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Primary production in a tropical large lake: The role of phytoplankton composition

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HIGHLIGHTS

- We provide a 7-year dataset of primary production in a tropical great lake.
- Specific photosynthetic rate was determined by community composition.
- Annual primary production varied between 143 and 278 mg C m⁻² y⁻¹.
- Pelagic production was highly sensitive to climate variability.

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ABSTRACT

Phytoplankton biomass and primary production in tropical large lakes vary at different time scales, from seasons to centuries. We provide a dataset made of 7 consecutive years of phytoplankton biomass and production in Lake Kivu (Eastern Africa). From 2002 to 2008, bi-weekly samplings were performed in a pelagic site in order to quantify phytoplankton composition and biomass, using marker pigments determined by HPLC. Primary production rates were estimated by 96 in situ ¹⁴C incubations. A principal component analysis showed that the main environmental gradient was linked to a seasonal variation of the phytoplankton assemblage, with a clear separation between diatoms during the dry season and cyanobacteria during the rainy season. A rather wide range of the maximum specific photosynthetic rate (P_{Bm}) was found, ranging between 1.15 and 7.21 g carbon g⁻¹ chlorophyll *a* h⁻¹, and was best predicted by a regression model using phytoplankton composition as an explanatory variable. The irradiance at the onset of light saturation (I_k) ranged between 91 and 752 μE m⁻² s⁻¹ and was linearly correlated with the mean irradiance in the mixed layer. The inter-annual variability of phytoplankton biomass and production was high, ranging from 53 to 100 mg chlorophyll *a* m⁻² (annual mean) and from 143 to 278 g carbon m⁻² y⁻¹, respectively. The degree of seasonal mixing determined annual production, demonstrating the sensitivity of tropical lakes to climate variability. A review of primary production of other African great lakes allows situating Lake Kivu productivity in the same range as that of lakes Tanganyika and Malawi, even if mean phytoplankton biomass was higher in Lake Kivu.

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1. Introduction

Contrary to common assumptions on the constancy of ecological conditions in tropical lakes, pelagic primary production may vary considerably in African great lakes, at different time scales, from seasons to centuries (Melack, 1979; Cohen et al., 2006). At long time scales, Indian Ocean surface temperatures, determining rainfall, are the primary influence on East African climate (Tierney et al., 2013), which largely determines water column processes in the great Rift lakes (e.g. Johnson

and Odada, 1996; Plisnier, 2000; MacIntyre, 2012). At a seasonal scale, the main driver of pelagic primary production is the alternation of wet and dry seasons, with changes in relative humidity and wind velocities: typical wet season conditions induce thermal stratification of the water column, which reduces nutrient supply in the euphotic zone. Dry season conditions tend to reduce the temperature–density gradient and higher wind velocities result in deep vertical mixing of the water column, increasing nutrient supply in the euphotic zone, inducing a dry season phytoplankton peak (Hecky and Kling, 1987; Spigel and Coulter, 1996).

Phytoplankton composition also depends on the alternation of stratified conditions in the rainy season with the deep mixing that occurs in the dry season: the seasonal mixing event not only increases the supply of dissolved nutrients in the euphotic zone, but also results in a rise of the ratio between mixed layer depth (Z_m) to the euphotic layer depth

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(Zeu) (Sarmiento et al., 2006). In these conditions, phytoplankton is subjected to potential light limitation, leading to diatom dominance (Reynolds, 2006a). By contrast, in the shallow mixed layer of the rainy season, the lower Zm:Zeu ratio selects for high-light adapted phytoplankton such as green algae and cyanobacteria. The trade-off between high light and nutrient limitation in the rainy season and low light and high nutrients during the dry season has been documented in classic studies in African lakes (e.g. Hecky and Kling, 1987; Kilham et al., 1986) and is a key to understanding shifts in phytoplankton composition in these lakes.

Estimates of annual primary productivity in tropical lakes have been usually based on measurements of phytoplankton photosynthesis carried out over sufficiently long periods to capture the seasonal variations of incident light, water transparency, temperature, nutrients and phytoplankton biomass. Examples of this approach can be found in Lewis (1974) in Lake Lanao (Philippines), in Talling (1965) for several East African lakes, in Hecky and Fee (1981), Sarvala et al. (1999) and Stenuite et al. (2007) for Lake Tanganyika, in Guildford et al. (2007) for Lake Malawi and in Silsbe et al. (2006) for Lake Victoria. Such studies derived photosynthetic parameters (P_{Bm} , the maximum specific photosynthetic rate, and lk or α , a measure of the photosynthetic efficiency) from in situ incubations. If the irradiance at the onset of light saturation (lk) describes the regulatory response of the phytoplankton photosynthesis to the light climate, P_{Bm} relates to the efficiency of the light harvesting system. Main environmental factors influencing P_{Bm} in cultures are temperature and nutrient availability (Geider and MacIntyre, 2002). A reduction of P_{Bm} is observed in nutrient-limited algae (Geider et al., 1998; Greene et al., 1991). At the community level, it has occasionally been demonstrated that larger cells sustain higher P_{Bm} than smaller cells (Cermeño et al., 2005; Peltomaa and Ojala, 2010), but field studies attempting to relate the compound photosynthetic response on the taxonomic composition of the phytoplankton assemblage are rare (Segura et al., 2013). However, phytoplankton composition matters, as

shown by experimental studies on pure cultures, which have provided evidence of significant variation of photosynthetic parameters among taxonomic groups (Falkowski and Raven, 2007; Kirk, 1994; Reynolds, 2006a).

Pigment-based analysis of phytoplankton composition may provide an adequate framework to relate community composition to photosynthesis parameters. Phytoplankton pigments, determined by high performance liquid chromatography (HPLC) analysis, have been used widely for assessing biomass at the class level, with many applications in marine, estuarine, and freshwater environments (e.g., review in Sarmiento and Descy, 2008). The assessment of algal abundance from pigment concentrations uses different techniques, involving ratios of marker pigments to chlorophyll *a* (Chl*a*) (Mackey et al., 1996). As it is based on a fast, automatic and reliable analytical technique, the pigment approach has been largely used in oceanographic studies and monitoring programs (Jeffrey et al., 1997), as well as in large lake studies (Descy et al., 2005; Fietz and Nicklish, 2004; Fietz et al., 2005; Sarmiento et al., 2006).

We applied a pigment approach in Lake Kivu, a great and deep (maximum depth of 489 m) meromictic lake of the East African Rift (Fig. 1). Lake Kivu is located north of Lake Tanganyika, at 1463 m above sea level. The mixolimnion (i.e. the upper layer of a meromictic lake) alternates between periods of complete mixing down to maximum 65 m and periods of stratification during which nutrients become depleted in the euphotic zone (Sarmiento et al., 2006; Schmid and Wüest, 2012). Whereas moderate to severe P-limitation of phytoplankton prevails during most of the year (Sarmiento et al., 2009, 2012), N-limitation may occur in the stratified rainy season, as denitrification takes place within the oxic–anoxic transition zone (Llirós et al., 2012). By contrast, the monimolimnion, i.e. the lower layer that never mixes with surface waters, is rich in nutrients and dissolved gases (Degens et al., 1973; Schmid et al., 2005). Pelagic primary production in Lake Kivu exhibits substantial variation at the seasonal scale, but also between years

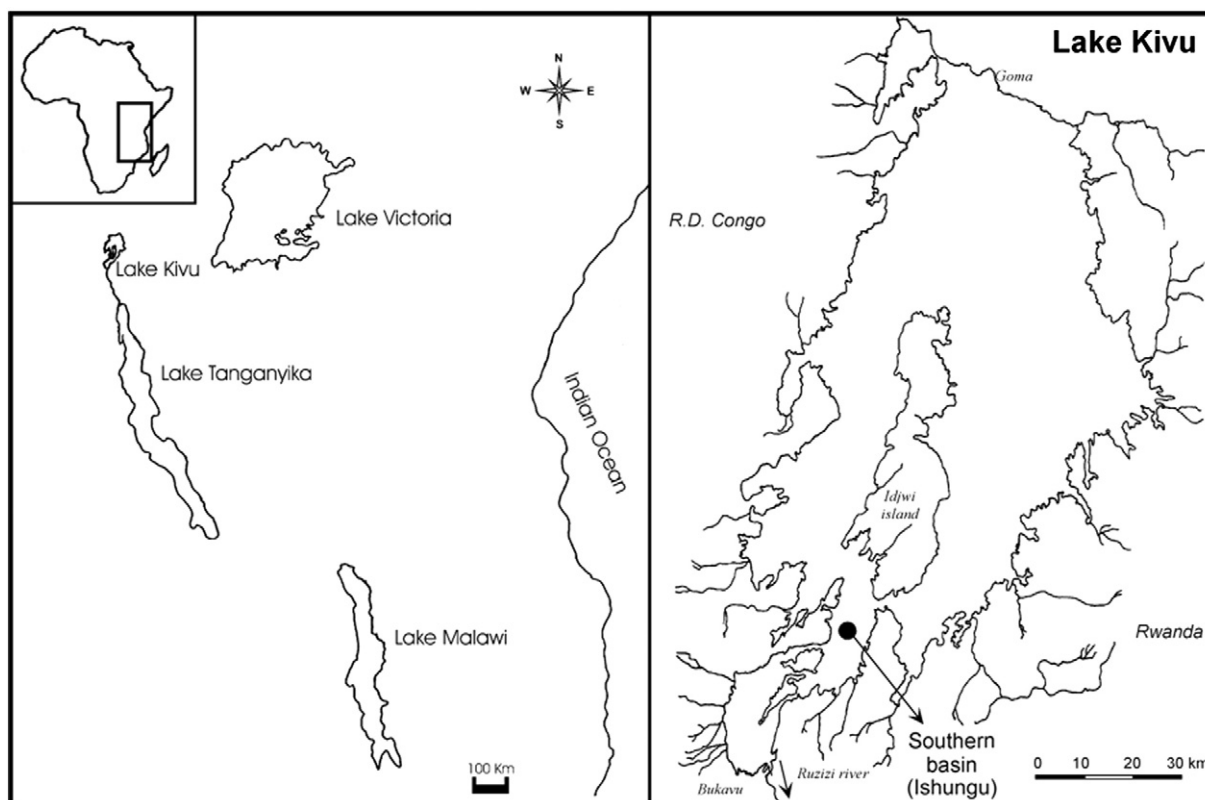


Fig. 1. Location of Lake Kivu in East Africa (left panel) and the sampling site (Ishungu, southern basin).

(Sarmiento et al., 2012), as shown by the variable height of the dry season Chla peak. Phytoplankton composition also varies seasonally in a typical way, with diatoms and cryptophytes being more abundant in the dry season, and cyanobacteria better developed in the rainy season (Sarmiento et al., 2006, 2007).

Our working hypothesis was that in this tropical great lake, phytoplankton composition, along with water transparency and depth of the mixed layer, is a key factor determining pelagic photosynthesis. We used a long-term database of in situ photosynthesis measurements and phytoplankton composition, determined by HPLC analysis of marker pigments, to demonstrate that the photosynthetic parameters, P_{Bm} and I_k , can be derived from quantitative composition of the phytoplankton assemblage, allowing accurate prediction of daily and annual primary production.

2. Material and methods

2.1. Sampling

The study site was located in the southern basin (Ishungu) of Lake Kivu (2.34°S, 28.98°E) (Fig. 1). General physico-chemical characteristics of the lake's water are described elsewhere (e.g. Borges et al., 2011; Descy et al., 2012; Sarmiento et al., 2006; Schmid et al., 2005). Limnological observations were made twice a month from March 2002 to November 2009. First, vertical profiles of temperature were obtained with a Hydrolab DS4a probe or a Yellow Springs Instrument 6600 V2 probe. The mixed layer depth, Z_m , was determined at each occasion as the depth with the maximum downward temperature change per meter, based on the fact that salinity has a marginal effect on density gradient in the top 65 m (Schmid and Wüest, 2012). Water samples were collected at discrete depth intervals (0, 5, 10, 15, 20, 25, 30, 40, 50 and 60 m depth) using a 6 L Van Dorn bottle. For each sampling depth, at least 3 L of water were filtered on Macherey-Nägel (Düren, Germany) GF5 filters (average retention capacity of 0.4 μm) which were immediately frozen at -20°C for pigment analysis. For the primary production incubation (see below), a pooled sample was constituted on each sampling occasion from discrete samples (2 L) spaced every 5 m in the mixed layer. In addition, at least 3 L of water was filtered from the pooled mixed layer sample for pigment analysis and 2 L was filtered on a pre-combusted GF5 filter for particulate carbon (C), nitrogen (N) and phosphorus (P) analyses. Filters were kept frozen until analysis.

2.2. Phytoplankton biomass

Chla was used as an index of phytoplankton biomass (Reynolds, 2006a). Total phytoplankton biomass and the contribution of the different algal groups were achieved by HPLC analysis of marker pigments. It was demonstrated that the accuracy of Chla and chemotaxonomic carotenoid quantification by HPLC is less than 10 and 25%, respectively (Claustre et al., 2004). Data were subsequently processed with CHEMTAX (for CHEmical TAXonomy) (Mackey et al., 1996), as described in Descy et al. (2005) and Sarmiento et al. (2006). CHEMTAX is a computer program that allows allocating Chla among different algal groups defined by a suite of markers. From an initial ratio matrix (or input matrix) usually derived from pure cultures of phytoplankton, the program uses an iterative process to find the optimal pigment:Chla ratios and generates the fraction of the total Chla pool belonging to each pigment-determined group (Mackey et al., 1996). A supplementary 50 mL sample was preserved immediately after collection with Lugol's solution and neutral formaldehyde (2–4% final concentration) for microscopic identification of main taxa, according to Sarmiento et al. (2007). Phytoplankton biomass was expressed either as mg Chla m^{-3} or as mg Chla m^{-2} , by integrating the Chla measurements at the different sampled depths over the whole mixolimnion (0–65 m).

2.3. Primary production

The primary production rate was determined in 96 field photosynthesis-irradiance incubations. Eighteen 120-mL (from 2003 to 2005) or 20 180-mL (from 2006 to 2008) glass flasks were filled with water from the pooled mixed layer sample and 50 μCi of $\text{NaH}^{14}\text{CO}_3$ was added into each flask. Duplicate sets of bottles were placed into a ten-case floating incubator providing a range from 0 to 90% of natural light energy and incubated in situ at mid-day for ~ 2 h just below the surface. Incident light was monitored by a Li-Cor (Lincoln, Nebraska, USA) quantum sensor throughout the incubations.

The incubation was stopped by adding neutral formaldehyde and the phytoplankton was collected on Macherey-Nägel GF5 filters. Filters were rinsed with HCl 0.1 N and the radioactivity of the filters was measured using a Beckman scintillation counter (LS 6000 SC) with Filter-Count (Packard) as scintillation cocktail and the external standard method for quench correction. The specific photosynthetic rate of individual bottle i , P_i (in $\text{mg C mg}^{-1} \text{Chla h}^{-1}$), was calculated following Steeman-Nielsen (1952). Dissolved inorganic carbon (DIC, in mg C L^{-1}) was computed from pH and total alkalinity (TA) measurements using the carbonic acid dissociation constants of Millero et al. (2006). Measurements of TA were carried out by open-cell titration with HCl 0.1 M according to Gran (1952) on 50 mL water samples.

For each experiment, the maximum specific photosynthetic rate P_{Bm} (in $\text{mg C mg}^{-1} \text{Chla h}^{-1}$) and the irradiance at the onset of light saturation I_k ($\mu\text{E m}^{-2} \text{s}^{-1}$) were determined by fitting P_i to the irradiance gradient provided by the incubator I_i ($\mu\text{E m}^{-2} \text{s}^{-1}$), using the Vollenweider's (1965) equation, with the photo inhibition parameters set to 1:

$$P_i = 2P_{Bm} \frac{\frac{I_i}{2I_k}}{1 + \left(\frac{I_i}{2I_k}\right)^2} \quad (1)$$

Fitting was performed using the Gauss-Newton algorithm for non-linear least squares regression with the help of the STATISTICA 10[®] software (StatSoft France). The vertical light attenuation coefficient (Kirk, 1994), K_e (m^{-1}), was calculated from simultaneous measurements of surface irradiance with a Li-Cor LI-190 Quantum Sensor and underwater PAR measurements with a submersible Li-Cor LI-193SA Spherical Quantum Sensor. K_e was derived from the slope of the semi-logarithmic regression between relative quantum irradiance and depth (from 0 to 20 m). From 2003 to 2006, K_e was derived from Secchi depth, SD (m), using a conversion factor $K_e = -\ln(0.25)/SD$ obtained by calibration with PAR downward attenuation ($n = 16$, Pearson $r = 0.81$, $p < 0.001$). The euphotic depth, Z_{eu} , was defined as the depth at which light is 1% of subsurface light. The average light in the mixed layer, I_{Zm} (in $\mu\text{E m}^{-2} \text{s}^{-1}$), was calculated according to Riley (1957):

$$I_{Zm} = \frac{I_s(1 - e^{-Z_m K_e})}{Z_m \cdot K_e} \quad (2)$$

where I_s is the mean solar flux at the surface of the lake (24 h average) and Z_m is the depth of the mixed layer. I_s was calculated for a theoretical cloudless atmosphere for the appropriate latitude (Fee, 1990).

Daily depth-integrated primary production (DPP, in $\text{g C m}^{-2} \text{d}^{-1}$) was determined using photosynthetic parameters P_{Bm} and I_k , Chla biomass vertical profile, vertical light attenuation coefficient K_e and continuous surface irradiance data (Kirk, 1994), calculated for a theoretical cloudless atmosphere for the appropriate latitude (Fee, 1990):

$$\text{DPP} = \int_0^{24\text{h}} \int_0^{Z_m} 2P_{Bm} B_z \frac{\frac{I_{z,t}}{2I_k}}{1 + \left(\frac{I_{z,t}}{2I_k}\right)^2} dz dt \quad (3)$$

Table 1
Description of the variables used for modeling primary production.

Symbol	Description	Unit	Data source
B_z	Chlorophyll <i>a</i> biomass at depth <i>z</i>	mg Chla m^{-3}	Field observations
DPP	Daily depth-integrated primary production	$g\ C\ m^{-2}\ d^{-1}$	Eq. (3)
$I_{0,t}$	Surface irradiance at time <i>t</i>	$\mu E\ m^{-2}\ s^{-1}$	Solar modeling (Fee, 1990)
I_k	Irradiance at the onset of light saturation	$\mu E\ m^{-2}\ s^{-1}$	Field experiment or Eq. (5)
I_s	Mean solar flux at the surface of the lake during the day (24 h average)	$\mu E\ m^{-2}\ s^{-1}$	Solar modeling (Fee, 1990)
I_{zm}	Average light in the mixed layer	$\mu E\ m^{-2}\ s^{-1}$	Eq. (2)
$I_{z,t}$	Irradiance at depth <i>z</i> and time <i>t</i>	$\mu E\ m^{-2}\ s^{-1}$	Eq. (4)
K_e	Vertical light attenuation coefficient	m^{-1}	Field observations
P_{Bm}	Maximum specific photosynthetic rate	$mg\ C\ mg^{-1}\ Chla\ h^{-1}$	Field experiment or Eq. (6)
PCAaxis1	Score of pigment-based phytoplankton composition on the 1st axis of the PCA	No unit	HPLC analyses of field samples
PCAaxis2	Score of pigment-based phytoplankton composition on the 2nd axis of the PCA	No unit	HPLC analyses of field samples
Z_m	Mixed layer depth	m	Field observations

with:

$$I_{z,t} = 0.95 I_{0,t} e^{-K_e z} \quad (4)$$

All symbols and units are described in Table 1.

2.4. Particulate CNP

Particulate C and N were analyzed using a Carlo-Erba NA1500 elemental analyzer. Particulate P was analyzed by spectrophotometric determination of phosphate after digestion with potassium persulfate and boric acid (Valderrama, 1981). The elemental ratios were expressed as the mean ratio in molar units of the different sampling dates.

2.5. Statistical analysis

A principal component analysis (PCA) was performed on the relative contribution of the different phytoplankton groups to Chla resulting from the CHEMTAX processing. In total, 1387 individual HPLC samples from Lake Kivu were used. The PCA was carried out with the help of the CANOCO software (ter Braak and Šmilauer, 2002) after centering and standardization of the relative contributions to total Chla biomass. Results of the PCA ordination, i.e. sample scores along the first factorial axis, were used as independent variables to explain the maximum specific photosynthetic rate, P_{Bm} , of the different photosynthesis experiments. The reason for using the PCA axes instead of phytoplankton relative class abundances was to avoid autocorrelation between independent variables (Legendre and Legendre, 1998). The effects of the season along PCA axes were tested using Student's *t* statistical tests. Simple and multiple linear regressions were performed to explain variations of photosynthetic parameters, I_k and P_{Bm} , with, respectively, light conditions in the water column and phytoplankton community composition and CNP ratios. Multiple linear regressions were achieved using a forward stepwise selection of explanatory variables. Statistical tests, i.e. simple and multiple linear regressions and Student's *t*-test, were carried out with the help of the STATISTICA 10[®] software (StatSoft France). Daily primary production was calculated using Eq. (4) with observed or statistically-derived photosynthetic parameters. A sensitivity analysis of the primary production model was performed by replacing each variable by its mean in turn, while holding all other variables at their original values. The mean absolute relative error of daily primary production was then computed for each variable.

3. Results

Phytoplankton composition and biomass are presented in Fig. 2. The community was dominated by cyanobacteria, diatoms and cryptophytes. A seasonal peak higher than 100 mg Chla m^{-2} was observed at the end of the dry season (July–August) in 2003, 2004 and more spectacularly in 2008. A lower dry season peak was observed in

2006 and 2007. These peaks were mainly constituted of diatoms (essentially *Nitzschia bacata* Hust. and *Fragilaria danica* Lange Bert.). By contrast, cyanobacteria developed best during the rainy season, from October to May. The most common cyanobacteria taxa present in Lake Kivu were *Planktolyngbya limnetica* Lemm., *Synechococcus* spp. and various *Microcystis* species. The cryptophyte *Rhodomonas* was present throughout the year.

The inter-annual variability of phytoplankton biomass was relatively high, with the lowest mean annual biomass observed in 2005 with 53 mg Chla m^{-2} and the highest in 2008 with 100 mg Chla m^{-2} . The inter-annual coefficient of variation (CV) from 2002 to 2008 was 21%.

The seasonal variation of the mixed layer depth is presented in Fig. 2C. The dry season (from June to August) was characterized by a deeper mixed layer, although this pattern was not consistent over the years.

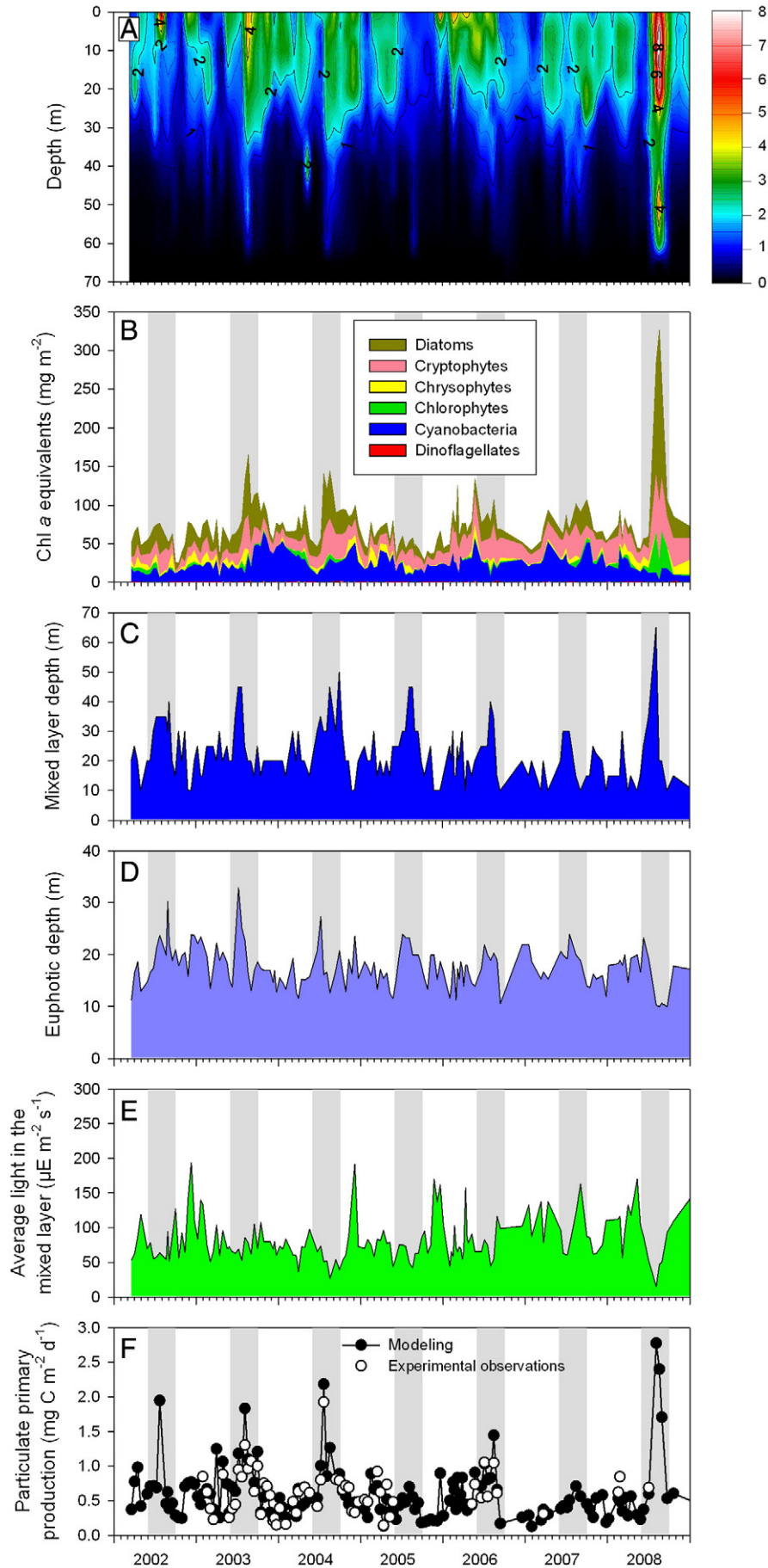
The PCA carried out on the relative contribution of each phytoplankton group to the total Chla biomass confirmed that the first component was linked to the seasonal variations (Fig. 3). The first axis, which represents 30.5% of the total variance, separates diatoms and chlorophytes from cyanobacteria. This axis clearly separates rainy season samples, with generally negative values (mean value, -0.19), from dry season samples, with positive values (mean value, $+0.31$) (Student's *t*-test, $p < 0.001$). The second axis collects 22.0% of the total variance and dissociates cryptophytes from the other groups. This axis is independent on the seasonal succession (Student's *t*-test, $p = 0.112$).

The depth of the euphotic zone, Z_{eu} , ranged between 8.3 and 28.5 m (median, 17.6 m) (Fig. 2D). The highest transparencies were observed at the end of the rainy season, in June, and sometimes in July and August, depending on the year. As expected, phytoplankton biomass directly influenced water transparency (Fig. 4).

Mean (\pm standard deviation) seston C, N and P concentrations were 458 (± 113) $\mu g\ C\ L^{-1}$, 56 (± 12) $\mu g\ N\ L^{-1}$ and 5.2 (± 1.8) $\mu g\ P\ L^{-1}$. Seasonal variations of the seston C:N:P molar ratios are presented in Fig. 5. The C:N ratio (mean 10.1, min–max 6.3–14.4) was largely influenced by season, with lower values at the end of dry season (July–August) than in the rest of year ($p < 0.005$). Nevertheless, dry season values (June–August) were the most variable, depending on the year. The C:P ratio (mean 263, min–max 130–447) was also largely influenced by season, with decreasing values from December to June and increasing values from July to November. The seasonal pattern was consistent over the years.

The photosynthetic parameters were estimated at 96 occasions from 2002 to 2008. An example of the photosynthesis vs irradiance curve we usually obtained is illustrated in Fig. 6. The fitting to the Vollenweider's model (Eq. (1)) was usually good, with a $R^2 > 0.95$. The irradiance at the onset of light saturation, I_k , ranged between 91 and 752 $\mu E\ m^{-2}\ s^{-1}$ (mean 318 $\mu E\ m^{-2}\ s^{-1}$). It was linearly correlated to the mean irradiance in the mixed layer, I_{zm} (Fig. 7).

The maximum specific photosynthetic rate, P_{Bm} , ranged between 1.15 and 7.21 $g\ C\ g^{-1}\ Chla\ h^{-1}$ (mean 3.57 $g\ C\ g^{-1}\ Chla\ h^{-1}$). Simple and multiple linear regressions were tested to explain the variability of



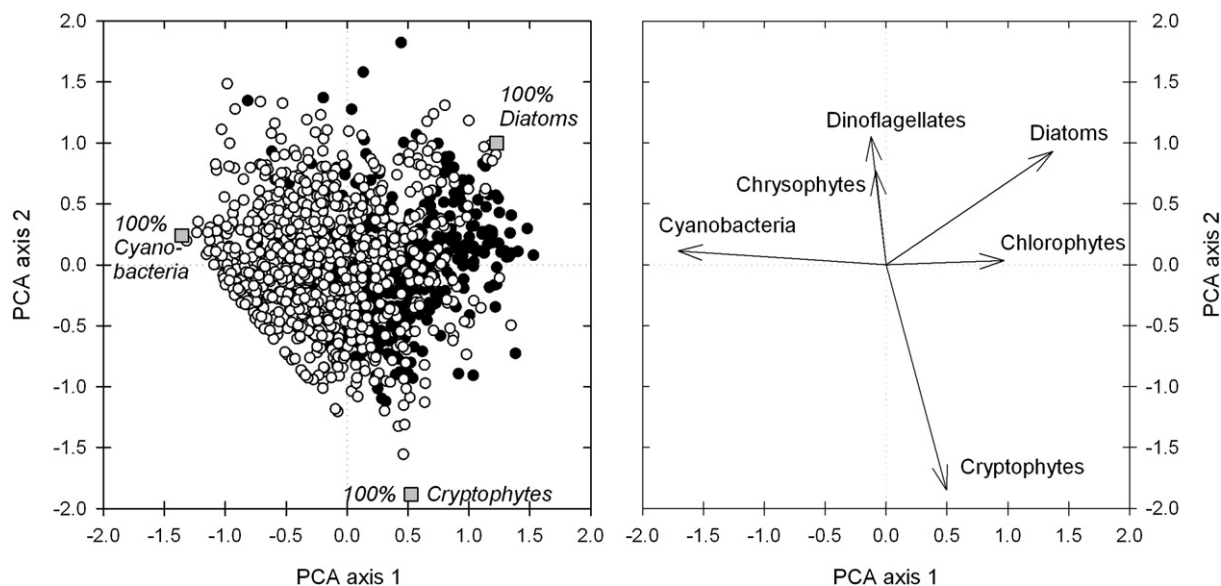


Fig. 3. Principal component analysis (PCA) of the relative contribution of the main phytoplankton groups to chlorophyll *a* from Lake Kivu, Ishungu station (southern basin); left panel: diagram of the samples on the two first axes of the PCA, showing a clear separation depending on season (open circles: samples from the rainy season; black circles: dry season) and the position of hypothetical “pure” phytoplankton group samples; right panel: diagram of the phytoplankton groups on the two first axes of the PCA.

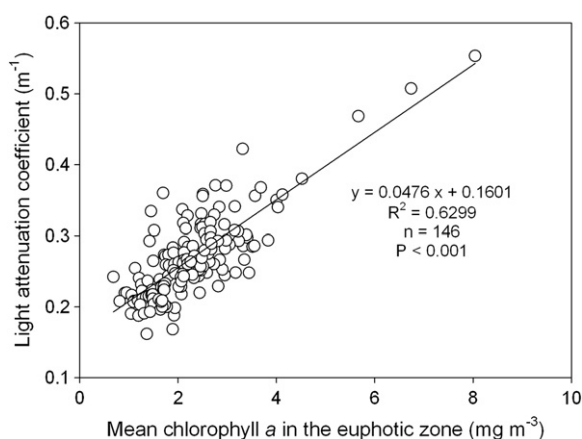


Fig. 4. Linear regression of the vertical attenuation of light against mean chlorophyll *a* concentration in the euphotic layer in Lake Kivu, Ishungu station (southern basin), 2002–2008.

P_{Bm} using phytoplankton composition, represented by the sample position along the first 4 axes of the PCA, and C:N and C:P ratios as explanatory variables. P_{Bm} was significantly correlated with axis 1 ($r = 0.779$; $p < 0.001$) and axis 2 ($r = 0.321$; $p = 0.001$) of the PCA. P_{Bm} was also negatively correlated with seston C:P ratios ($r = -0.448$; $p < 0.001$). A multiple linear regression was constructed with a forward stepwise selection of significant variables (Table 2). A single model with the first two axes of the PCA, significant at the 0.05 probability level, explained around 66% of the P_{Bm} variance (Table 2 and Fig. 8). As the C:P ratios were negatively correlated with the first PCA axis ($r = -0.49$, $p < 0.001$), both variables explained a common variance of P_{Bm} . This explains why the C:P ratio was not significant to explain P_{Bm} when the first PCA axis was already included in the regression model.

P_{Bm} was positively correlated with the sample score along the first and the second axes of the PCA: this results from the fact that P_{Bm} was

higher for a phytoplankton assemblage dominated by diatoms than when phytoplankton was dominated by cyanobacteria and/or cryptophytes. Three fictive HPLC samples with communities composed exclusively of cyanobacteria, diatoms or cryptophytes were added as passive samples in the PCA (see Fig. 3). The position of these communities along the first 2 axes was used within the multiple linear regression model presented in Table 2, to calculate the P_{Bm} values for “pure” communities in Lake Kivu. The calculated P_{Bm} was $1.13 \text{ g C g}^{-1} \text{ Chla h}^{-1}$ for cyanobacteria, $2.36 \text{ g C g}^{-1} \text{ Chla h}^{-1}$ for cryptophytes, and $7.21 \text{ g C g}^{-1} \text{ Chla h}^{-1}$ for diatoms.

The daily primary production was calculated based upon observed and statistically-derived photosynthetic parameters. I_k was modeled using the linear regression model including I_{zm} as single explanatory variable (Fig. 7):

$$I_k = 43.7 + 3.67I_{zm} \quad (5)$$

and P_{Bm} values were obtained from the multiple linear regression model presented in Table 2:

$$P_{Bm} = 3.56 + 2.001 \text{ PCAaxis1} + 1.196 \text{ PCAaxis2}. \quad (6)$$

Daily primary production results are presented in Fig. 2F. The mean daily primary production based upon observed photosynthetic parameters was $0.620 \text{ g C m}^{-2} \text{ d}^{-1}$ (range 0.142–1.924). Daily primary production values calculated from observed or statistically-derived photosynthetic parameters were highly correlated ($R^2 = 0.787$) and not statistically different (Student’s t-test for paired samples, $n = 59$, $P = 0.206$). Annual primary production was then calculated based on statistically-derived photosynthetic parameters. The mean annual primary production from 2002 to 2008 was $213 \text{ g C m}^{-2} \text{ y}^{-1}$. The inter-annual variation was important (CV = 25%), with a minimum value of $143 \text{ g C m}^{-2} \text{ y}^{-1}$ in 2007 and a maximum value of $278 \text{ g C m}^{-2} \text{ y}^{-1}$ in 2008.

Input variables of the primary production model are the phytoplankton biomass (Chla), the photosynthetic parameters (P_{Bm} and I_k), the

Fig. 2. (A) Vertical distribution of phytoplankton biomass (Chlorophyll *a*, mg m^{-3}), (B) areal chlorophyll *a* concentrations and biomass composition from marker pigment analysis, (C) depth of the mixed layer, (D) depth of the euphotic layer, (E) average light in the mixed layer, (F) daily depth-integrated primary production with photosynthetic parameters estimated from in situ ^{14}C incubations (white circles) or with photosynthetic parameters calculated from Eqs. (5) and (6) (black circles with lines), during the 2002–2008 period in Lake Kivu, Ishungu station (southern basin). The gray boxes identify the main dry season periods.

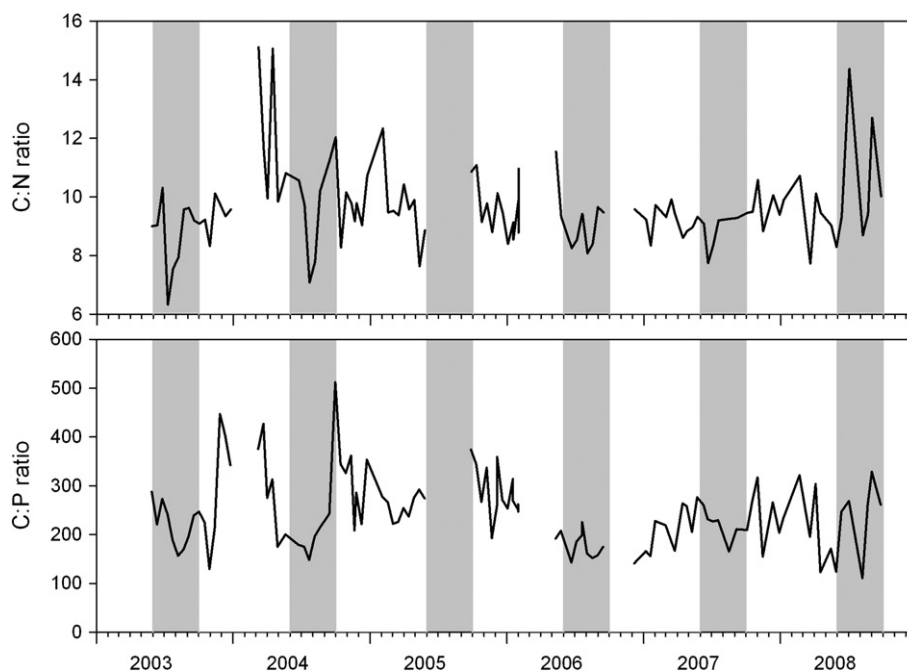


Fig. 5. C:N:P elemental ratios (atomic values) of epilimnetic seston in Ishungu station (southern basin) of Lake Kivu from 2003 to 2008. The gray boxes identify the main dry season periods.

depth of the mixed layer (Z_m), the vertical light attenuation coefficient (K_e), and indirectly (via its influence on P_{Bm}) the phytoplankton community composition (PCAaxis1). Results of the sensitivity analysis of the primary production model are presented in Table 3. Chla was the most influential variable of the daily primary production, followed by the photosynthetic parameters. The physical variables, such as Z_m and K_e had only minor influence.

4. Discussion

In this study, we present results on phytoplankton assemblage, biomass and production obtained during a 7-year continuous survey in Lake Kivu, a large tropical lake of East Africa. Such a dataset is unique for East African Great lakes and provides evidence for substantial variations of phytoplankton biomass and production between years. From these data, we developed an empirical model of planktonic primary

production which can be used for deriving photosynthetic parameters based upon phytoplankton community composition and light conditions.

In Lake Kivu, phytoplankton generally peaks in the main dry season (June–September) (Fig. 2), when enhanced lake evaporation causes a significant heat loss from the lake surface, allowing a reduction of the thermal gradient in the mixolimnion (Sarmiento et al., 2006). Surface waters are then mixed with deeper waters enriched in nutrients, allowing adequate conditions for phytoplankton development. Community is then dominated by diatoms, which sustained a higher specific photosynthetic rate, P_{Bm} ($7.21 \text{ g C g Chla}^{-1} \text{ h}^{-1}$), than the other taxonomic groups. During the rest of the year, i.e. from September to June, stable density stratification is usually observed within the mixolimnion, with varying depths of the surface mixed layer of typically around 10–30 m (Fig. 2). During this time, nutrient supply for primary production is scarce (Pasche et al., 2012; Sarmiento et al., 2012) and phytoplankton becomes nutrient-limited (Fig. 5). Cyanobacteria with a low P_{Bm} ($1.13 \text{ g C g Chla}^{-1} \text{ h}^{-1}$) then dominated the community.

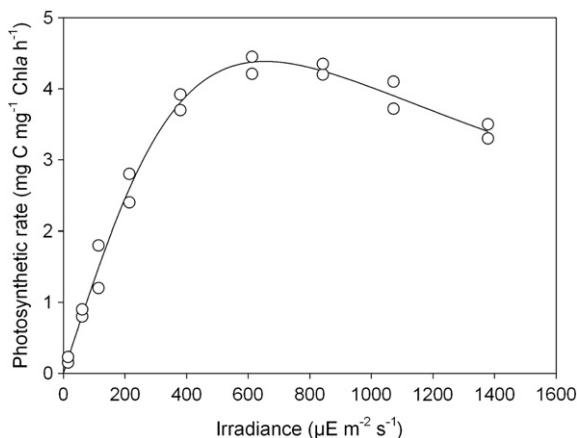


Fig. 6. Example of a photosynthesis–light relationship obtained from an in situ radiocarbon incubation under light saturation in Lake Kivu (July 3rd, 2008). White circles are for the rates estimated from the incubated bottles while the line shows the rates estimated from Vollenweider's equation (Eq. (1)) fitted to the incubation results ($R^2 = 0.989$).

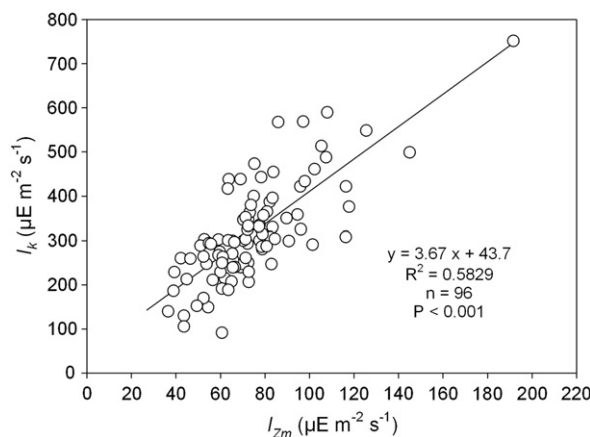


Fig. 7. Linear regression of the onset of light saturation of the phytoplankton (I_k) against average light in the mixed layer (I_{zm}); data from ^{14}C incubations in Lake Kivu, Ishungu station (southern basin), 2002–2008.

Table 2

Results of multiple linear regressions with forward stepwise selection between P_{Bm} as dependent variable and sample coordinates along the first 4 axes of the PCA with HPLC results and seston C:P and C:N ratios as explanatory variables, $n = 96$.

Variables	Coefficient	P	R ²
Origin	+3.560	<0.001	0.658
PCAaxis1	+2.001	<0.001	
PCAaxis2	+1.196	<0.001	

P_{Bm} was significantly correlated to both intracellular nutrient quota and phytoplankton taxonomic composition described by the principal components of a PCA. As the effects of nutrient supply and phytoplankton taxonomic composition are confounded in our field study, we cannot distinguish their respective role in controlling P_{Bm} . It was demonstrated that N limitation in microalgae limits the amount of Chla and RubisCO, the key enzyme involved in photosynthetic fixation of carbon dioxide (CO₂) (Geider and MacIntyre, 2002; Turpin, 1991) and that P_{Bm} parallels N content in N-limited algae (Geider et al., 1998). Moreover, P starvation limited also P_{Bm} and the contribution of RubisCO to cell protein in *Dunaliella tertiolecta* Butcher (Geider et al., 1998).

Nevertheless, the best prediction of P_{Bm} in Lake Kivu was obtained by a regression model including the first principal component of a PCA analysis, used as synthetic descriptor of the phytoplankton taxonomic composition. This approach generated estimates of P_{Bm} which depended primarily on the dominant phytoplankton groups according to season. We were able to calculate P_{Bm} specific to each important taxonomic group: 1.13 g C g Chla⁻¹ h⁻¹ for cyanobacteria, 2.36 for cryptophytes, and 7.21 for diatoms. The physiological basis for these large differences among phytoplankton depends on inorganic C fixation mechanisms and therefore on the specific properties of RubisCO, as discussed by Tortell (2000). Indeed, RubisCO exists in different forms in photosynthetic organisms (Falkowski and Raven, 2007) and differs largely in affinity and specificity for CO₂. The specificity is measured by the ratio between the CO₂ fixation rate and the O₂ fixation rate when CO₂ and O₂ are at limiting concentrations: the higher the value of the ratio, the higher the affinity for CO₂ relative to O₂ (Falkowski and Raven, 2007). Most cyanobacteria, including *Synechococcus* sp., abundant in tropical lakes (Sarmiento, 2012), have high affinity and low specificity, whereas diatoms are among the eukaryotes having the lowest affinity and highest specificity (Falkowski and Raven, 2007; Tortell, 2000). This would give diatoms a higher inherent capacity for C-fixation relative to photorespiration and may explain the high P_{Bm} we found for this phytoplankton group.

The irradiance at the onset of light saturation, I_k , was highly correlated to the average light in the mixed layer, I_{Zm} (Fig. 7). For a given taxon,

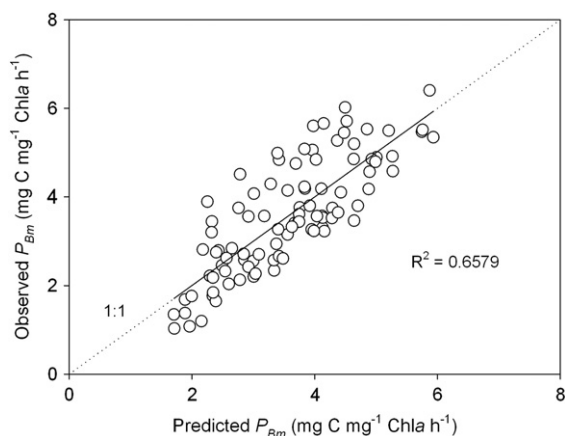


Fig. 8. Plot of observed vs predicted photosynthetic capacity (P_{Bm}) of the phytoplankton in Lake Kivu, Ishungu station (southern basin), 2002–2008.

Table 3

Sensitivity analysis of the daily primary production model. Each variable was replaced by its mean in turn while holding all other variables at their original values. The main absolute relative error of daily primary production (MARE, in %) was computed for each variable. A high value indicates that the model is sensitive to the variable. Variables are classified by decreasing order of MARE.

Variables	Mean	MARE
Biomass	0 m: 2.44 mg Chla m ⁻³ 10 m: 2.26 mg Chla m ⁻³ 20 m: 1.95 mg Chla m ⁻³ 30 m: 1.12 mg Chla m ⁻³ 40 m: 0.55 mg Chla m ⁻³ 50 m: 0.32 mg Chla m ⁻³ 60 m: 0.17 mg Chla m ⁻³	38%
P_{Bm}^a	3.57 mg C mg ⁻¹ Chla h ⁻¹	27%
K_e (only directly) ^b	0.26 m ⁻¹	18%
I_k^c	318 μE m ⁻² s ⁻¹	17%
Z_m^d	21.6 m	17%
K_e^e	0.26 m ⁻¹	10%

^a P_{Bm} in the model is predicted by the algae community composition.

^b K_e influences the daily primary production both directly and indirectly (through its influence on I_k); in this line only the direct effect is evaluated.

^c I_k in the model is predicted by I_{Zm} , which is calculated from Z_m and K_e .

^d Z_m in the model influences I_{Zm} and therefore I_k .

^e The direct and indirect effects of K_e on the daily primary production is evaluated.

I_k is influenced by both temperature and available light (Kirk, 1994). Given the small range of temperature variation in tropical lakes, it is expected that I_k would be best predicted by available light in the mixed layer, which is itself, given by the relative constancy of I_0 in tropical regions, governed by the depth of the mixed layer (Z_m) and by the vertical light attenuation coefficient (K_e). A low I_k is characteristic of phytoplankton adapted to low light, i.e. able of developing their maximal photosynthetic rate at low mean irradiance induced by deep mixing, and having accessory photosynthetic pigments. This situation occurs in deep tropical lakes in the dry season conditions, selecting for diatoms, which are also favored by increased nutrient supply and reduced sedimentation losses (Reynolds, 2006b). In contrast, high I_k occurred in Lake Kivu when I_{Zm} was high due to stratification of the mixolimnion reducing the mixing depth, selecting for high-light-adapted phytoplankton, able to face N depletion, such as cyanobacteria. So, to a large extent, the variation of I_k in deep tropical lakes reflects seasonal variations of the environmental factors that contribute to determine the phytoplankton assemblage (Stenuite et al., 2007).

A key feature of Lake Kivu, already pointed out by Spigel and Coulter (1996), is the weak thermal gradient in the mixolimnion, due to its location at high altitude, where air temperature is lower than in the regions of the other East African great lakes. Then the density gradient in surface waters is always weak (Schmid and Wüest, 2012). Stratification conditions are therefore not constant during the rainy season and short mixing events may alternate with episodes of stratification (Fig. 2C). This leads to short periods of phytoplankton development out of the dry season, as observed by example during the rainy season 2006. On average, half of the annual primary production occurred nevertheless during the 4 months of the dry season. But exceptions to this general pattern are not rare: dry season phytoplankton peaks were not observed during 3 years (2002, 2005 and 2007) out of 7 (Fig. 2). Consequently, the absence of the dry season peak directly heavily impacted the mean annual primary production. For example, the absence of a complete mixing within the mixolimnion during the dry season 2007 led to a low annual primary production (143 g C m⁻² y⁻¹) compared to the situation in 2008 where a complete overturn of the mixolimnion was observed during the dry season, producing a high phytoplankton biomass over the whole mixed layer and an annual production of 278 g C m⁻² y⁻¹.

This demonstrates the sensitivity of tropical lakes to climate variability, as emphasized by several authors (e.g. Johnson and Odada, 1996; Descy and Sarmiento, 2008). If the weather conditions leading to the

Table 4

Volumetric (average in the euphotic zone) and total areal chlorophyll *a* (Chl_a) concentrations, mean annual primary production (PP) in the pelagic zone of the East African great lakes. ⁽¹⁾ Sarmento et al. (2012) and unpublished results (Jean-Pierre Descy, pers. comm.), ⁽²⁾ volumetric Chl_a from Descy et al. (2005), areal Chl_a and CNP data from Descy et al. (2006), PP data from Stenuite et al. (2007); ⁽³⁾ Bergamino et al. (2010) and unpublished results (Nadia Bergamino, pers. comm.); ⁽⁴⁾ Degenbol (1993); ⁽⁵⁾ Guildford et al. (2000); ⁽⁶⁾ Patterson et al. (2000); ⁽⁷⁾ Guildford et al. (2007); ⁽⁸⁾ Mugidde (1993); ⁽⁹⁾ Guildford and Hecky (2000); ⁽¹⁰⁾ Mugidde (2001); ⁽¹¹⁾ Silsbe (2004) using a photosynthetic quotient of 1.

		Chl _a (mg m ⁻³)	Chl _a (mg m ⁻²)	PP (g C m ⁻² y ⁻¹)
L. Kivu (southern basin)	2002	1.77	57	223
	2003	2.31	80	264
	2004	2.55	83	236
	2005	1.63	53	153
	2006	2.58	74	192
	2007	2.04	73	143
	2008	2.89	100	278
	Mean	2.23	74	213
L. Kivu (eastern basin) ⁽¹⁾	2005	2.11	91	
	2006	1.94	63	
	2007	2.03	65	
	2008	2.10	88	
	Mean	2.03	77	
L. Tanganyika (off Kigoma) ⁽²⁾	2002	0.64	36.4	123
	2003	0.59	37.3	130
	2004		35.8	
L. Tanganyika (off Mpulungu) ⁽²⁾	2002	0.71	38.3	175
	2003	0.73	41.3	205
	2004		34.4	
L. Tanganyika (whole lake) ⁽³⁾	2003	1.06	42.9	236
L. Malawi (pelagic) ⁽⁴⁾	1977–1981		27.0	271
	1990–1991	0.51	23.0	
	1992			329
	1993			518
	1997–2000	0.86	34.4	169
L. Victoria (near offshore) ⁽⁸⁾	1989–1991	24.5	330.8	1903 ^a
	1990	26.5		
	1992–1996			
	1994–1998	13.5		
L. Victoria (lake-wide averages) ⁽¹¹⁾	2000 ^b	10.7	116.5	1302/366 ^c
	2001 ^d	10.5	106.9	1350/236 ^c

^a Gross primary production estimated by the O₂ light and dark technique and converted into C using a photosynthetic quotient of 1.

^b Mean of the February and August 2000 cruises.

^c Respectively, gross and net primary productions estimated by the O₂ light and dark technique and converted into C using a photosynthetic quotient of 1.

^d Mean of the February and August 2001 cruises.

seasonal mixolimnion cooling and overturn are well understood, regional drivers of the inter-annual variability of the limnology of Lake Kivu are not yet explored. The East African climate was shown to be highly sensitive to sea-surface temperatures in the tropical Atlantic and Indian Oceans (Nicholson, 1996; Tierney et al., 2013). For example, the weather of the area centered around Lake Tanganyika is influenced by the El-Niño Southern Oscillation but timing and magnitude of this teleconnection are controlled by the local climate system (Plisnier et al., 2000).

Table 5

P values from Mann–Whitney *U* tests performed between individual East African great lakes for the variables and data presented in Table 4. Significant values at the 0.05 level are in bold.

	Volumetric Chl _a	Areal Chl _a	Net PP
Lake Kivu vs Lake Tanganyika	0.003	<0.001	0.234
Lake Kivu vs Lake Malawi	0.041	0.014	0.165
Lake Kivu vs Lake Victoria	0.003	0.014	0.241
Lake Tanganyika vs Lake Malawi	0.846	0.030	0.111
Lake Tanganyika vs Lake Victoria	0.012	0.023	0.118
Lake Malawi vs Lake Victoria	0.081	0.081	0.817

A comparison of phytoplankton biomass and production data from East African Great Lakes shows that volumetric and areal biomass in Lake Kivu was higher than in lakes Tanganyika or Malawi but lower than in Lake Victoria (Tables 4 and 5). However, the annual primary production in Lake Kivu was in the same range as that in lakes Tanganyika or Malawi and no statistical difference can be observed between the phytoplankton production of these lakes (Table 5). Severe eutrophication of Lake Victoria, resulting into the highest pelagic Chl_a biomass for the East African great lakes (Table 4), arose from an important increase of human-population and agricultural activity from the 1930s onwards in its drainage basin (Verschuren et al., 2002). Higher phytoplankton biomass is still observed in the littoral areas and in closed bays (see e.g. Silsbe et al., 2006). Despite this higher Chl_a concentration in Lake Victoria, the net particulate primary production in the pelagic of Lake Victoria is surprisingly in the same range as those of the other East African Great Lakes (Tables 4 and 5). This low net productivity is most probably caused by self-shading, reducing the euphotic layer and inducing low light availability, as described for many other eutrophic lakes (e.g. Hubble and Harper, 2001; Vareschi, 1982).

Higher nutrient concentrations are usually observed in surface waters of Lake Kivu than in Lake Tanganyika (Sarmento et al., 2006). Soluble reactive phosphorus (SRP) in the euphotic zone of Lake Kivu was on average 0.44 μM in rainy season and 0.75 μM in dry season in 2002–2005; mean SRP in the euphotic layer of Lake Tanganyika was 0.19 and 0.43 in rainy season and dry season, respectively, in 2002 off Kigoma (Sarmento et al., 2006). The average dissolved inorganic nitrogen (DIN) in Lake Kivu was 2.42 and 3.29 μM in the rainy season and the dry season, respectively. This contrast with lower DIN in Lake Tanganyika off Kigoma (mean rainy season DIN: 0.48 μM; mean dry season DIN: 0.69 μM). In Lake Malawi, annual means of total P and total N were 0.25 and 6.7 μM, respectively (Guildford et al., 2000). So, if Lake Kivu presents higher P concentrations in surface waters than in lakes Tanganyika and Malawi, Lake Malawi presents higher N concentrations than the other two lakes. Nevertheless phytoplankton of the three lakes present periods of single or combined N and/or P limitations (De Wever et al., 2008; Guildford et al., 2003; Sarmento et al., 2012). Differences in nutrient concentrations, and especially P, between these lakes may help to explain the higher phytoplankton biomass we observed in Lake Kivu compared to lakes Tanganyika and Malawi.

An alternative but not exclusive hypothesis is linked to the food web structure, which allows a lower grazing pressure from the metazooplankton in Lake Kivu than in the other large Rift lakes. In 1959, *Limnothrissa miodon* Boulenger, a clupeid endemic to Lake Tanganyika, was introduced into Lake Kivu (Snoeks et al., 2012) in order to fill the empty pelagic niche and provide proteins for the local population. The planktivorous “Tanganyika sardine” may have led to the extinction of the cladoceran *Daphnia curvirostris* Eylmann, an efficient grazer and nutrient recycler (Dumont, 1986), which was presumably present in the lake in the 1950s. The current zooplankton is dominated by cyclopoid copepods, which are less efficient grazers (Isumbisho et al., 2006). Further, predation by the sardine has led to a reduction of zooplankton biomass, which has reduced the top-down control over phytoplankton (Darchambeau et al., 2012). The absence of an efficient grazer in Lake Kivu, as those present in lakes Tanganyika and Malawi, may help to explain why phytoplankton biomass observed in Lake Kivu is relatively high, despite phytoplankton productivity is of the same magnitude as in lakes Malawi and Tanganyika.

Huge amounts of CO₂ and methane (CH₄) (300 km³ and 60 km³, respectively, at 0 °C and 1 atm) are dissolved in the deep water layers of Lake Kivu (Degens et al., 1973; Schmid et al., 2005). Around one third of CH₄ originates from acetoclastic methanogenesis of sedimentary organic material, the other two thirds is produced by reduction of geogenic CO₂ (Schoell et al., 1988; Pasche et al., 2011). Deep gas concentrations increased by 15–20% for CH₄ and 10% for CO₂ in the past 30 years (Schmid et al., 2005). In an attempt to explain the increase of CH₄ concentrations in deep waters, Schmid et al. (2005) simulated the

CH₄ production along the 990 last years. They concluded that the historical CH₄ production rate rose from an historical constant production rate of 30 g C m⁻² y⁻¹ to 100 g C m⁻² y⁻¹ between 1974 and 2004. Such a 3-fold increase would have been possible if an equivalent increase of primary production in the mixolimnion had occurred. In order to evaluate a possible increase of primary production in the lake, few historical data are available: Degens et al. (1973) and Jannasch (1975) reported a range of mean daily production of, respectively, 1.03–1.44 g C m⁻² d⁻¹ and 0.66–1.03 g C m⁻² d⁻¹, whereas Descy (1990) measured a rate of 0.33 g C m⁻² d⁻¹ in the pelagic zone. According to our estimates, the present daily primary production in Lake Kivu spans over a wide range of values, from 0.14 to 1.92 g C m⁻² d⁻¹, with a mean of 0.62 g C m⁻² d⁻¹. This range of variation covers well the few historic observations, allowing the conclusion that there was no important change of the lake's primary production in the pelagic zone over the last 40 years.

Other hypotheses than lake eutrophication for explaining the CH₄ increase should then be envisaged. These hypotheses would involve an increased net sedimentation flux of C and nutrients due to environmental modifications as observed from analyses of sediments cores (Pasche et al., 2010, 2011). Among these modifications, the introduction of the Tanganyika sardine, *L. miodon*, at the end of the 1950s might have been a key event leading to ecological and geochemical changes. The possible consequences of this introduction, involving a trophic cascade effect with a reduction of the grazing pressure on phytoplankton and a subsequent increase of net sedimentation of organic matter, are further discussed by Darchambeau et al. (2012) and Descy et al. (2012). However, the extent of the changes in the food web is still difficult to evaluate from the present data, and an improved understanding will likely result from further paleolimnological studies based on various proxies of past productivity and phytoplankton composition.

Conflict of interest

There is no conflict of interest.

Acknowledgments

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