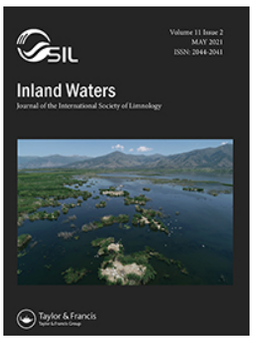

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Phytoplankton pigment analysis as a tool for monitoring a tropical great lake, Lake Kivu (East Africa)

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ABSTRACT

Lake Kivu, East Africa, is a deep oligotrophic and meromictic lake containing high amounts of dissolved methane (~55–60 km^3) and carbon dioxide (~300 km^3) in its deep waters. Methane harvesting for energy production began in 2015, and a monitoring programme was set up to assess possible disturbance on the ecosystem. Phytoplankton biomass and composition was assessed twice per month or monthly at 2 monitoring sites between June 2005 and December 2019, based on HPLC analysis of chlorophyll *a* (Chl-*a*) and marker pigments. This long-term series shows that significant changes occurred around 2010 in the lake phytoplankton, with a notable increase of Chl-*a* and changes in the assemblage toward an increase in non-motile green algae and diatoms. To assess possible changes due to methane harvesting, we compared 2 periods, 2012–2014 and 2018–2019. Chl-*a* concentration decreased slightly in 2018–2019 compared to the reference period of 2012–2014, and significant changes occurred in composition of the phytoplankton assemblage. In terms of relative contribution to Chl-*a*, diatoms increased from 26% to 46%, whereas green algae decreased ~2-fold, from 35% in 2012–2014 to 18% in 2018–2019. Multivariate analyses showed that phytoplankton composition was influenced by seasonal and interannual variations of limnological variables related to changes in meteorological factors. To assess possible future changes due to methane exploitation, we recommend increasing sampling frequency and taxonomic resolution, as well as improving environmental data acquisition.

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algal strategies; limnology; long-term data; meteorology; methane harvesting

Introduction

Integration of changes in the ecological status of lakes by phytoplankton assemblages have been well demonstrated by studies that interpreted long time series from temperate lakes, reporting changes due to oligotrophication (e.g., Ruggiu et al. 1998, Anneville et al. 2002), global warming (e.g., Stenuite et al. 2007, de Senerpont-Domis et al. 2013, Sarmento et al. 2013), or combined effect of eutrophication and global warming (Pomati et al. 2017). In tropical lakes, long time series are rare; comprehensive phytoplankton surveys, if available, are usually separated by long periods of time, and interpretation of temporal changes in a single lake is limited by lack of environmental data or insufficient sampling. These shortcomings occurred, for instance, in Lake Malawi and Lake Tanganyika studies (see review by Descy and Sarmento 2008), despite the availability of some past and recent comparable data on phytoplankton composition. In Lake Victoria, much of the assessment of major causes for the lake's eutrophication was from paleolimnological studies, which allowed reconstruction of the history of the changes (Verschuren et al. 2002, Stager et al. 2009, Hecky et al. 2010), even though data from the 1960s and 1990s had previously provided some evidence of the many pressures on the lake and its resources.

In Lake Kivu, in East Africa, the oxic surface waters are separated from the anoxic deep waters by a chemocline. The deep waters of the lake contain a high amount of dissolved methane (CH_4; ~55–60 km^3) and carbon dioxide (CO_2; ~300 km^3), with a reported high risk for local populations in the case of a release event (Schmid et al. 2005, Nayar 2009). The gas also represents an opportunity for the region to exploit this available energy source for economic development. Methane gas exploitation started in 2008 with the first pilot plant named Kibuye Power 1 (KP1), which stopped production in 2016. In recent years, gas exploitation increased. The KivuWatt power plant started CH_4 harvesting in 2015 with a production capacity of 26.2 MW and will

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reach 100 MW in the coming years, according to the Rwanda Energy Group (REG) projections. Wüest et al. (2012) provided a comprehensive account of the process of gas extraction and different scenarios that considered the need to maintain the salinity gradient and to protect the ecosystem of surface waters. Briefly, the process of gas extraction involves pumping water into a pipe lowered into the deep "resource zone," below 270 m depth, where the highest gas concentration occurs. Hydrostatic pressure decreases as the flow is driven to the surface, forming gas bubbles; separation of the poorly soluble CH_4 from CO_2 and other solutes occurs in a separation chamber. The remaining soluble gases, essentially CO_2 and hydrogen sulfide (H_2S), are washed with surface water and released at ~60 m depth. The degassed water, which contains high concentrations of salts and nutrients, must then be reinjected into the deep layers to maintain the salinity gradient and thus stability of the water column (Wüest et al. 2012). Reinjection is also necessary to prevent release of nutrient-rich water into the biozone, which would trigger catastrophic eutrophication, resulting not only in phytoplankton blooms and changes in composition, but also reduced oxygenation in the mixolimnion (Descy et al. 2015), which would likely destroy the fishery. Among the uses of the lake resources, the fishery, mainly based on the Tanganyika sardine (*Limnothrissa miodon*), is particularly important. Since the 1960s, the fishery has become a key resource for the human population, with a yield reaching 10 000 ton yr^{-1} for the whole lake, close to the annual sardine production of 8000–9600 ton (~38 kg ha^{-1} yr^{-1}) estimated from hydroacoustic surveys (Guillard et al. 2012, Snoeks et al. 2012).

In parallel to methane gas pilot harvesting, the biological monitoring of Lake Kivu began in 2012 with a baseline project, supported by the Belgian Technical Cooperation (BTC, now ENABEL [Agence Belge de Développement]), as a reference to assess future changes in the lake ecosystem due to CH_4 exploitation, climate change, and anthropisation (Descy and Guillard 2014). This first project aimed to gather available scientific knowledge on the lake before intensive gas harvesting. Since then, monitoring has continued through the Lake Kivu Monitoring Program (LKMP), with a special emphasis on plankton survey and analysis, at 2 sites with CH_4 development (i.e., near Kibuye and Gisenyi, Rwanda). Because lake productivity is driven by climatic factors (Darchambeau et al. 2013, Loiselle et al. 2014), the fish stock and the fishery yield are expected to respond to changes in phytoplankton and zooplankton production, driven by climate variability at the regional scale.

Since 2002, phytoplankton studies have been conducted in Lake Kivu (Sarmento et al. 2012, Rugema et al. 2019) using high performance liquid chromatography (HPLC) to determine phytoplankton marker pigments. This technique, which can estimate phytoplankton biomass at the class level, was developed in the marine environment (Wright and Jeffrey 2006) and applies as well to estuarine and fresh waters (Fietz and Nicklisch 2004, Descy et al. 2005, Fietz et al. 2005, Sarmento et al. 2006, review in Sarmento and Descy 2008). Monitoring phytoplankton biomass and composition in Lake Kivu, based on the use of specific marker pigments of these classes over 12 years, allowed Rugema et al. (2019) to detect dramatic changes in phytoplankton community structure of Lake Kivu, which they attributed to a change in the water column mixing pattern, depending on large-scale climate variability. That study demonstrated the potential of using pigment-based analysis of phytoplankton composition, complemented by data from microscopy, as a tool to monitor environmental changes in this tropical lake at different time scales. The approach, largely consisting of combining the marker pigment approach with identification of the most abundant taxa at the microscope, is similar to that proposed by Sarmento and Descy (2008), who aimed to assess the ecological status of reservoirs within the implementation of the EU Water Framework Directive.

In this study, we present long-term data (2005–2019) available for the northern and eastern basins of Lake Kivu and compare data collected in 2018–2019 with those from 2012–2014, before the large-scale development of CH_4 exploitation. The main objective of the study was to assess changes possibly due to CH_4 exploitation, taking into account the influence of limnological and meteorological factors.

Material and methods

Study sites

Lake Kivu is a large (2450 km^2) and deep (maximum depth of 489 m) meromictic lake of the East African Rift (Fig. 1) at 1463 m a.s.l. The study sites (Fig. 1) were located in the northern basin (near Gisenyi 1.07°S, 29.23°E) and the eastern basin (near Kibuye 2.10°S, 29.20°E), the same as those surveyed by Rugema et al. (2019).

Methods

Sampling was conducted monthly throughout 2018 and 2019, starting in January 2018 and ending in December

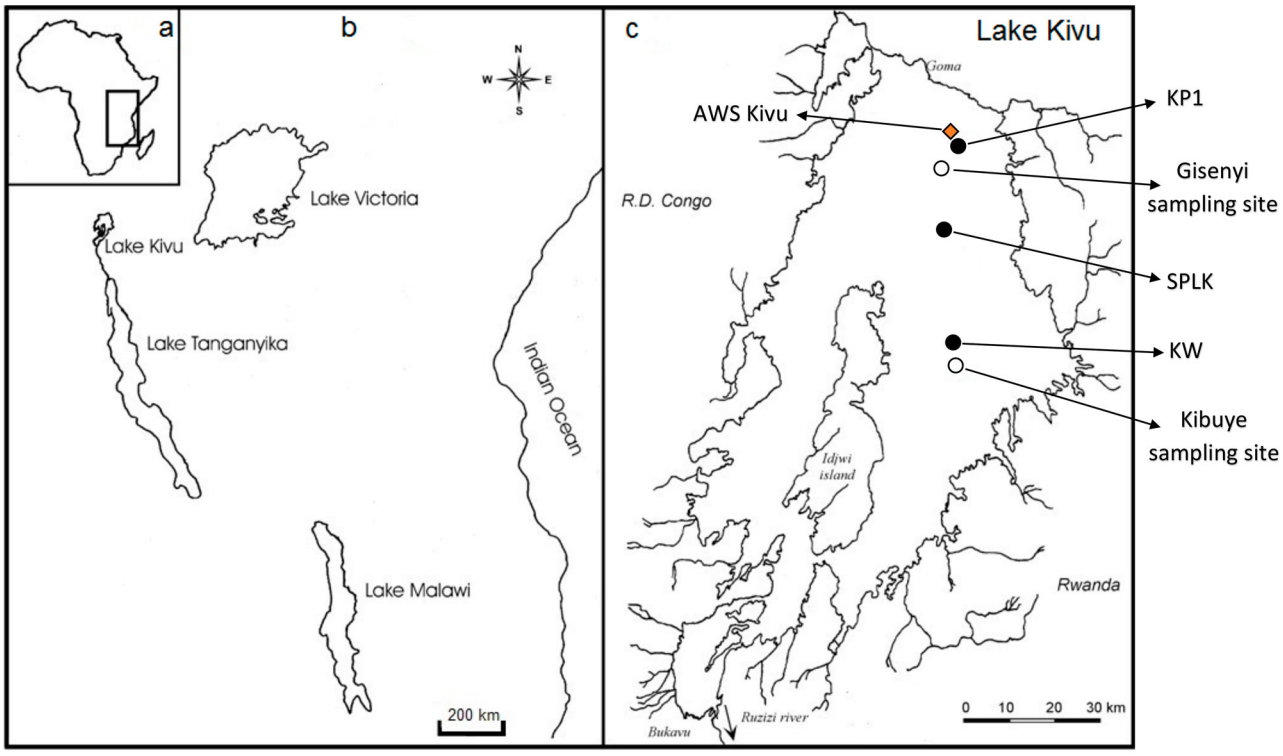

Figure 1. (a) Location of the East African Great Lakes area. (b) Location of Lake Kivu among the East African great lakes. (c) Lake Kivu, with location of the monitoring sites (open circles) of the automatic weather station (AWS Kivu; diamond) and of the gas harvesting platforms (closed circles). KP1: Kibuye Power 1; SPLK: Shema Power Lake Kivu; KW: KivuWatt.

2019. The sampling methods were the same as in Rugema et al. (2019), with water samples collected in a 5 L Niskin bottle from 2 floating platforms at 5 m intervals in the 0–40 m layer and at 10 m intervals in the 40–60 m layer. Sea & Sun CTD M725 and 257 multiparameter probes (Trappenkamp, Germany) were used to acquire vertical profiles of temperature, dissolved oxygen, pH, and conductivity in the mixolimnion, with casts down to 100 m depth. The mixed layer depth (*Z*m) was determined based on temperature and oxygen vertical profiles. The depth of the euphotic zone (*Z*eu; the depth at which light is attenuated to 1% of subsurface PAR) was estimated from Secchi depth using conversion coefficients determined several times during 2012–2014 from simultaneous measurements with Li-Cor (Lincoln, NE, USA) surface and submersible quantum sensors (e.g., Darchambeau et al. 2014).

Pigment extraction was carried out in 90% HPLC-grade acetone following Sarmento et al. (2006), after filtration of 3 L lake water from each sampling depth on Macherey-Nägel GF5 filters (Düren, Germany; average retention capacity 0.4 µm). Chlorophyll *a* (Chl-*a*) and phytoplankton marker pigments were measured by HPLC analysis of phytoplankton extracts according to Sarmento et al. (2006), using the Wright et al. (1991) gradient elution method with a Waters Alliance (Milford, MA, USA) system equipped with a 2998 photodiode array detector installed at the LKMP laboratory on the shore of Lake Kivu (Rubavu, Rwanda). Equipment was calibrated using commercial external standards (DHI, Denmark) of all key chlorophylls (*a*, *b*, and *c*2) and carotenoids used as markers of phytoplankton classes (Table 1).

Phytoplankton abundance at the class level was estimated from pigment concentrations using CHEMTAX 1.95 software (Wright and Jeffrey 2006), which uses a steepest descent algorithm to optimise the marker pigments to Chl-*a* ratios, given in an input ratio matrix (Mackey et al. 1996). The result is the contribution of different phytoplankton classes to Chl-*a* as well as a final ratio matrix containing the optimised ratio values. Successive runs, using each time the output ratio matrix as input ratio matrix, can be conducted to minimise the root mean square (RMS). The input ratios were determined according to data in literature from field studies in deep tropical lakes (Descy et al. 2005, Sarmento et al. 2006, Rugema et al. 2019) as well as laboratory studies (Lauridsen et al. 2011). Taking into account variations of pigment ratios with depth, as well as possible pigment degradation, we performed separate CHEMTAX runs on the 0–30 m samples and used the output ratio matrix

Table 1. Initial ratio matrix with the initial values of the ratio between each marker pigment and chlorophyll *a* used in the CHEMTAX processing of the pigment data from Lake Kivu during the 2 periods of monitoring (2012–2014 and 2018–2019); peri = peridinin; fuco = fucoxanthin; neo = neoxanthin; myxo = myxoxanthophyll; viol = violaxanthin; allo = alloxanthin; lut = lutein; zea = zeaxanthin; echi = echinenone; BPcar = βψ-carotene; acar = α-carotene; chl_*c* = chlorophyll *c*1–*c*2; chl_*b* = chlorophyll *b*; chl_*a* = chlorophyll *a*.

Class / pigment	peri	fuco	neo	myxo	viol	ddx	allo	lut	zea	echi	Bpcar	acar	chl_*c*	chl_*b*	chl_*a*
green algae	0.0000	0.0000	0.0202	0.0000	0.0794	0.0000	0.0000	0.1405	0.0478	0.0000	0.0000	0.0000	0.0000	0.2300	1.0000
chrysophytes	0.0000	0.3000	0.0000	0.0000	0.1500	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.1000	0.0000	1.0000
cryptophytes	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.2016	0.0000	0.0000	0.0000	0.0000	0.0140	0.0510	0.0000	1.0000
cyanobacteria_T1	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.7952	0.0000	0.0000	0.0000	0.0000	0.0000	1.0000
cyanobacteria_T2	0.0000	0.0000	0.0000	0.6027	0.0000	0.0000	0.0000	0.0000	0.2569	0.0477	0.0000	0.0000	0.0000	0.0000	1.0000
diatoms T1	0.0000	0.2286	0.0000	0.0000	0.0000	0.0971	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0382	0.0000	1.0000
diatoms T2	0.0000	0.4000	0.0000	0.0000	0.0000	0.2920	0.0000	0.0000	0.0000	0.0000	1.0017	0.0000	0.0841	0.0000	1.0000
dinoflagellates	0.6290	0.0000	0.0000	0.0000	0.0000	0.2500	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.1500	0.0000	1.0000

of these runs as input ratio matrix for the deeper samples, with a stronger constraint on the limits of ratio optimisation. Using this procedure, we determined Chl-*a* biomass of green algae, chrysophytes, diatoms (2 pigment types, diatoms T1 and T2; Sarmento et al. 2006), cryptophytes, dinoflagellates, and cyanobacteria (2 pigment types, cyanobacteria T1 and T2). The initial ratio matrix used for processing the pigment concentrations with CHEMTAX was recorded (Table 1). The marker pigment data collected from October 2012 to September 2014 by Rugema et al. (2019) were reprocessed using the same procedure. The total number of individual samples processed for the 2 monitoring periods was 1132.

According to Sarmento et al. (2007) on taxa identification in Lake Kivu, which has a remarkably low phytoplankton diversity, these phytoplankton groups can be assigned to the following taxa: diatoms T2 correspond to *Urosolenia* sp.; diatoms T1 are mostly long needle-shaped *Nitzschia* and *Fragilaria*; green algae are essentially nonmotile desmids (mainly *Cosmarium laeve*) and a small coccal form; cyanobacteria T1 are picoplankton (*Synechococccus* spp.); and cyanobacteria T2 are slender filamentous forms, some with heterocytes, which allow efficient N_2-fixation. Rugema et al. (2019) discussed the ecological strategies of the most abundant groups.

Data gathering and processing

The dataset combined available data from the 2 monitoring sites, focusing on the 2 distinct monitoring periods: 2012–2014, corresponding to the BTC baseline and used as a reference ($n = 56$, "reference period" in the following text), and 2018–2019 ($n = 46$). Given their similarity (Rugema et al. 2019), the data from the 2 sites were merged (i.e., inserted into a single time series). The phytoplankton data were Chl-*a* concentration (μg L^{-1}) and the biomass of phytoplankton classes (μg L^{-1}), averaged for the 6 sampling depths between 0 and 20 m, corresponding roughly to the euphotic zone (average [standard deviation] 16.1 [2.5] m).

The available limnological measurements were: mixed layer depth (*Z*m, m), maximum temperature in the mixolimnion (Max_T, °C), minimum temperature in the mixolimnion (Min_T), Delta_T (Max-T – Min_T), Secchi depth (Secchi, m), depth of the euphotic zone (*Z*eu, m), and the *Z*m:Zeu ratio. Detailed meteorological data were obtained from an automatic weather station (AWS Kivu; Rooney et al. 2018) deployed on the Rwanda Energy Company (REC) platform ~3 km near Gisenyi (Rwanda). Since 9 October 2012, AWS Kivu has provided quasi-continuous high-quality

observations of near-surface meteorology including 4-component radiation, with a time step of 15 s. These data were processed to determine average values, for the 6 days preceding phytoplankton sampling, of air temperature (°C), relative air humidity (%), incoming shortwave radiation (solar radiation, W m^{-2}), wind speed (m s^{-1}), and rainfall (mm h^{-1}). A few meteorological data were missing for the end of 2019 because of errors in data transfer.

The final data matrix contained 82 observations of limnological, meteorological, and planktological variables. Using the R 3.5 (R Development Core Team 2010) and the *ADE4* package (Chessel et al. 2004), we performed principal component analyses (PCA) on the abiotic and phytoplankton data to examine changes between the 2 periods of observation. We also performed a redundancy analysis (RDA) to identify the key environmental variables driving the biomass of the phytoplankton classes.

We also used the complete phytoplankton dataset for the Rwandese part of the lake, containing 2507 single samples, collected twice per month or monthly since June 2005, with, however, gaps in the measurements from September 2008 until the end of 2009 as well as from mid-2015 to mid-2017. The data were averaged over the 0–20 m layer as for the 2 monitoring periods, providing a matrix of 227 observations.

Results

Variations of Chl-*a* concentration and of the abundance of the most important classes occurred over 2005–2019 (Fig. 2–3). Chl-*a* (Fig. 2) showed long-term variation superimposed on the seasonal variation, with maxima reached during the dry season (Jun–Sep). As previously reported by Rugema et al. (2019), an increase in phytoplankton abundance began ~2010. The changes are more conspicuous when the different phytoplankton groups are considered (Fig. 3). Green algae and diatoms (Fig. 3) presented a similar long-term increase, with biomass peaks of variable importance occurring in the dry seasons. The increase was particularly important for green algae, which had low abundance in the pre-2010 period and from 2010 became a major group constituting the main part of the Chl-*a* peaks, along with the diatoms. Similar to Chl-*a*, both groups exhibited some interannual variability. By contrast, the phytoplankton groups known to be best adapted to stratified conditions (Reynolds 2006), cyanobacteria T2 and to a lesser extent cryptophytes (Fig. 3), had an opposite pattern of development over time, with maxima before 2010 and a conspicuous decline afterward. Cyanobacteria T1 significantly increased from 2010 on, similar to green algae and diatoms.

Total phytoplankton biomass (as Chl-*a*; Fig. 4) was slightly but significantly ($p < 0.001$) lower in 2018–2019 (2.54 [0.74] µg L^{-1}) than in the reference period (2.86 [0.63] µg L^{-1}), a difference resulting from variation of the most abundant phytoplankton groups (Fig. 4), green algae and cyanobacteria T2, which both decreased in the second monitoring period. By contrast, the contribution of diatoms and cyanobacteria T1 to total phytoplankton (Fig. 4) increased in 2018–2019. In terms of relative contribution to Chl-*a*, diatoms increased from 26% to 46%, whereas green algae decreased ~2-fold, from 35% in 2012–2014 to 18% in 2018–2019.

Multivariate analyses (Fig. 5–6) showed seasonal and interannual variations for the 2 monitoring periods and allowed us to relate the response of total phytoplankton biomass and phytoplankton groups to environmental variables. PCA (Fig. 5) was conducted on the whole dataset but separated abiotic variables (Fig. 5a–b) from biotic variables (Fig. 5c–d). Both types of variables showed major seasonal variation; for example, the highest *Z*m and *Z*m:*Z*eu ratio occurred during the dry season, and the stronger Delta_T (hence the thermal stratification) occurred during the rainy season, when relative humidity and air temperature were highest. In parallel, phytoplankton groups that exhibited their

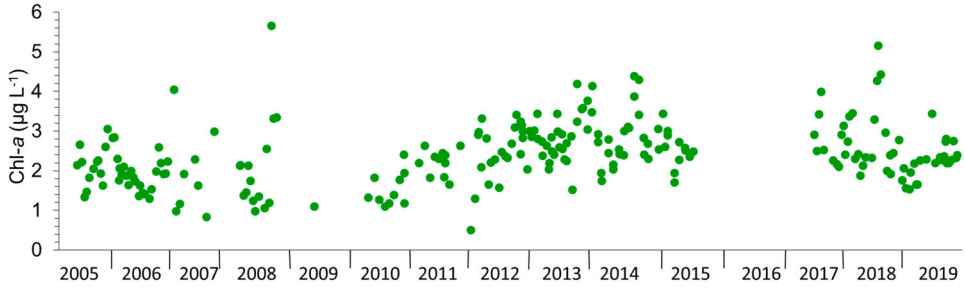

Figure 2. Average concentration of chlorophyll *a* (Chl-*a*; proxy of total phytoplankton biomass) in the euphotic layer of Lake Kivu from June 2005 to December 2019; the data from the 2 sampling sites near Gisenyi and Kibuye were merged. The 2 main gaps in the time series correspond to missing data.

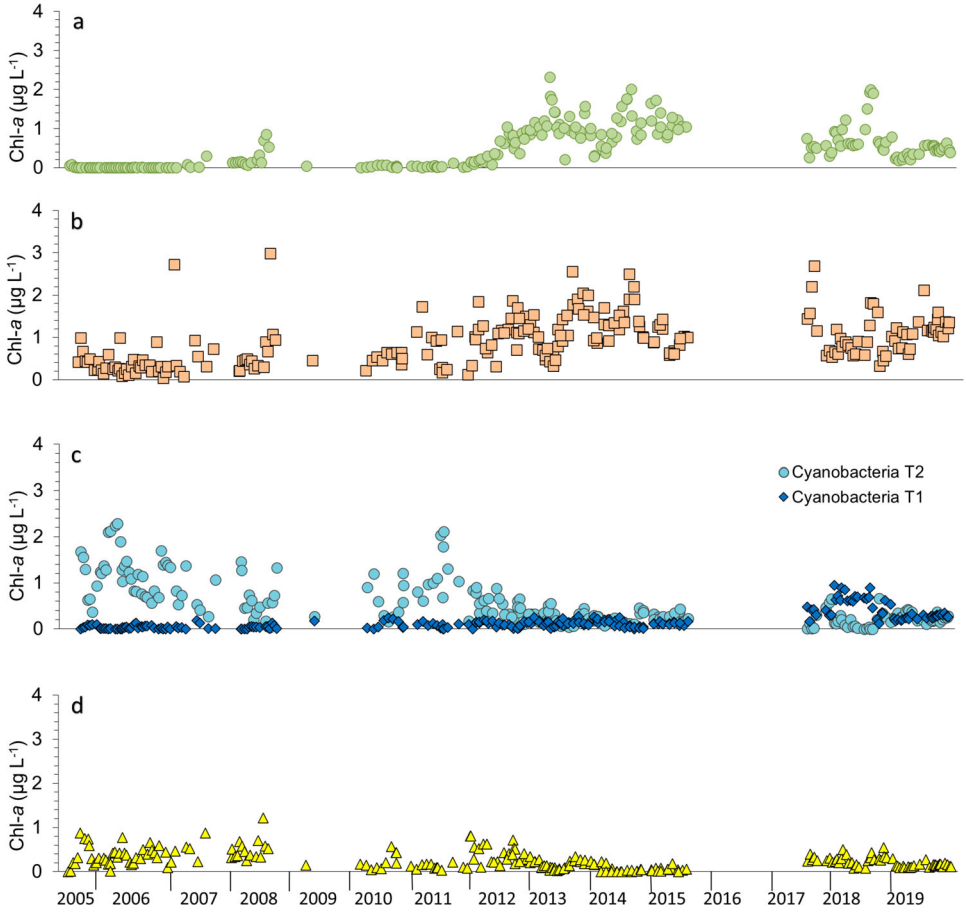

Figure 3. Average abundance of (a) green algae, (b) diatoms, (c) cyanobacteria (pigment type 1 [T1], and pigment type 2 [T2]), and (d) cryptophytes, expressed as Chl-*a* concentration, in the euphotic layer of Lake Kivu, from June 2005 to December 2019; the data from the 2 sampling sites near Gisenyi and Kibuye were merged. The 2 main gaps in the time series correspond to missing data.

maxima in the dry season (green algae, diatoms, and cyanobacteria T1) separated from those that developed best in stratified conditions (cyanobacteria T2, cryptophytes, and dinoflagellates; Fig. 4d). By contrast, the differences between the 2 observation periods were better represented by the PCA run on the biotic variables (Fig. 5c). The RDA (Fig. 6) effectively separated the 2 periods, indicating a greater success of diatoms and cyanobacteria T1 in 2018–2019 and a better success of the green algae in 2012–2014. Although the percentage of variance of the biotic variables explained by the environmental variables was low (~30%), the RDA diagram suggests that green algae were closely dependent on Zm and wind velocity and that solar radiation might have directly affected the abundance of dinoflagellates and cyanobacteria T2.

Discussion

In this study devoted to the setup of a monitoring programme based on phytoplankton assessment using HPLC analysis of marker pigments, we provided evidence of a substantial interannual variability of phytoplankton biomass and composition, needed to assess the potential impact of harvesting gas resources on the lake ecosystem. Tropical lakes, given their usually weak thermal gradient, respond quickly in changes in atmospheric conditions that may be driven by climate variability (e.g., Nicholson 1996, Thiery et al. 2015). This response may be particularly strong for Lake Kivu, given its location at relatively high altitude, which determines a mean surface temperature of ~24 °C and a thermal gradient in the mixolimnion in the rainy season of ~2 °C (Schmid and Wüest 2012). These characteristics result in a high interannual variability of the intensity of dry season mixing, which drives phytoplankton biomass and primary production (Darchambeau et al. 2014). Darchambeau et al. (2013) observed statistically highly significant correlations between intra- and inter-annual variations of water column stability, the dry season Chl-*a* peaks, and tropical ocean climate indexes. Because productivity of consumers in Lake Kivu seem to be bottom-up controlled (Isumbisho et al. 2006), zooplankton biomass and the

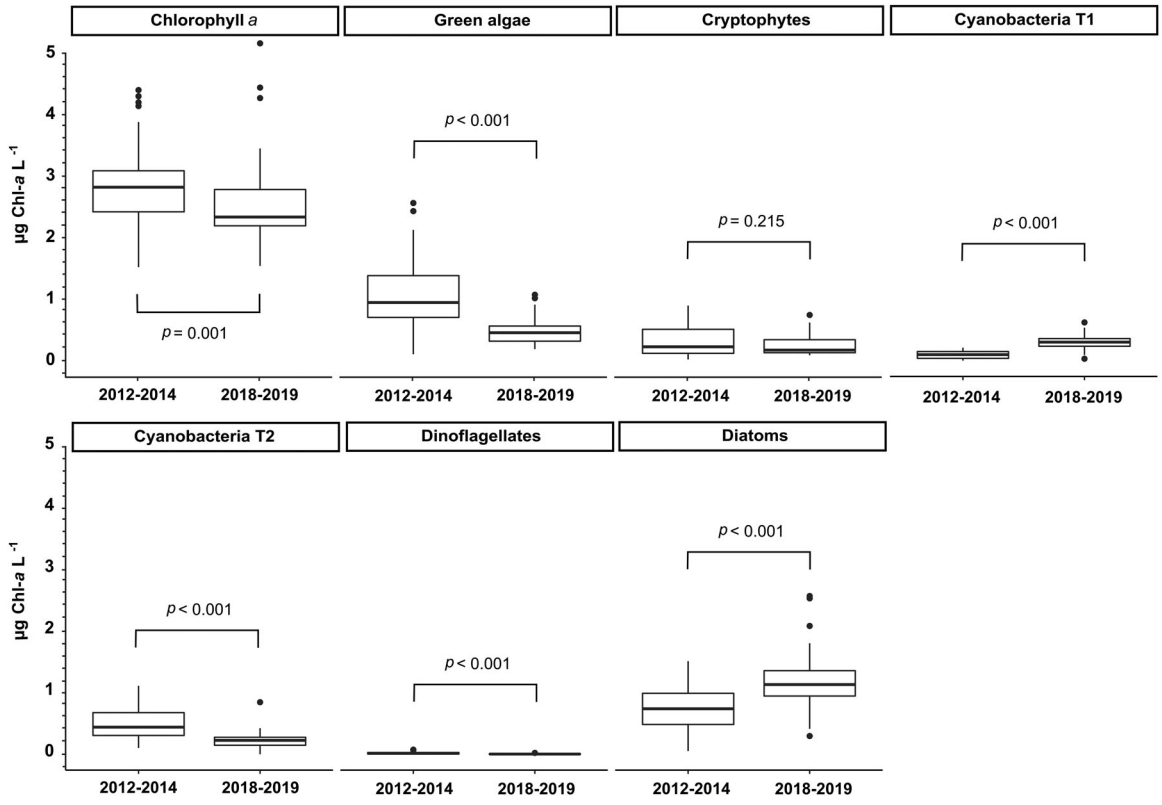

Figure 4. Box-plots of chlorophyll *a* concentration and phytoplankton groups abundance (expressed as chlorophyll *a* concentration) in Lake Kivu, from the lake monitoring near Kibuye and Gisenyi in 2012–2014 and in 2018–2019. Dark lines represent the median, and the middle boxes encompass 50% of the observations from lower (25%) to upper (75%) quartiles. The upper and lower whiskers, respectively, describe the extreme quartiles. Outliers are displayed as closed circles. Stars indicate statistical significance at $*p < 0.05$, $**p < 0.01$, and $***p < 0.001$ tested with a Wilcoxon-Mann-Whitney test.

fish stock are also likely affected by variation in the regional climate. Fish surveys have been conducted by LKMP to assess possible impact on the sardine fishery (Descy and Guillard 2014), and recent surveys provided evidence of variation in fish stock, in parallel with the change in phytoplankton composition and biomass (Tessier et al. 2020).

Rugema et al. (2019) reported that a shift in limnological conditions in the mixolimnion occurred in Lake Kivu around 2010, driving the changes in phytoplankton resulting from a decrease of the lake stability, likely related to a decadal climate variability. The data presented here confirm that the recent lake phytoplankton was still in a state dominated by the groups benefiting from vertical mixing at different time scales. In contrast with the changes in phytoplankton abundance and composition since 2010, no major change has occurred in the surface waters of Lake Kivu since the baseline study of 2012–2014, used as a reference to evaluate the possible impact of CH_4 exploitation (particularly the operation of the KivuWatt plant near Kibuye since late 2015). To date, total phytoplankton biomass assessed by the Chl-*a* concentration has not increased; instead, we observed a slight decrease in the 2018–2019 period, along with some changes in the contribution of the main phytoplankton groups. Compared to 2012–2014, diatom and cyanobacteria T1 biomass in 2018–2019 has increased, whereas that of green algae has significantly decreased. These changes were not an artefact of calculation that may arise when processing the pigment concentration with CHEMTAX; fucoxanthin, the main marker of diatoms, nearly doubled in 2018–2019 (mean 0.34 µg L^{-1}) compared to the baseline period (0.19 µg L^{-1}). The average concentration of lutein, a marker for green algae, declined from 0.19 to 0.07 µg L^{-1}; a similar decrease, by a factor of ~3, occurred for the average Chl-*b* (also specific to green algae) concentration. Based on the characteristics and life strategies of the main taxa belonging to these classes, one can hypothesise that a change of water column mixing dynamics may have occurred. A greater success of the diatoms may be the result of a deeper mixed layer during the dry season; planktonic diatoms need deep vertical mixing to remain in suspension and are able to achieve high photosynthesis and growth rate at low light exposure, which is associated with the higher

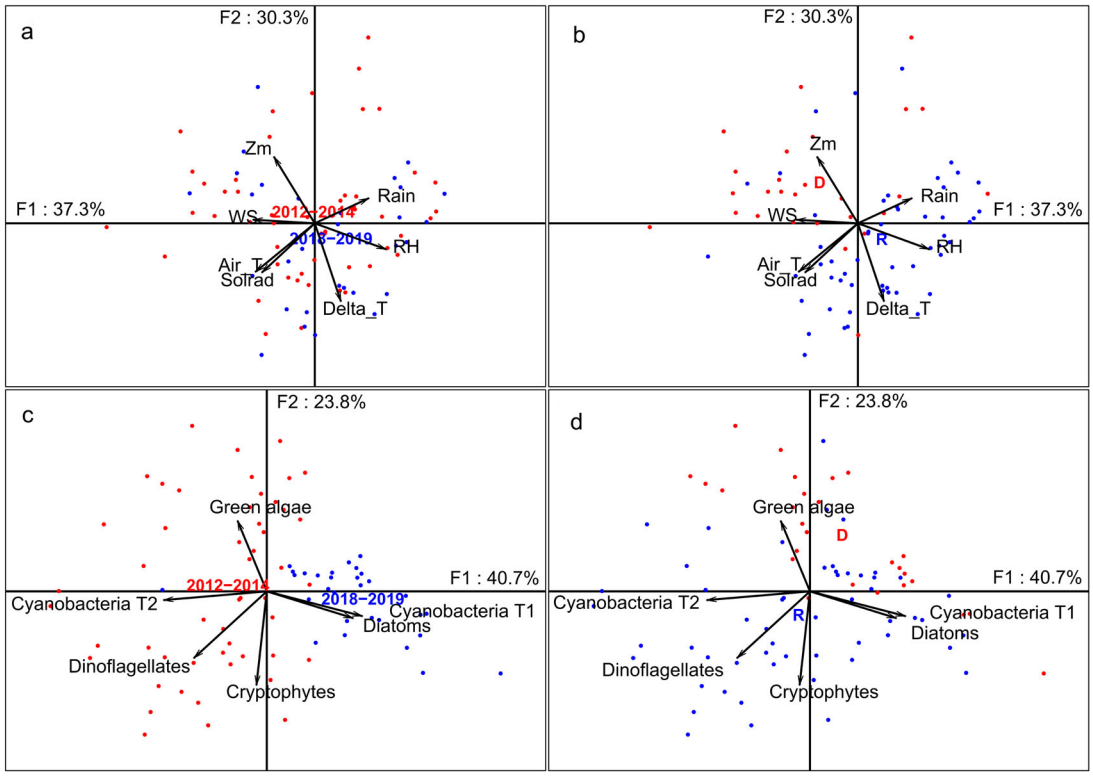

Figure 5. Ordination on the 2 first axes of the principal component analysis (PCA) of the (a and b) limnological and meteorological data and the (c and d) phytoplankton biomass data of the 2012–2014 and 2018–2019 periods in Lake Kivu. Sampling points are linked by (a and c) periods or (b and d) season. Centroids are indicated by year labels 2012–2014 (red) or 2018–2019 (blue) and R for rainy season (blue) and D for dry season (red). Delta_T = water temperature Max – Min (°C), Zm = mixed layer depth (m), Air_T = air temperature (°C), RH = relative air humidity (%), Solrad = incoming shortwave radiation (W m^{-2}), WS = wind speed (m s^{-1}), and Rain = rainfall (mm h^{-1}); see "Data gathering and processing" for more information.

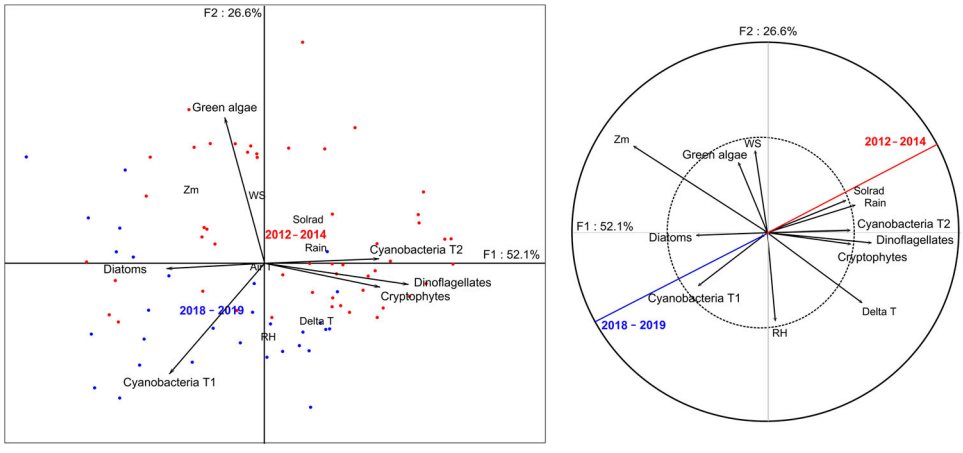

Figure 6. Ordination depicting the first 2 axes of the redundancy analysis (RDA) of the phytoplankton biomass data and the limnological and meteorological data of the 2012–2014 and the 2018–2019 periods in Lake Kivu. Positions of the species assemblages are framed by arrows. Position of observations are indicated in red for 2012–2014 and blue for 2018–2019. The first axis (F1) encompassed 52.0% of the projected inertia and the second axis (F2) 26.6%. The limnological and meteorological variables explained 29.7% of the variance of the biomass of the phytoplankton classes. Right figure focuses on correlations between the environmental and biological variables on the 2 axes of the redundancy analysis. Delta_T = water temperature Max – Min (°C), Zm = mixed layer depth (m), Air_T = air temperature (°C), RH = relative air humidity (%), Solrad = incoming shortwave radiation (W m^{-2}), WS: wind speed (m s^{-1}), and Rain = rainfall (mm h^{-1}); see "Data gathering and processing" for more information.

Zm:*Zeu* ratio (Reynolds 2006). At the same time, the greater availability of nutrients due to deeper vertical mixing allows diatoms to achieve a higher growth rate and to contribute to the Chl-*a* dry season peaks. In this way, diatoms are best equipped to face the trade-off of "low light–high nutrients," a key driver of phytoplankton production in African Great Lakes (Hecky and Kling 1987). The green algae identified in Lake Kivu are mainly coccal (Sarmento et al. 2007), and these non-motile forms also need vertical mixing to remain in suspension. Rugema et al. (2019) reported a rise of the biomass of the green algae in Lake Kivu, which they interpreted as the result of a change in mixing regime dynamics in the lake, similar to the process of atelomixis reported in tropical shallow lakes (Barbosa and Padisák 2002, Barbosa et al. 2013). The decline of green algae we observed in 2018–2019 was possibly the result of a reduction of the frequency and intensity of wind-driven non-seasonal mixing episodes. Indeed, the most significant result of the RDA may be that green algae were dependent on mixed layer depth and wind speed, the primary driver of vertical turbulent mixing. Therefore, we hypothesise that a change in wind pattern may have been a key factor contributing to the recent decline of green algae because reduced turbulence would directly affect green algae sedimentation losses. Because samples for microscopy were lacking, we could not check whether species composition remained the same as in 2012–2014. However, the changes reported earlier for Lake Kivu (Rugema et al. 2019) did not indicate a change of biodiversity but a change in abundance of taxa previously reported by Sarmento et al. (2007).

Our data analysis did not include other factors that can explain the change in phytoplankton composition in the lake, such as nutrient concentrations. In the deep oligotrophic East African Great Lakes, such as Lake Tanganyika or Lake Malawi (Hecky and Kling 1987, Bootsma et al. 2003), nutrient availability to phytoplankton is mostly driven by internal loading and therefore by vertical mixing at different time scales. External nutrient inputs from the watershed have proportionately little influence on pelagic processes, as in Lake Kivu (Muvundja et al. 2009), which has a small watershed and few small tributaries, and a high nutrient concentration in the deep waters compared to those in the surface waters (Pasche et al. 2012). In these conditions, a release of nutrient-rich waters from the CH_4 extraction plants—by accident or from a too shallow reinjection process—to the surface waters is expected to result in a dramatic increase of phytoplankton biomass and change of composition toward taxa thriving in nutrient-rich waters, such as some diatom or cyanobacteria taxa. We expect the changes in phytoplankton related to a catastrophic eutrophication would be much larger than the relatively small changes related to the weather variability evidenced in our study. Moreover, superficial release of degassed saline deep waters would increase water column stability of the mixolimnion, generating conditions potentially favouring bloom-forming cyanobacteria (Reynolds 2006), with further alteration of water quality.

Conclusions and guidelines for future monitoring

This study demonstrates that the monitoring programme based on HPLC analysis of Chl-*a* and marker pigments is adequate for detecting changes in phytoplankton biomass and composition, currently mostly driven by variations of meteorological factors that determine limnological processes. In particular, the nearly stable Chl-*a* concentration suggests no change has yet occurred in the lake's mixolimnion that could be attributed to the operation of gas extraction plants.

However, a valid comparison with earlier data will not be possible unless regular monitoring of all relevant variables is ensured. Sampling phytoplankton and measuring environmental variables (including nutrients) twice a month (rather than monthly) would be more appropriate to detect and interpret phytoplankton variations. Indeed, in the future, differentiating changes brought about by plant operation from those due to other environmental changes will be necessary, which will require fine interpretation based on the ecological strategies at species or genus level. One key asset for monitoring Lake Kivu is a database on phytoplankton and limnological variables dating back to 2002 for the southern basin and to 2005 for the northern and eastern basins, using the same techniques. Such a database is unique for an African Great Lake and will be, provided that the observations are pursued in the future, an important dataset to assess the impact of global change on a lake ecosystem and ensure water resource conservation and management in a region where data are usually lacking (Robarts and Zohary 2018).

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No potential conflict of interest was reported by the author(s).

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