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Diversity and ecology of phytoplankton in Lake Edward (East Africa): Present status and long-term changes

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ABSTRACT

Lake Edward is one of the African Rift Valley lakes draining into the Nile River basin. We conducted three sampling series in Lake Edward in October-November 2016, March-April 2017 and January 2018, in distinct seasonal conditions and in several sites varying by depth and proximity to river outlets, including the Kazinga Channel, which connects the hypertrophic Lake George to Lake Edward. The phytoplankton was examined using microscopy and marker pigment analysis by high performance liquid chromatography (HPLC) and subsequent CHEMTAX processing for estimating abundance of phytoplankton groups. Chlorophyll *a* concentration in the pelagic and littoral open lake sites barely exceeded 10 μg L^{-1} whereas, in contrast, in the semi-enclosed Bay of Katwe influenced by the Kazinga Channel chlorophyll *a* was up to 100 μg L^{-1}. Despite substantial seasonal variations of limnological conditions such as photic and mixed layer depths, cyanoprokaryotes/cyanobacteria represented on average 60% of the phytoplankton biomass, followed by diatoms, which contributed ~25% of chlorophyll *a*, and by green algae, chrysophytes and cryptophytes. 248 taxa were identified with clear prevalence of cyanobacteria (104 taxa), from the morphological groups of coccal and filamentous species (non-heterocytous and heterocytous). The high proportion of heterocytous cyanobacteria, along with a relatively high particulate organic carbon to nitrogen (C:N) ratio, suggest N limitation as well as light limitation, most pronounced in the pelagic sites. During the rainy season, the most abundant diatoms in the plankton were needle-like *Nitzschia*. Comparison with previous studies found differences in water transparency, total phosphorus, and phytoplankton composition.
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Introduction

Phytoplankton community structure strongly influences the direction and efficiency of the energy transfer through aquatic food webs (Reynolds, 2006). However, when being set against the constraints of the environmental conditions in nature, the phytoplankton community of any given site becomes specific in composition and abundance, which generally varies conspicuously both in space and through time. Therefore, the diversity and dynamics of phytoplankton populations are scientifically intriguing, and there are "good reasons to seek an understanding of the basis of phytoplankton dynamics in nature" (Reynolds, 2006, p. 286). This is especially valid for tropical phytoplankton, which remains far less studied in comparison with its temperate counterparts. Differences in the level of knowledge concern also different tropical regions and sites, including the phytoplankton of the fascinating African Great lakes in the East African Rift (Talling, 2006, 2011; Hecky and Kling, 1987). This rift system dominated the past 45 million years of geological history of the African continent (Ebinger, 2006) associated with volcanic activities during the last 30 million years (Foley, 2006) and had a strong influence on its biological history (de Lamme and de Dapper, 2006).

The first scientific studies on African aquatic ecosystems were essentially devoted to surveys of biodiversity and to geological research and explorations, dating back to the end of the 19th

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century and the beginning of the 20th century (review by Talling, 2006). Famous examples were the quest for the source of the Nile River (Speke, 1863) or the research on the origin of the oldest and largest lakes, Lake Tanganyika and Lake Malawi (Cunnington, 1920). Soon the interest for inventories of the endemic fish fauna of these great lakes developed; several expeditions enriched museum collections of fishes and various invertebrate groups. Modern studies, starting around 1925, have addressed a more comprehensive approach, devoted to understanding ecosystem function and productivity, in a context of aquatic resources exploitation and management (Talling, 2006).

This study investigates the diversity and ecology of phytoplankton of Lake Edward (also known as Rutanzige, Edward Nyanza or Idi Amin Dada; Beadle, 1981), which has been much less studied in comparison with nearby lakes of the Rift region (Beadle, 1981). The first published data on the planktonic algae of Lake Edward could be traced back to the end of the 1940s and were based on 47 samples (8 of which were net samples) collected from the lacustrine phytoplankton in 1935–1936 during the Belgian expedition led by Damas (1938). The studies were oriented mainly towards recent species composition and reported 273 species, varieties and forms identified by the leading taxonomists of that period: Cyanoprokaryota/Cyanobacteria – 34 (Frémy, 1949), Chlorophyta – 47 (Conrad, 1949a; Pascher, 1949a) and Streptophyta – 7 (Conrad, 1949c), Ochrophyta – 184 (4 from Xanthophyceae – Conrad, 1949b; Pascher, 1949b, and 180 from Bacillariophyceae – Hustedt, 1949). These numbers were obtained after taxonomic updating of the original data (Stoyneva-Gärtner and Descy, 2018). Some additional planktonic algae were found by the same authors in the qualitative samples from visible algal layers, or in the benthic samples collected during the Damas Mission (Stoyneva-Gärtner and Descy, 2018). Although quantitative data were not provided, the frequency of occurrence was commented on by the authors for the majority of algae species, or could be estimated from the species lists. Later, Verbeke (1957) published some limnological data, albeit with few data on phytoplankton. Hecky and Kling (1987) reported the phytoplankton composition from whole water samples collected in the southern part of the lake and they showed the quantitative dominance of green and blue-green algae, with 28 species.

In contrast to the different qualitative or semi-quantitative records on the phytoplankton of Lake Edward, there were few published quantitative data on total biomass and on the contribution of the different phytoplankton classes. This lack of data hampers interpretation of changes reported over the past decades, in particular the observation that fisheries have declined (Orach-Meza et al., 1989; Crespi and Ardizzone, 1995), for which the underlying causes (e.g. a decrease in lake productivity related to environmental changes, or an increase in fishing pressure and poaching) remain to be determined. The decline of the fish yield started in the 1960s, and followed a drastic reduction of the population of *Hippopotamus* in the Virunga National Park (Languy and de Merode, 2009), which borders the western shore of the lake. It is suspected that this may have contributed to a reduction of the nutrient transfer from the land to the lake waters, affecting the nutrient loading and thus the lake productivity. However, other environmental changes may have been involved and the fishery may also have suffered from mismanagement and overexploitation resulting from the unrest in the North Kivu region in Democratic Republic of the Congo. Regarding the lake limnological and chemical properties, Lehman et al. (1998) reported chlorophyll *a* and nutrient concentrations, and compared them to data from earlier studies (Verbeke, 1957; Talling and Talling; 1965). They mentioned a substantial decline in chlorophyll *a* and total phosphorus (TP) in Lake Edward since the 1950s and 1960s (Talling, 1965), consistent with a decrease in lake productivity.

The present work is the first comprehensive study of the phytoplankton diversity and dynamics in Lake Edward based on modern algal taxonomy and limnological methods. Our objective is to fill the gaps in the knowledge of the phytoplankton composition and biomass of this large tropical lake and ultimately to contribute to the understanding of the ecosystem processes involved in the reported decline of the lake productivity.

Material and methods

Study site

Lake Edward – one of the Great lakes of Western Rift (or Albertine Rift, the western branch of the east African Rift) – is about 80.8 km long and has a maximum width of 39.5 km (Fig. 1). This tropical lake with a northern shore just few kilometers south of the equator covers a total surface area of 2243 km^2 and lies at an altitude of 912 m a.s.l. (Russell and Johnson, 2006). The deepest area (maximum depth is 117 m) is a trench only 5 km off the western shore from which the escarpment rises precipitously to highlands exceeding 2500 m in altitude, while the eastern side of this trench is much less steep and rises with an almost uniform gradient for more than 30 km under water to the Uganda shore (Beadle, 1981). The main inflows are the River Nyamugasani, which drains the south-western part of the Ruwenzori mountains and the Ishasha, Rutshuru and Rwindi Rivers flowing through the Kigezi and Rwanda highlands and the Virunga volcanoes in the south (Beadle, 1981). The annual contribution from the Kazinga Channel (36 km long with a maximum width of less than 1 km), which connects lakes Edward and George, is approximately one third of the total inflow from rivers and is roughly equivalent to that from direct precipitation (Russell and Johnson, 2006). The water residence time of Lake Edward is ~25 years. In the Edward-George basin the annual rainfall is generally low (650–900 mm; Beadle, 1981). The outflow of Lake Edward is the Semliki (also Semuliki) River, which flows out Lake Edward at Ishango in the northwest and flows into Lake Albert. In Lake Edward, the fish fauna consists of more than 50 species and it is well populated by invertebrates (Verbeke, 1957).

Sampling strategy and analysis

The study is based on 137 samples collected from Lake Edward in October-November 2016, March-April 2017 and January 2018, carried out in the framework of the HIPE (Human impacts on ecosystem health and resources of Lake Edward) research project supported by the Belgian Scientific Policy Office (BELSPO). The two first campaigns were conducted in the rainy season (October-November 2016, March-April 2017) and the third one in the dry season. (January 2018). A variety of sites in littoral and pelagic zones were sampled along two depth gradients in the Ugandan part of Lake Edward and Katwe Bay (Fig. 1). Lake George and the Kazinga Channel, which flows into Lake Edward, were sampled during the three sampling campaigns. In January 2018, a deeper station (90 m deep) located in the Congolese waters was also sampled once (Fig. 1).

Secchi disk depth (SD) was determined at every sampling site. The vertical light attenuation coefficient in water (k; m^{-1}) was directly measured at different sites with a spherical underwater quantum sensor (Li-COR Li-193SA). Intercalibration with Secchi depth measurements enabled the following equation (R^2 = 0.97):

$$k = 1.141 * (1/SD)$$

with Secchi depth expressed in m.

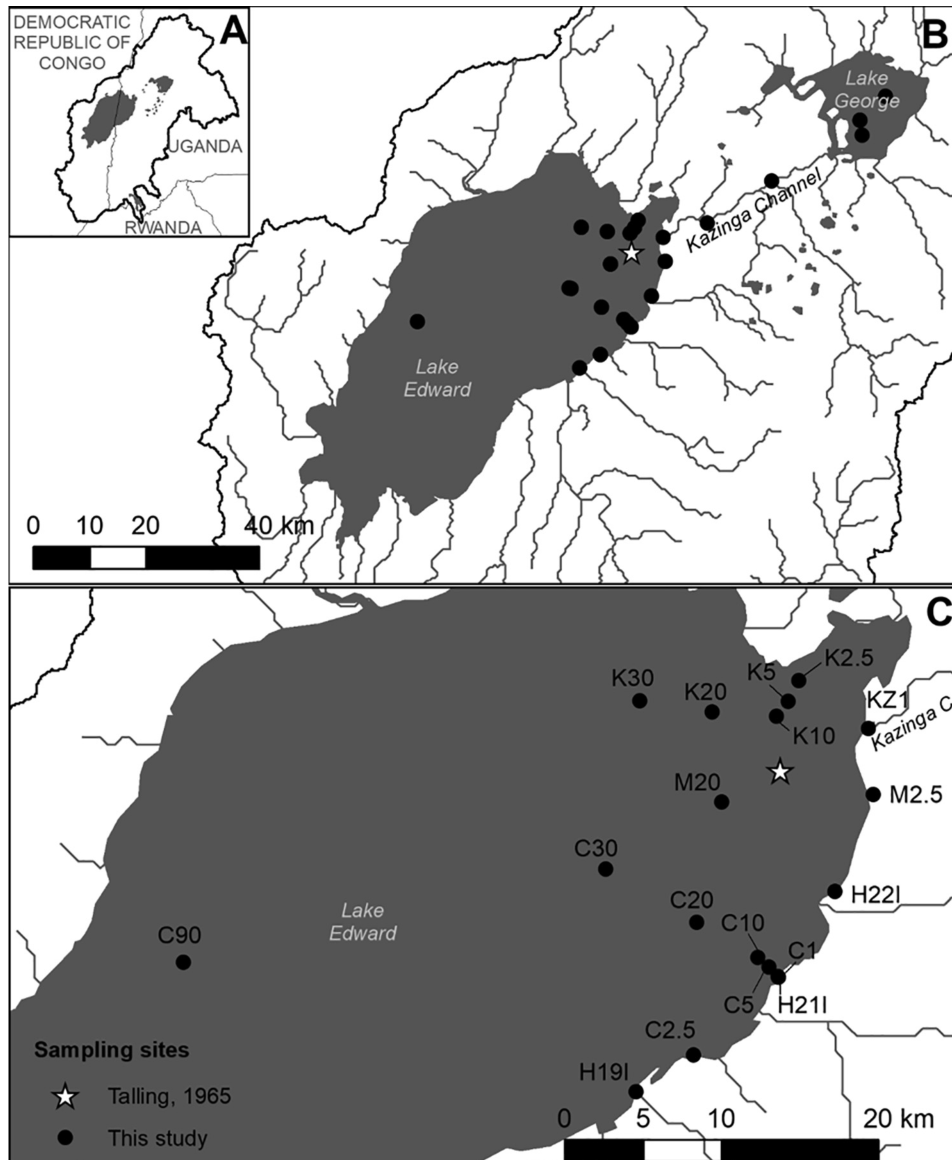

Fig. 1. Location of Lake Edward and of the study sites. A. Location of Lake Edward in East Africa; B: Lake Edward basin, with the inflowing rivers, Lake George and the Kazinga Channel; C: Location of the sampled sites. The dots indicate the study sites (figures giving depth at the sampling site); the star shows the location of Talling's (1965) sampling site.

The euphotic zone (Z_{eu}), defined as the depth illuminated by 1% of surface light, was then determined as:

$$Z_{eu} = -\ln(0.01)/k$$

Vertical profile of temperature, conductivity, dissolved oxygen concentration (DO) and pH were measured in situ with a YSI EXO2 multiparametric probe. The depth of the mixed layer (Z_m) was determined from the temperature profile at every sampling station.

Water was collected with a Niskin bottle at a depth interval of 2.5 m between 0 and 5 m, and at an interval of 5 m between 5 m and the bottom of the lake. At each sampling depth, a variable amount of water was filtered on a pre-combusted 25 mm glass fibre filters (Sartorius GF5, 0.7 μm nominal pore size) for particulate organic carbon (POC), particulate nitrogen (PN) and particulate phosphorus (PP) analyses. Filters were dried and then kept in small Petri dishes until later analysis. Filters for POC and PN determination were decarbonated with HCl fume prior to measurement using a EA 1110 elemental analyser coupled to a Delta V Advantage isotope ratio mass spectrometer (Thermo). PP was measured by spectrophotometry of phosphate using the molybdate blue-ascorbic acid reaction (APHA, 1998) after persulphate digestion (Valderrama, 1981). Molar C:N and C:P ratios were used as indicators of phytoplankton nutrient status. Samples for total suspended matter (TSM) concentration were filtered on a pre-weighed 47 mm glass fibre filters (Sartorius GF5, 0.7 μm nominal pore size), dried, and subsequently weighed to determine the TSM load.

For dissolved inorganic nutrients (NO_3^-; NO_2^-; NH_4^+; soluble reactive phosphorus (SRP)), 50 mL of water was filtered on a 0.2 μm polyethylsulfone syringe filter and preserved frozen until measurement by colorimetry according to standard techniques. The sum of NO_3^-, NO_2^- and NH_4^+ was considered as the dissolved inorganic nitrogen content (DIN). NH_4^+ concentration was determined using the dichloroisocyanurate-salicylate-nitroprussiate colorimetric method (Standing Committee of Analysts, 1981). NO_3^- and NO_2^- were determined with the sulphanilamide colorimetric method, after cadmium reduction for NO_3^- (APHA, 1998). SRP was determined by spectrophotometry using the ammonium molybdate-

potassium antimonyl tartrate method (Murphy and Riley, 1962). The sum of PP and SRP was considered as total phosphorus (TP). Measurements of total alkalinity (TA) were performed by automated electrotitration on 50 mL filtered (0.2 μm) samples with HCl 0.1 mol L^{-1} as the titrant. The equivalence point was determined from pH between 4 and 3 with the Gran method (Gran, 1952). In addition, data were quality checked with certified reference material obtained from Andrew Dickinson (Scripps Institution of Oceanography, University of California, San Diego, USA). Typical reproducibility of TA measurements was better than ±3 μmol L^{-1}. The dissolved inorganic carbon (DIC) concentration was computed from water temperature, pH and TA measurements using the carbonic acid dissociation constants of Millero et al. (2006) and the CO_2 solubility from Weiss (1974), implemented in the CO_2SYS software (Lewis et al., 1998).

Absorbance from 200 to 700 nm was recorded on a Perkin Elmer UV/vis 365 spectrophotometer using a 1 cm quartz cuvette. Napierian absorbance at 350 nm, a proxy for CDOM content, was then calculated according to:

$$a_{350} = \ln(10) \times A_{350}/L,$$

where a_{350} is the absorption coefficient at 350 nm (m^{-1}), A_{350} the measured absorbance at 350 nm and L (m) the length of the optical cell.

Pigments and phytoplankton diversity

A variable volume of water was filtered on Macherey-Nägel (Düren, Germany) 47 mm GF5 filters (nominal pore size 0.7 μm) on which pigment extraction was performed in 90% HPLC-grade acetone, following Sarmento et al. (2006). Phytoplankton biomass and composition were assessed throughout the study by determination of chlorophyll *a* (Chla) and marker pigments by high performance liquid chromatography (HPLC). HPLC analysis of phytoplankton extracts was performed using the Wright et al. (1991) gradient elution method, with a Waters system comprising a Photodiode DA detector and a fluorescence detector. Calibration was made using commercial external standards (DHI, Denmark). For estimating phytoplankton abundance at the class level, pigment concentrations were processed with the CHEMTAX software (Mackey et al., 1996), following a procedure similar to that of Descy et al. (2005), allowing estimating Chla biomass of green algae, chrysophytes, diatoms, cryptophytes, dinoflagellates and cyanobacteria, taking into account possible variation of pigment ratios with depth. Phytoplankton biomass was expressed per unit volume (μg Chla L^{-1}). Based on knowledge of the phytoplankton composition in Lake Edward analyzed using microscopy (see below), the following phytoplankton groups were considered according to their pigment composition (see Wright and Jeffrey, 2006):

- Diatoms and chrysophytes, which have chlorophylls *c* and share fucoxanthin as main marker pigment; diatoms also have diadinoxanthin and diatoxanthin; due to analytical problems of the HPLC technique (i.e. the incomplete separation of myxoxanthophyll and violaxanthin or diadinoxanthin), the two classes could not be separated by the CHEMTAX processing; however, as no chrysophytes were detected by microscopy in the lake samples, "diatoms + chrysophytes" could be safely considered as diatoms;
- Green algae, which have chlorophyll *b*, lutein, neoxanthin, zeaxanthin, and violaxanthin
- Cyanobacteria type 1 (T1), which have zeaxanthin at high concentration
- Cyanobacteria type 2 (T2), which have echinenone and often aphanizophyll and/or myxoxanthophyll in addition to zeaxanthin
- Cryptophytes, with chlorophyll *c*, alloxanthin, and α–carotene
- Dinoflagellates, with chlorophyll *c*, peridinin, and diadinoxanthin

Twenty-nine additional 500 mL water samples were taken at 1 m depth in the sites sampled during the three campaigns, preserved with formalin and settled to a final volume of approximately 25 mL for microscopical analysis of phytoplankton composition. The algal identification was based on conventional light microscopy (LM) in combination with scanning electron microscopy (SEM) for diatom determination. The work was done on fixed material on non-permanent slides using LM microscopes Motic BA 4000. Images were taken with Moticam 2000 camera supplied by Motic Images 2 Plus software program. Diatom permanent slides were obtained after digestion with hydrogen peroxide and mounting with Naphrax, and examined with a 100X objective under phase contrast on a Leitz Diaplan standard microscope, equipped with a Euromex camera using the Image Focus 4 software. The determination was based on standard taxonomic sources (Krammer and Lange-Bertalot, 1991, 1997a,b, 2004; Komárek and Fott, 1983, Komárek and Anagnostidis, 1999, 2005; Komárek, 2013, Moestrup and Calado, 2018) with use of recently published updating papers (for details see Stoyneva-Gärtner and Descy, 2018). The latin names were checked using AlgaeBase (Guiry and Guiry, 2019), CyanoDB 2.0 (Hauer and Komárek, 2019) and DiatomBase (Kociolek et al., 2018). A detailed analysis of the algal flora of the lake, with comparison with earlier reports can be found in Stoyneva-Gärtner and Descy, (2018).

Nutrient limitation assays

Nutrient limitation of phytoplankton in a pelagic site in Lake Edward (M20 in Fig. 1) was assessed during the rainy (March-April 2017) and dry (January 2018) seasons. Twelve 500-mL polycarbonate bottles (Nalgene) were filled with water collected in the epilimnion and amended in triplicate with either 1 mL of a solution of $NaNO_3$ (+N treatment, 55 μmol L^{-1} final concentration), NaH_2PO_4 (+P treatment, 15 μmol L^{-1} final concentration), $NaNO_3$ and NaH_2PO_4 (+NP, final concentration of 55 μmol L^{-1} of $NaNO_3$ and 15 μmol L^{-1} of NaH_2PO_4), or 1 mL of mQ water (control treatment). Directly after the nutrient addition, every bottle was spiked with 1 mL of a solution of $NaH^{13}CO_3$ to a final concentration of 0.8 mmol L^{-1}(~10% of the total DIC pool) and incubated for 24 h at in situ temperature (26 °C) and under constant light conditions provided by a Philips 55 W PLL-deluxe bulb (250 μmol photons m^{-2} s^{-1}). Prior to starting the incubation, an exetainer vial (12 mL, Labco) poisoned with 50 μL of $HgCl_2$ was filled with water from every bottle in order to determine the exact ^{13}C enrichment of the dissolved inorganic carbon pool ($\delta^{13}C$-DIC_i). The stable C isotope composition of the DIC was determined as described in detail in Morana et al. (2015). The initial concentration (POC) and the stable C isotope composition of the POC ($\delta^{13}C$-POC_i) was also determined filtering 50 mL of water through a precombusted 25 mm glass fibre filter (0.7 μm nominal porosity). At the end of the incubation (24 h), the incorporation of the ^{13}C tracer into the POC (δ ^{13}C-POC) was assessed in every bottle filtering 50 mL of water in duplicate through precombusted 25 mm glass fibre filter (0.7 μm nominal porosity). Filters were dried, decarbonated with HCl fuming and analysed with the above-mentioned EA 1110 elemental analyser coupled to a Delta V Advantage isotope ratio mass spectrometer (Thermo).

The amount of C incorporated into the POC (CFix) during the incubation (t = 24 h) was calculated as:

$$CFix = (POC * (\delta^{13}C - POC - \delta^{13}C - POC_i))/(t \times (\delta^{13}C - DIC_i - \delta^{13}C - POC_i))$$

Statistics and data analysis

A data matrix including 137 observations from the three sampling series was constructed, containing the limnological and physical-chemical variables relevant for the phytoplankton ecology. Phytoplankton variables were biomass of the phytoplankton classes, as determined with CHEMTAX, expressed as chlorophyll *a* ($\mu g\ L^{-1}$). Most data processed in statistical analyses were selected in the epilimnion in the 0–5 m layer (n = 37 for the rainy season samplings, 32 for the dry season sampling) to reflect the conditions and the biomass in the euphotic zone (whole-lake average ~6 m), rather than in the whole water column. Due to the bathymetry of the lake, the depth of about half of sampling sites did not exceed 6.1 m, so that the water column was in contact with the sediment at all times (even though a diurnal stratification could develop during the day in the top 5 m, see Fig. 2). These sites were therefore considered as being in the littoral zone (n = 23), even though they could be situated far away from the shore. Some of these shallow sites, located in the Katwe Bay, under the influence of the plume of the Kazinga Channel, were considered separately (n = 10), due the large inputs from the Channel into the Bay. The rest of the sampling sites, with a depth range between 10 and 85 m, were considered as pelagic sites (n = 40). The data matrix was further reduced to 40 observations by averaging the 0–5 m values, in order to perform redundancy discriminant analysis (RDA). The RDA was performed to reveal relationships between phytoplankton class relative abundance and some predictive environmental variables. RDA was performed with R software (R Core Team, 2018) using the vegan package (Oksanen et al., 2019). All concentrations data were log-transformed prior to RDA. In addition to RDA, non-parametric bivariate analyses (Mann-Whitney statistical tests) were used to estimate if hydrological seasons or if the sampling sites locations had significantly influenced the concentration of a given environmental variable. An outlier identification was performed to remove outliers from the subsequent Mann-Whitney tests. Outlier identification analyses were performed using the ROUT method implemented in the Prism 7 software (Motulsky and Brown, 2006).

Results

Representative limnological profiles of the pelagic zone of Lake Edward (at site C30, see Fig. 1) are presented in Fig. 2, which essentially shows the difference in mixed layer depth (MLD) between the rainy and dry seasons. Temperature (range was 25.5–27.8 °C) and DO profiles indicated a weak thermal gradient between 15 m and 20 m depth in rainy season conditions, and the absence of gradient in dry season conditions (Fig. 2). Accordingly, DO, conductivity, soluble substances and biomass were distributed in a mixed layer of maximum 18 m in the rainy season and of 55 m in the dry season (Fig. 2). The pH was high throughout the lake surface layers (range in the littoral and pelagic sites was 8.6–9.1; Table S1), due to high TA (7.9–8.5 mmol L^{-1}; Table S1). Consequently, dissolved CO_2 corresponded on average to 0.2% of the total DIC, while HCO_3^- and CO_3^{2-} represented on average 95.1% and 4.7%, respectively. Mean values and range of the different parameters measured in Lake Edward, Lake George and the Kazinga Channel are given in Table S1 (see SI1).

Figs. 3 to 6 illustrate the range of different variables (Z_{eu}, Z_m:Z_{eu}, DIN, SRP, Chla, C:N, C:P) according to season (rainy and dry) and/or location (Katwe bay, littoral and pelagic sampling sites). Secchi depth was between 17 cm and 69 cm in Katwe Bay, 68 cm and 149 cm in the littoral sites, and 107 cm and 232 cm in the pelagic sites (Table S1). The depth of the euphotic layer did not vary significantly depending on seasons (Z_{eu} was 6.2 ± 1.7 m and 5.8 ± 2.2 m in the rainy and dry seasons, respectively), but differed strongly depending on site locations, with large differences among the Katwe Bay (1.9 ± 0.8 m, n = 6), littoral (4.3 ± 1.0 m, n = 14) and pelagic (7.2 ± 1.4 m, n = 20) sites (Fig. 3a). By contrast, for the MLD: euphotic depth ratio (Z_m:Z_{eu}) difference was significant only between the pelagic (2.3 ± 0.7, n = 19) and littoral (0.8 ± 0.2, n = 14) sampling sites (Fig. 3b). Consequently, the exposure of the phytoplankton to light in the water column differed greatly between sites but not between seasons. Applying the mean surface irradiance during the 3 sampling series (736–832 $\mu E\ m^{-2}\ s^{-1}$, data not shown), the mean irradiance in the water column (estimated according to Kirk, 1994) in Katwe Bay was 100–114 $\mu E\ m^{-2}\ s^{-1}$, 182–205 $\mu E\ m^{-2}\ s^{-1}$ in the littoral sites and 60–68 $\mu E\ m^{-2}\ s^{-1}$ in the pelagic sites. In contrast, in the deepest site (90 m) sampled in the dry season, the exposure of phytoplankton to light in the mixed layer was ~20 $\mu E\ m^{-2}\ s^{-1}$, with a Zm:Zeu ratio of 8.4.

Dissolved nutrients and Chla concentrations exhibited significant differences between seasons (Fig. 4). Dissolved forms of N and P were at their lowest concentration during the dry season, irrespective of the sampling location, whereas Chla was higher in the dry (Fig. 4c; 10.7 ± 5.6 $\mu g\ L^{-1}$, n = 27) than in the rainy season (Fig. 4c; 6.8 ± 2.7 $\mu g\ L^{-1}$, n = 35). Regarding nutrient concentration and Chla according to site, the littoral zone had higher DIN (Fig. 5a; 3.3 ± 1.4 $\mu mol\ L^{-1}$, n = 13) than pelagic sites (Fig. 5a; 2.1 ± 1.0 $\mu mol\ L^{-1}$, n = 37) and Katwe Bay (Fig. 5a; 2.0 ± 1.1 $\mu mol\ L^{-1}$, n = 10). The situation was similar for SRP (Fig. 5b; 1.3 ± 0.9 $\mu mol\ L^{-1}$, 0.9 ± 0.2 $\mu mol\ L^{-1}$ and 0.3 ± 0.2 $\mu mol\ L^{-1}$ for littoral pelagic sites, and Katwe bay respectively), although the difference pelagic-littoral was not statistically significant. In contrast, pelagic (Fig. 5c; 8.0 ± 3.9 $\mu g\ L^{-1}$, n = 44), and littoral (Fig. 5c; 8.4 ± 3.7 $\mu g\ L^{-1}$, n = 17), sites had similar mean Chla concentration much lower than Katwe Bay (Fig. 5c; 50.4 ± 31.8 $\mu g\ L^{-1}$, n = 10), which likely received biomass and nutrients from the outlet of the Kazinga Channel (Chla was up

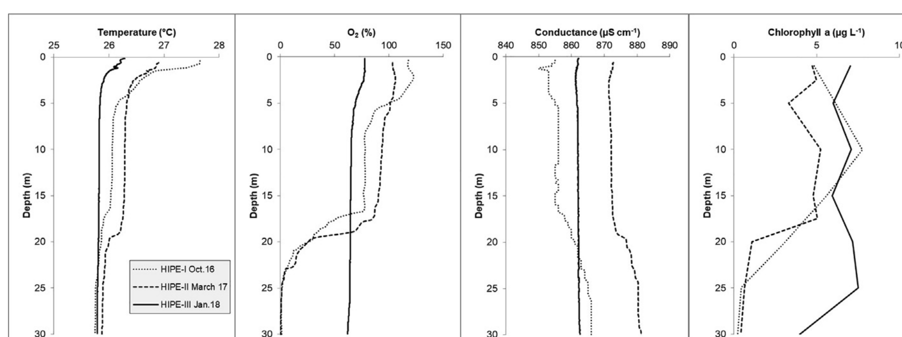

Fig. 2. CTD and chlorophyll *a* vertical profiles during the 3 cruises on Lake Edward at a pelagic site (C30, see Fig. 1). The two first campaigns (HIPE 1 and 2), were conducted in the rainy season, and the third one (HIPE 3) in the dry season.

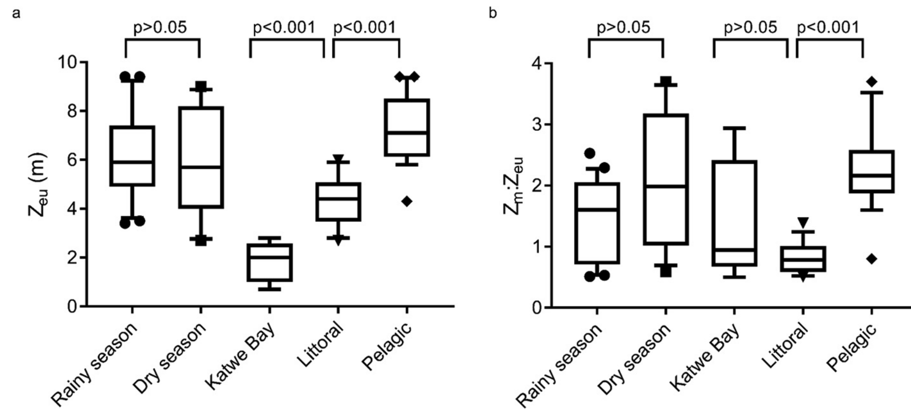

Fig. 3. Box-plots of the depth of the euphotic zone (Zeu) and of the mixed layer depth: euphotic depth ratio (Zm:Zeu) in Lake Edward, in the rainy season, the dry season, the Katwe Bay, the littoral zone and the pelagic zone. A Mann-Whitney test was applied to assess the significance of the difference between seasons and sites.

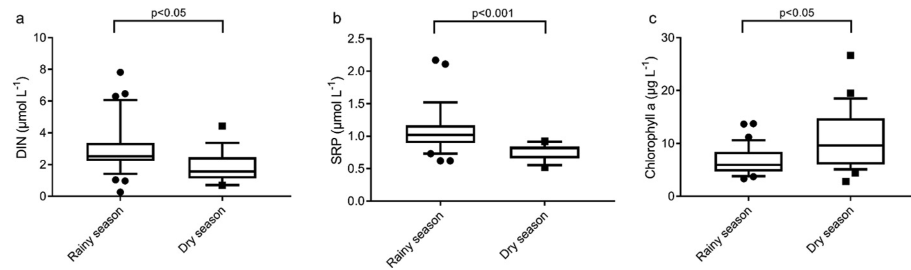

Fig. 4. Box-plots of dissolved inorganic nitrogen (DIN), soluble reactive phosphate (SRP) and Chlorophyll *a* in Lake Edward, in the rainy and the dry season. A Mann-Whitney test was applied to assess the significance of the difference between seasons.

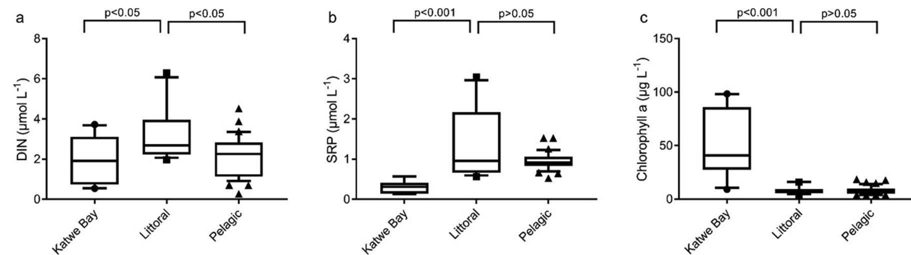

Fig. 5. Box-plots of dissolved inorganic nitrogen (DIN), soluble reactive phosphate (SRP) and Chlorophyll *a* in Lake Edward, in the Katwe Bay, the littoral zone and the pelagic zone. A Mann-Whitney test was applied to assess the significance of the difference between sites.

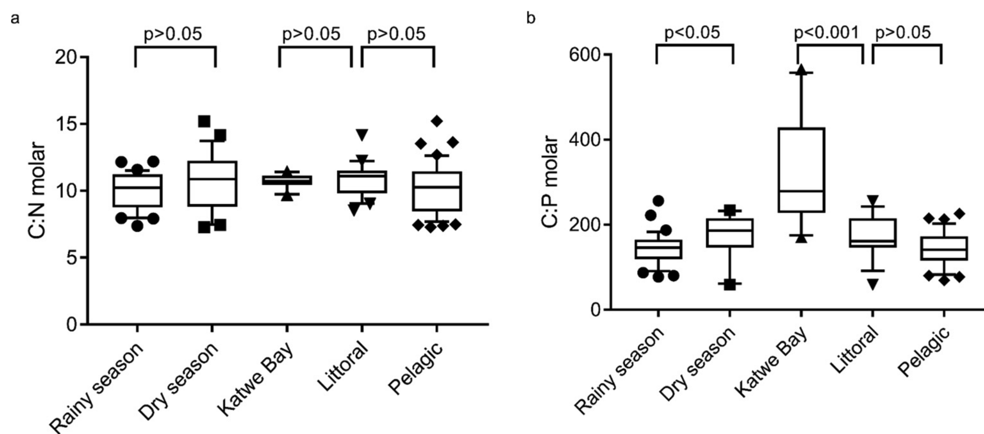

Fig. 6. Box-plots of the seston C:N and C:P ratios in Lake Edward, in the rainy season, the dry season, in the Katwe Bay, the littoral zone and the pelagic zone. A Mann-Whitney test was applied to assess the significance of the difference between seasons and sites.

to 255 μg L^{-1}). The C:N molar ratio was quite constant (Fig. 6a; mean range from 10.1 ± 1.3 to 10.8 ± 1.3) across seasons and sites), whereas C:P molar ratios were more variable (Fig. 6b; mean range from 144 ± 40 to 318 ± 128): they differed significantly between seasons and between Katwe Bay and the other sites. These C:P molar ratios were similar in pelagic (Fig. 6b; 144 ± 40, n = 33) and littoral (Fig. 6b; 168 ± 49, n = 15) sites and did not differ much from the Redfield ratio, whereas they were higher in Katwe Bay (Fig. 6b; 318 ± 128, n = 10), suggesting extreme P limitation. A few data from Lake George were also available: mean Chla was 190.7 ± 114.3 μg L^{-1} (n = 7) in Lake George, and 128.9 ± 114.3 μg L^{-1} in the Kazinga Channel (n = 8).

Based on biomass estimates from the marker pigments, phytoplankton was dominated in the whole lake by two classes (Fig. 7), cyanobacteria and diatoms. Cyanobacteria were most abundant in Katwe Bay, with 90% of Chla, and also dominated in the littoral and pelagic sites (~60% of Chla on average). Cyanobacteria T1 were always more abundant than cyanobacteria T2 (Fig. 7). Diatoms were represented in similar proportion in the pelagic (27.7% of Chla on average) and the littoral sites (24.7% of Chla), and less abundant in the Katwe Bay (7.7% of Chla on average; Fig. 7). In the different sampling sites, green algae were the least abundant group, followed by cryptophytes and euglenophytes (Fig. 7). Cyanobacteria were by far the most developed group in Lake George (98.6 ± 2.4% of Chla) and in the Kazinga Channel (96.1 ± 5.0% of Chla).

Microscopical examinations of the lake phytoplankton confirmed the dominance of cyanobacteria and diatoms in Lake Edward, and recorded a total of 248 species, varieties and forms from 6 divisions (Table 1): Cyanoprokaryota/Cyanobacteria – 104, Chlorophyta – 66, Streptophyta – 3, Pyrrhophyta (dinoflagellates) – 4, Euglenophyta – 1 and Ochrophyta – 70 (Bacillariophyceae (diatoms) – 68, Xanthophyceae – 2). The heterocytous species from the filamentous genera *Raphidiopsis* and *Anabaenopsis* were abundant, in combination with small coccoid colonial algae from the genera *Microcystis, Merismopedia, Aphanocapsa, Aphanothece* and *Anathece*. For diatoms, the most important were species of the genus *Nitzschia*, the most abundant being the needle-like *N. spiculum* and *N. bacata*, although *N.* cf. *lacuum* (=*N. fonticola* sensu Hustedt, 1949) and *N. tropica* could occur in large numbers in some samples. Centric diatoms were represented by *Cyclostephanos damasii* and *Stephanodiscus* cf. *minutulus*; they occurred in a relatively high number of samples, but they were much less abundant than the needle-like *Nitzschia*. Lake George and presumably the Kazinga Channel had a different species composition from that of Lake Edward: both water bodies were dominated by *Microcystis*, with high proportion of small coccal (*Gloeothece*, *Chroococcus*) and tiny filamentous non-heterocytous cyanoprokaryotes (*Planktolyngbya*) with very low contribution of heterocytous genera like *Raphidiopsis* and *Anabaenopsis*. Despite the connection through Kazinga Channel, the floristic similarity between lakes George and Edward was very low (only 11%).

The RDA performed on the relative abundance of the phytoplankton groups and on some predictive environmental variables (Fig. 8) explained a large part of the total variance within the data set (~71% associated with the two first factorial axes). The main environmental variables contributing to the abundance of the two major phytoplankton classes (i.e., cyanobacteria and diatoms) were Z_{eu} (euphotic layer), which was negatively correlated with TSM, a_{350}, C:P, SRP and pH (Fig. 8). C:N ratio explained well cyanobacteria T2 (Fig. 8). The non-linear regression of Z_{eu} against TSM was quite good (Fig. 9a; R^2 = 0.72), whereas Chla was not a good predictor of Z_{eu} (Fig. 9b; R^2 = 0.36). An additional result of interest was the linear regression of Chla against POC (Fig. 9c), with a slope (i.e. an average POC:Chla ratio) of 124 and a Y-intercept of 1.2 mg L^{-1} (R^2 = 0.53). Using 124 as a conversion coefficient estimating phytoplankton carbon gave a mean contribution of phytoplankton biomass to POC of 47.4 ± 18.2%.

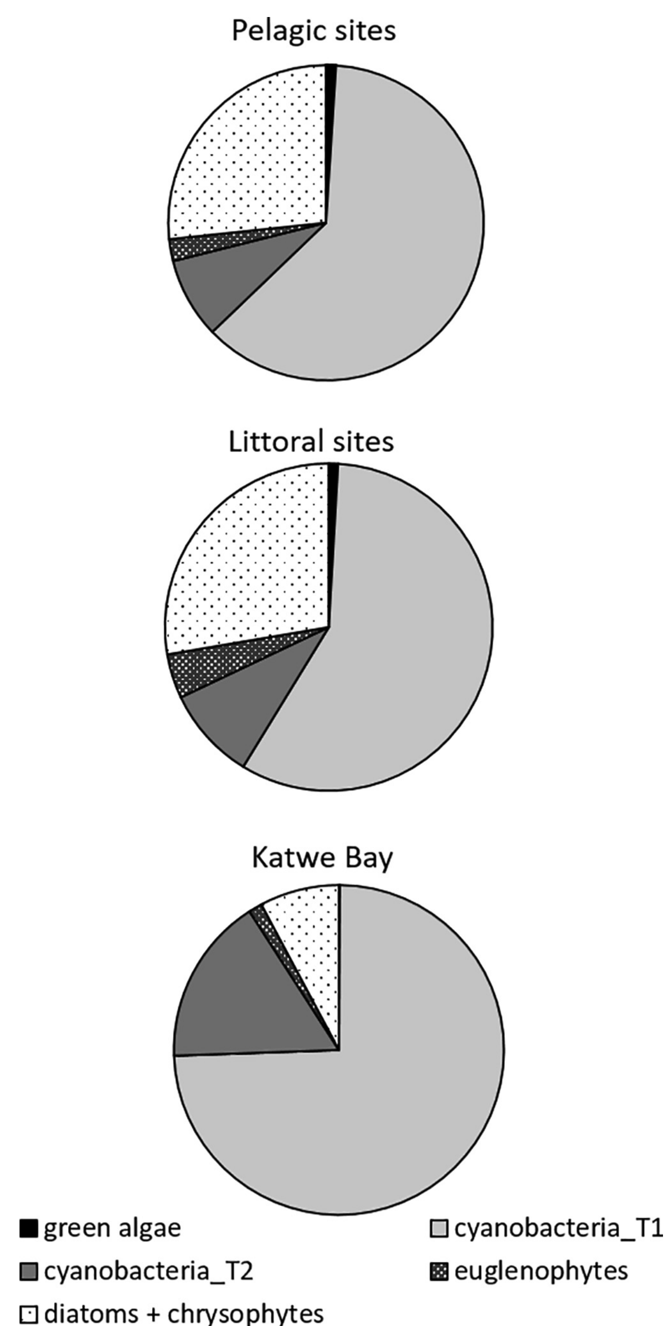

Fig. 7. Mean relative abundance of phytoplankton classes in Lake Edward, expressed as percentage contribution to chlorophyll *a* concentration.

The nutrient limitation experiment showed that primary production was always significantly higher (~2 fold) in the bottles amended with NO_3^- (+N, +NP) than in the control and bottles amended with only PO_4^{3-} (Fig. 10).

Discussion

We report a large number of observations made during three sampling series on phytoplankton ecology and diversity in an African great lake, Lake Edward, with some data on Lake George and the Kazinga Channel, which connects the two lakes (Table S1, see Electronic Supplementary Material (ESM) SI1). We show a clear

Table 1
Summary of phytoplankton diversity in Lake Edward: comparison of the data from the Damas' mission (1939), from Hecky and Kling (1987) and from the HIPE project (this study). For details see Stoyneva-Gärtner and Descy (2018).

	Damas 1935–1936	Hecky and Kling 1972	HIPE 2016–2018	Total taxa
CYANOPROKARYOTA	46	11	104	134
EUGLENOPHYTA	8	0	1	8
PYRHHOPHYTA	1	0	4	5
CRYPTOPHYTA	0	1	0	1
OCHROPHYTA	249	0	70	287
Tribophyceae	9	0	2	11
Chrysophyceae	3	0	0	3
Synurophyceae	1	0	0	1
Bacillariophyceae	236	0	68	274
CHLOROPHYTA	65	13	66	131
STREPTOPHYTA	8	3	3	14
Total taxa	*377*	*28*	*248*	580

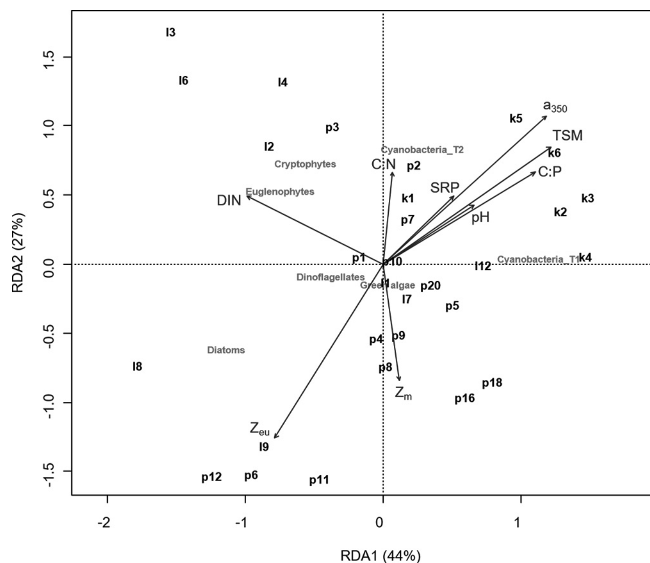

Fig. 8. Results of the redundancy discriminant analysis (RDA) of Lake Edward environmental and phytoplankton data: plot of variables and sites on the two first factors. Environmental variables are indicated as vectors (arrows): Zeu: euphotic layer depth; Zm: mixed layer depth; DIN: dissolved inorganic nitrogen; SRP: soluble reactive phosphate; C:N: particulate carbon:nitrogen ratio; C:P: particulate carbon: phosphorus ratio; TSM: total suspended matter; a350: light absorption at 350 nm. l: littoral site; p: pelagic site; k: Katwe Bay site.

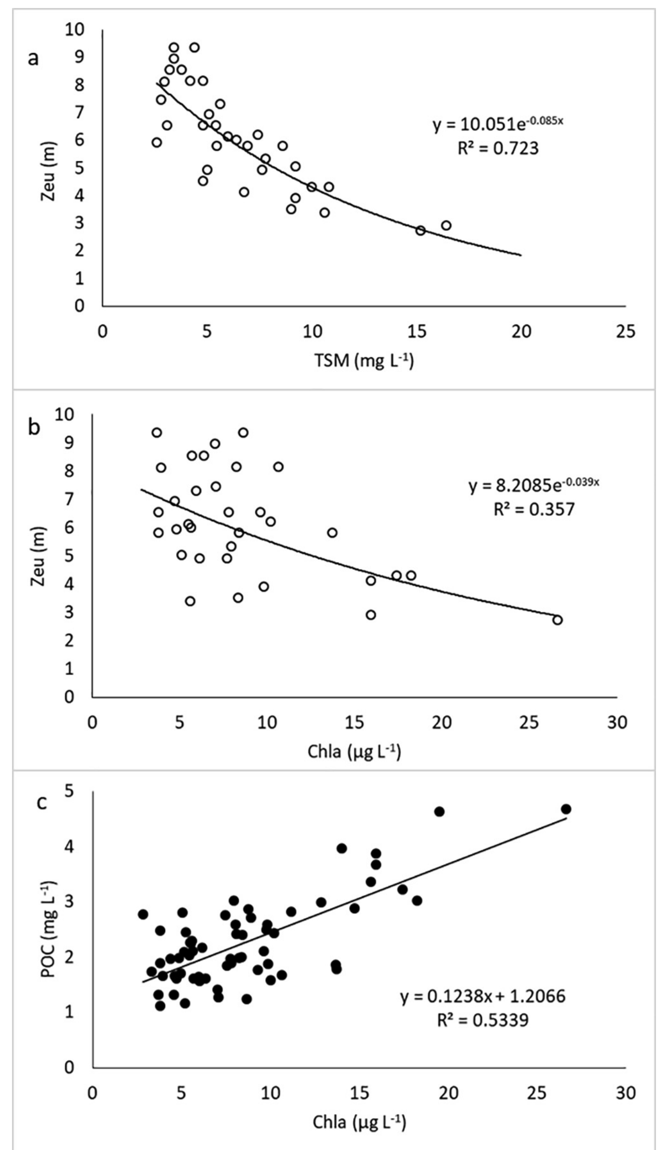

Fig. 9. Regression plots of (a) euphotic depth (Z_{eu}) vs. TSM, (b) Z_{eu} vs. chlorophyll *a* concentration and of (c) particulate organic carbon (POC) vs. chlorophyll *a* concentration. Equations and R^2 are indicated on the plots. The data are from the 0–5 m depth range and from the samples from the littoral and pelagic zones of Lake Edward, excluding the Katwe Bay sites.

dominance of two phytoplankton classes, cyanobacteria and diatoms (Fig. 7), both in terms of biomass and diversity (although green algae, despite their noticeably low abundance, were quite diverse). In contrast, Lake George and its connection to Lake Edward, the Kazinga Channel, are essentially dominated by colonial coccoid cyanobacteria, whereas Lake Edward has a great diversity of cyanobacteria taxa, including a significant proportion of heterocytous forms. Therefore, the input from the hypereutrophic Kazinga Channel, despite the fact that it contains a high biomass of cyanobacteria and that it represents 1/3 of the total river inflows to the Lake Edward, does not seem to provide an inoculum to Lake Edward, which has a different microflora.

Light availability limited by high TSM loading emerges as an important factor, contrasted among the shallow and deep sites with potential light limitation in the pelagic sites, due to the high Z_m:Z_{eu} ratio (Fig. 3b). Despite the fact that the euphotic layer did not vary significantly between seasons (Fig. 3a), the greater MLD in the dry season induced strong light limitation in the deep

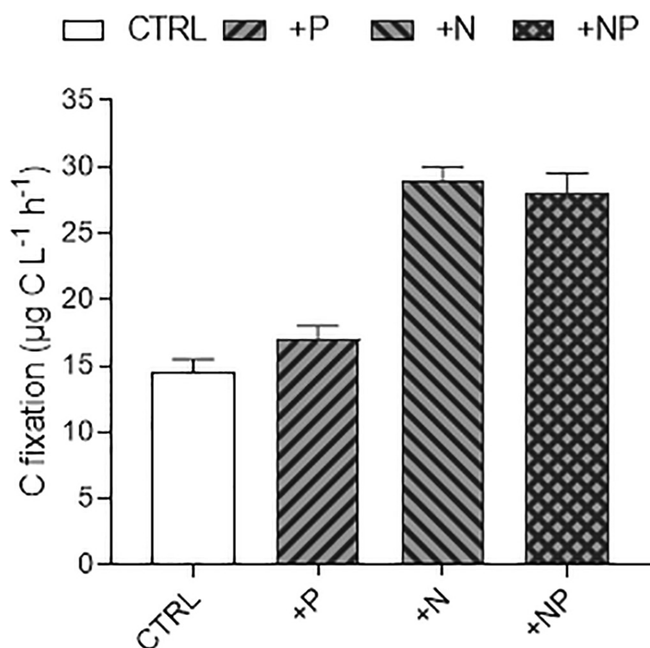

Fig. 10. Photosynthetic C fixation rates measured during a nutrient limitation experiment (24 h incubation under constant light irradiance) carried out with samples from a pelagic station in L. Edward (20 m max depth). Bottles were incubated without any amendment (CTRL treatment), or amended with an excess amount of NO_3^- (+N treatment), PO_4^{3-} (+P treatment), or both NO_3^- and PO_4^{3-} (+NP treatment). Error bars are the standard deviation calculated on triplicates.

pelagic sites, with a very low average light experienced by the phytoplankton. Although one would generally expect a positive selection for diatoms in such low-light conditions (Reynolds, 2006), here cyanobacteria increased the most in the dry season. This might be explained by several factors, among which phycobiliproteins, which provide cyanobacteria with an advantage for light absorption in the most penetrating wavelengths (Kirk, 1994). Also, many cyanobacteria species in the lake are thin filamentous forms, which provide these taxa with high surface-to-volume (S:V) ratio, favoring both light absorption and nutrient assimilation (Reynolds, 2006). Interestingly, the most abundant diatoms such as needle-like *Nitzschia spiculum* and *N. bacata* in Lake Edward have also high S:V ratio, which may be interpreted as a similar response to the environment. Another factor explaining the success of cyanobacteria is the N limitation in the whole lake evidenced by the C:N ratio (indicative of moderate limitation, see e.g. Guildford and Hecky, 2000). The effect of N limitation on the lake primary production was further evidenced by the nutrients addition experiments (Fig. 10). These assays clearly indicated that primary production increased significantly with N addition (and did not with P addition) illustrating therefore that Lake Edward was most likely to be N-limited during both rainy (March-April 2017) and dry (January 2018) seasons (Fig. 10). The hypothesis of N-limitation on phytoplankton growth is also supported by the notable presence of filamentous heterocyte-bearing species, providing evidence for N_2 fixation. Last but not least, cyanobacteria may be favored by the high pH and alkalinity of the lake water, as they are superior competitors for dissolved CO_2 and bicarbonate (Shapiro, 1997; Falkowski and Raven, 2007).

Contrary to the reports for other great lakes (e.g. Hecky and Kling, 1987), and despite expectations from remobilization of deep nutrients with deeper vertical mixing occurring in the dry season in deep tropical lakes, nutrient concentrations in the euphotic layer did not increase in the dry season in Lake Edward (Fig. 4a-b). On the contrary, DIN and SRP concentrations tended to decrease during the dry season whereas Chla increased (Fig. 4), suggesting that nutrient demand determined the concentration of DIN and SRP. DIN was higher in the littoral sites than in the pelagic sites and those of the Katwe Bay (Fig. 5a). Lower DIN in Katwe Bay may also have resulted, as for SRP, from the high demand from the large phytoplankton biomass. Epilimnion DIN was also lower in the pelagic sites, which may have resulted from stratification and from denitrification taking place in the hypolimnion and the sediment in the rainy season. Indeed, in the rainy season, the pelagic waters became anoxic below 20 m when the lake was stratified (Fig. 2), generating environmental conditions for denitrification to occur. In contrast, the relatively high concentration of SRP in the euphotic layer of the littoral and pelagic sites of Lake Edward (Fig. 5b) do not suggest that P could be limiting to phytoplankton growth, and this is confirmed by the C:P ratio close to the Redfield ratio (Fig. 6b) except in Katwe Bay where the high C:P was obviously driven by the high demand of the large biomass. However the conclusions on nutrient limitation based solely on seston nutrient ratios should be considered with care, as phytoplankton biomass represented on average about half of POC in pelagic and littoral waters of the lake.

Optical microscope observations showed a dominance of the phytoplankton community of Lake Edward by cyanobacteria in terms of biodiversity. Although the total number of planktonic species found in this study (248) was comparable to the number found in the samples from the Damas' mission (270), and while the main diatom taxa correspond to the list of Hustedt (1949), there appears to be a difference in the algal biodiversity, with a strong shift from diatom-rich towards cyanobacterial phytoplankton. For example, according to the data from the Damas' mission, cyanobacteria (Cyanoprokaryota) and diatoms (Bacillariophyceae) represented 12% and 66% of the total species composition, while in our study they formed 42% and 27%, respectively (Table 1). Among cyanoprokaryotes, the biodiversity of small coccal algae strongly increased; in our study they comprised 70% of the total cyanoprokaryote diversity in comparison with their contribution (32%) in the early 1930s (for details in species composition see Stoyneva-Gärtner and Descy, 2018). The contribution of green algae (divisions Chlorophyta and Streptophyta) to the general biodiversity also increased from 20% to 28% (Table 1). However, from these data, it is not possible to assess whether changes in phytoplankton abundance occurred since the 1930′s, as no cell counts nor chlorophyll *a* measurements were made at that time. To some extent, our results agree with those of Hecky and Kling (1987) who found cyanobacteria and green algal dominance in pelagic whole water samples from the southern part of the lake. Hecky and Kling (1987) did not mention the diatoms.

Other changes, with regard to biogeochemistry and phytoplankton, may have occurred over time in Lake Edward. An earlier comparison with historical data was attempted by Lehman et al. (1998), on the basis of a few measurements they carried out in March 1995. Although the historical record was also based on few and incomplete data, they were able to provide evidence for a decline in P concentration by a factor of 2 from the 1950s and 1960s, based on TP concentration (Table 2). Our nutrient and Chla data are in agreement with those from Lehman et al. (1998) and provide additional evidence, however based on few earlier data, for unchanged DIN concentration (Table 2). Given the lack of historical Chla measurements, it cannot be assessed whether the TP reduction resulted in lower phytoplankton biomass. However, a clue to a change can be found from monthly Secchi depth measurements made in 1952–1953 (Verbeke, 1957). Using these data and the formula we used for calculating k, the vertical attenuation coefficient, we found that the euphotic depth has declined since the 1950s (Table 2): it was close to 10 m at that time (compared with ~6 m today in the pelagic zone), indicating that a change has occurred in the transparency of the lake water, which is likely to have resulted in a reduction of the lake primary production. This

Table 2
Nutrients, Chla and vertical extinction coefficient (k): comparison with historical data. Verbeke's data date back from 1952 to 1953; k was calculated from Secchi depth (n = 11).

	NO_3^- µM	DIN µM	SRP µM	TP µM	Chla µg L^{-1}	k m^{-1}
Verbeke (1957)	1.61	3	2.90			0.48 ± 0.08
Talling (1965)	1.7		0.6	4.1		
Lehman et al. (1998)	<0.1		0.6	1.4	6.5–8.8	0.58–0.63
This study (pelagic)	1.4 ± 1.6	2.1 ± 1.0	0.9 ± 0.2	2.0 ± 0.9	8.0 ± 3.9	0.66 ± 0.14

change occurred in about four decades, from the middle to the end of the 20th century. We hypothesize that it resulted from an increase in TSM, which today is the main factor determining water transparency (Fig. 9), whereas in the 1960s, the attenuation coefficient in Lake Edward (as in lakes Albert and Victoria) was determined by Chla concentration (Lehman et al., 1998). Interestingly, a decrease of light in the water column might be an explanation for the very low green algal biomass we found in Lake Edward, whereas green algae were abundant in the 1970s (Hecky and Kling, 1987).

Conclusions

Present Lake Edward, according to Chla, TP and Secchi depth, can be considered as being in the upper mesotrophic range, as far as a classification developed for temperate lakes (e.g. Sigee, 2004) is applicable to tropical lakes. Its phytoplankton is dominated by cyanobacteria, both in terms of biomass and species richness. Diatoms rank second in terms of biomass, and green algae have high species diversity, but contribute little to total biomass. In contrast to larger and deeper African great lakes, such as the oligotrophic Lake Tanganyika, Lake Edward does not seem to exhibit a strong seasonality: in the largest and deepest lakes, deep mixing occurs in the dry season, when the temperature gradient is weaker, and increases availability of SRP and DIN, resulting in dry season chlorophyll *a* peaks. The rainy season stratification results in nutrient limitation, translating in lower Chla and changes in the structure of the phytoplankton assemblage, driven by light, nutrient limitation and zooplankton grazing (Hecky and Kling, 1987; Descy et al., 2005, 2010; Sarmento et al., 2006). In contrast, possibly due its closeness to the Equator and modest depth compared to its large neighbours, Lake Edward presents rather stable limnological and physical and chemical conditions, clearly favorable to cyanobacteria dominance. Although the historical record is incomplete, environmental changes may have occurred in the lake since the 1930s and the 1950s, as indicated by alterations of phytoplankton diversity and by biogeochemical changes, as well by a decline of the fishery yield. Available historical data suggest a possible change in the nutrient budget of the lake but also a decrease of water transparency, possibly due to higher suspended matter than in the past, which may have affected the lake primary productivity.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jglr.2020.01.003.

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