitoki, C. Weirich, J. Corman, D. Owage, M. Umami, E. Odada, J. Miruka, Z. Ogari, W. Smith, E. Rejmankova, and T. R. Miller. 2020. Harmful Algal Blooms Threaten the Health of Peri-Urban Fisher Communities: A Case Study in Kisumu Bay, Lake Victoria, Kenya. *Exposure and Health*.
- Rouso, B.Z., Bertone, E., Stewart, R., Hamilton, D.P., 2020. A systematic literature review of forecasting and predictive models for cyanobacteria blooms in freshwater lakes. *Water Res.* 182, 115959.
- Sébastien, L., Josse, J., Husson, F., 2008. FactoMineR: An R Package for Multivariate Analysis. *J. Stat. Softw.* 25 (1), 1–18.
- Silsbe, G.M., Hecky, R.E., Guildford, S.J., Mugidde, R., 2006. Variability of chlorophyll a and photosynthetic parameters in a nutrient-saturated tropical great lake. *Limnol. Oceanogr.* 51, 2052–2063.
- Sitoki, L., Kurmayer, R., Rott, E., 2012. Spatial variation of phytoplankton composition, biovolume, and resulting microcystin concentrations in the Nyanza Gulf (Lake Victoria, Kenya). *Hydrobiologia* 691, 109–122.
- Sterner, R.W., Keeler, B., Polasky, S., Poudel, R., Rhude, K., Rogers, M., 2020. Ecosystem services of Earth's largest freshwater lakes. *Ecosyst. Serv.* 41, 101046.
- Sun, J., Liu, D., 2003. Geometric models for calculating cell biovolume and surface area for phytoplankton. *J. Plankton Res.* 25, 1331–1346.
- Talling, J.F., 1957. Some Observations on the Stratification of Lake Victoria. *Limnol. Oceanogr.* 2, 213–221.
- Talling, J.F., 1987. The phytoplankton of Lake Victoria (East Africa). *Arch. Hydrobiol. Beihefte Ergebnisse der Limnologie* 25, 229–256.
- Uganda Bureau of Statistics 2017a. The National Population and Housing Census 2014 – Area Specific Profile Series – Kampala District, Kampala, Uganda. Accessed October 2020.
- Uganda Bureau of Statistics 2017b. The National Population and Housing Census 2014 – Area Specific Profile Series – Jinja District, Kampala, Uganda. Accessed October 2020.
- Utermöhl, H., 1958. Toward the improvement of the quantitative phytoplankton method. *Mitteilungen-Internationale Vereinigung für Limnologie* 9, 1–38.
- Verschuren, D., Johnson, T.C., Kling, H.J., Edgington, D.N., Leavitt, P.R., Brown, E.T., Talbot, M.R., Hecky, R.E., 2002. History and timing of human impact on Lake Victoria, East Africa. *Proc. R. Soc. Lond. B Biol. Sci.* 269, 289–294.
- Wetzel, R.G., Likens, G.E., 2000a. Composition and biomass of phytoplankton. In: *Limnological Analyses*. Springer, New York, pp. 147–174.
- Wetzel, R.G., Likens, G.E., 2000b. Inorganic Nutrients: Nitrogen, Phosphorus, and Other Nutrients. In: *Limnological Analyses*. Springer, New York, pp. 87–112.
- WHO, 2020. Cyanobacterial toxins: Microcystins. Background document for development of WHO Guidelines for Drinking-water Quality and Guidelines for Safe Recreational Water Environments. World Health Organization, Geneva.
- Whittaker, R.H., 1972. Evolution and measurement of species diversity. *Taxon* 21 (2–3), 213–251.
- Whittaker, R.J., Willis, K.J., Field, R., 2001. Scale and species richness: towards a general, hierarchical theory of species diversity. *J. Biogeogr.* 28 (4), 453–470.
- Wilson, M.V., Shmida, A., 1984. Measuring beta diversity with presence-absence data. *J. Ecol.*, 1055–1064.
- Worthington, E.B., 1930. Observations on the Temperature, Hydrogen-ion concentration, and other physical conditions of the Victoria and Albert Nyanzas. *Internationale Revue der gesamten Hydrobiologie und Hydrographie* 24, 328–357.