Chapter 5
Phytoplankton of Lake Kivu

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Abstract This chapter reviews taxonomic composition, biomass, production and nutrient limitation of the phytoplankton of Lake Kivu. Present Lake Kivu phytoplankton is dominated by cyanobacteria – mainly *Synechococcus* spp. and thin filaments of *Planktolyngbya limnetica* – and by pennate diatoms, among which *Nitzschia bacata* and *Fragilaria danica* are dominant. Seasonal shifts occur, with cyanobacteria developing more in the rainy season, and the diatoms in the dry season. Other groups present are cryptophytes, chrysophytes, chlorophytes and dinoflagellates. According to a survey conducted in the period 2002–2008, the composition of the phytoplankton assemblage was quasi homogeneous among lake basins. The mean euphotic depth varied between 17 and 20 m, and the increase in the ratio between mixed layer depth and euphotic depth to about 2 in the dry season may have selected for diatoms and cryptophytes, which tended to present their maximal development in this season, when cyanobacteria slightly decreased. Mean chlorophyll *a* concentration was 2.16 mg m^{-3}, and the mean daily primary production was 0.62 gC m^{-2} day^{-1} (range, 0.14–1.92), i.e. in the same range as in other large oligotrophic East African Rift lakes. Seston elemental

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ratios indicated a moderate P-deficiency during the dry, mixed season and a severe P limitation during part of the rainy, stratified season; the C:N ratio indicated a moderate N limitation throughout the year. Nutrient addition assays pointed to a direct N-limitation and co-limitation by P during rainy seasons and P or N limitation during dry seasons depending on the year. Thus, phytoplankton ecology in Lake Kivu does not differ from that of other Rift lakes, where seasonal variations result in a trade-off between low light with high nutrient supply and high light with low nutrient supply. Phytoplankton production in Lake Kivu is also similar to that of other Rift lakes, and nutrient limitation of phytoplankton growth may occur as a result of variable availability of N and P, as in Lakes Tanganyika and Malawi, even though the extent of P limitation seems greater in Lake Kivu.

5.1 Introduction

Because of its large size, substantial depth and consequently reduced littoral zone, the ecological functioning of the mixolimnion of Lake Kivu is dominated by pelagic processes, among which phytoplankton photosynthesis supplies the bulk of the organic carbon available for the food web. In this way, the pelagic ecosystem of Lake Kivu is not different from that of the other oligotrophic African Rift lakes, where strong seasonal changes occur, imposing contrasting constraints on phytoplankton growth, resulting in substantial shifts of the composition and biomass of the planktonic assemblages (Hecky and Kling 1987). Since the earlier studies carried out in the first half of the twentieth century, it was suspected that large variations of phytoplankton abundance occurred in Lake Kivu, but, besides taxonomic lists, few data were available (Beadle 1981). Despite the perception of its oligotrophic status by Damas (1937), Lake Kivu was described as more productive than Lake Tanganyika, based on few data on net plankton abundance (Hecky and Kling 1987). Indeed, subsequent studies confirmed that, in recent years, chlorophyll *a* concentration in the pelagic waters of Lake Kivu was two to three times as high as in Lake Tanganyika and Malawi (Sarmento et al. 2009). But is Lake Kivu "more eutrophic" than Lake Tanganyika (Sarvala et al. 1999)? Is its primary productivity higher than that of the other deep Rift lakes?

Here we review the literature on the autotrophic plankton of Lake Kivu: its taxonomic composition, abundance, production and ecology. Additionally, we summarise the results of the most complete limnological and planktological survey ever realised in Africa, and probably in a tropical lake. The first aim of this review is to establish a well-documented and updated picture of the pelagic phytoplankton of Lake Kivu, which can be used as a reference for the future generations of researchers and naturalists, as well as a baseline for the lake monitoring to evaluate potential effects of the ongoing gas extraction (Chap. 10).

5.2 Light Conditions

Light is an essential factor determining primary productivity and phytoplankton assemblages in aquatic systems (Reynolds 2006). Contrarily to the common sense, light limitation in tropical aquatic systems is relatively common: numerous shallow polymictic lakes receive large amounts of suspended matter due to erosion (e.g. Mukankomeje et al. 1993); in others, like Lake Victoria, phytoplankton is light-limited due to high biomass after eutrophication producing a self-shading effect (Mugidde 1993; Kling et al. 2001). In deep lakes light can equally become a limiting factor as soon as the depth of the upper mixed layer (Zm) reaches or exceeds the depth of the euphotic zone (Zeu), depth at which the light intensity drops to 1% of the surface incident light. In such periods, the Zm:Zeu ratio is larger than 1 and light harvesting by primary producers becomes a selective factor shaping phytoplankton composition (Sarmento et al. 2006).

In Lake Kivu, the Zm:Zeu ratio is often larger than 1, especially during the deep mixing periods, more frequent in the dry season (Fig. 5.1), when Zm often exceeds 50 m (typically occurring between June and September). Although water transparency is higher, on average, during the dry season (mean Zeu = 19.8 m) than during the rainy season (17.1 m), it is during that period that phytoplankton experiences the lowest light conditions, and this is reflected in shifts in the phytoplankton composition (discussed below).

The water transparency co-varies seasonally in a similar range in both the main basin and Ishungu basin (Fig. 5.1). However, the dry season winds may disproportionally affect the main basin, which is more exposed to wind than the Ishungu basin, resulting in more intense vertical mixing in the main basin (Fig. 5.1).

5.3 Taxonomic Composition

The first relevant scientific information concerning the plankton of Lake Kivu is from the mid 1930s, when H. Damas carried out an expedition to the "Parc National Albert" (Damas 1935–1936, 1937). The 55 net samples collected from Lake Kivu were studied by several phycologists and the results were published in two issues of the publication of the Institut of National Parks of Belgian Congo devoted to the Mission H. Damas: fasc. 8 "Süsswasser-Diatomeen" by Hustedt (1949) for the diatoms, and fasc. 19 "Algues et Flagellates" by Frémy et al. (1949) for several other groups of algae, namely Cyanobacteria (P. Frémy), Chrysophyta, Pyrrhophyta, Euglenophyta, Volvocales (A. Pascher), Heterokontae, Protococcales, Siphonocladales (W. Conrad). In the samples from Lake Kivu, 157 species and intraspecific taxa of diatoms were found (including benthic and epiphytic samples); 12 were described as new species. The most common diatoms in the main basin were *Nitzschia confinis* Hust., *N. lancettula* O. Müller, *N. tropica* Hust., *N. gracilis* Hantzsch and *Synedra* (now *Fragilaria*) *ulna* (Nitzsch) Ehrenb. Among the

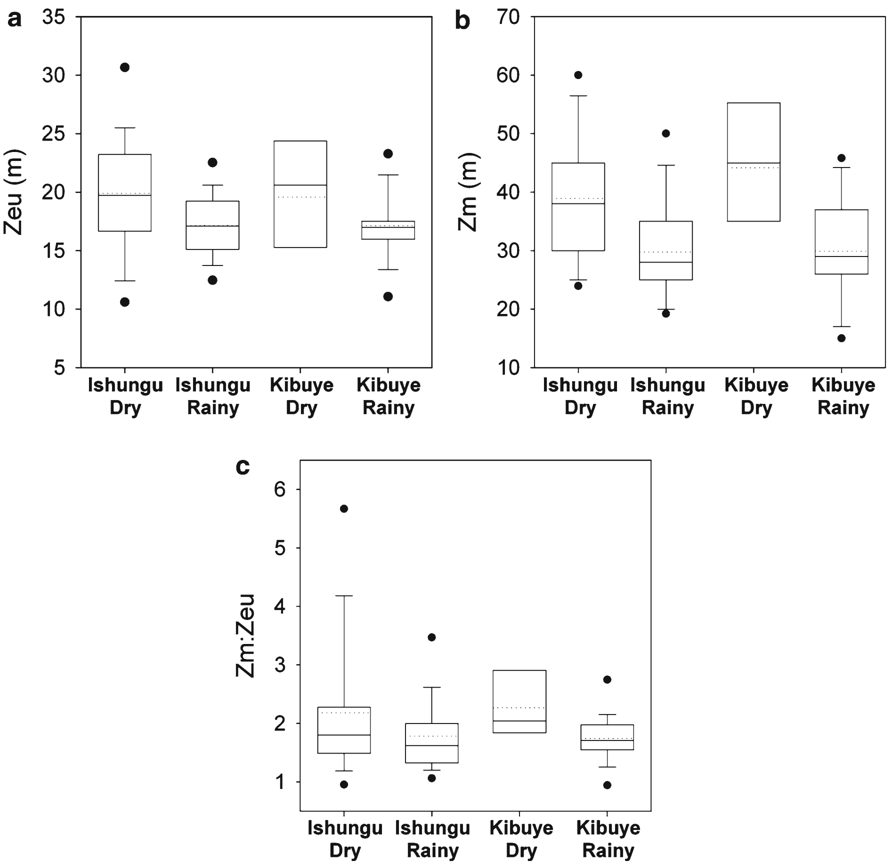

Fig. 5.1 Box plots of (**a**) the euphotic layer depth (Zeu), (**b**) the mixed layer depth (Zm) and (**c**) the Zm:Zeu ratios. Data from two sampling stations (located in Ishungu basin and in the main basin off Kibuye, see Fig. 2.1) and two seasons (rainy vs. dry) are compared. The central full line indicates the median value, the middle dotted line indicates the arithmetic mean values, the box indicates the lower and upper quartiles, the error bars indicate the 10th and 90th percentiles, and the dots correspond to the 5th and 95th percentiles

cyanobacteria, *Microcystis flos-aquae* (Wittrock) Kirchner was the most frequent, together with other *Microcystis* species, such as *M. aeruginosa* (Kütz.) Kütz. and *M. ichthyoblabe* Kütz., and a few planktonic *Lyngbya* (especially *L. circumcreta* West and *L. contorta* Lemm.). Among the other groups, *Botryococcus braunii* Kütz. and *Chlorella vulgaris* Beijerinck were rather abundant, together with several species of *Pediastrum* and *Scenedesmus*. Two new green algae were described from Lake Kivu: *Cosmarium kivuense* Conrad and *Scenedesmus cristatus* Conrad ex Duvigneaud. The data from the Damas' expedition were used by Van Meel (1954) in his book on the phytoplankton of East African great lakes, but without any new addition to the knowledge of the algal flora of Lake Kivu.

Later, in diatom physiology studies, Kilham et al. (1986) and Kilham and Kilham (1990) discussed the *Nitzschia* – *Stephanodiscus* dominance gradient in the sediments of the lake in the different basins, following a Si:P gradient, and Haberyan and Hecky (1987), in a paleoclimatological study, reported several diatoms and scales of *Paraphysomonas vestita* Stokes (Chrysophyceae) in sediments cores. Drastic changes were recorded around 5,000 years BP in the fauna and flora of the lake, in particular the disappearance of *Stephanodiscus astraea* var. *minutula* (Kütz.) Grunow (an uncertain taxon, see Spamer and Theriot 1997), and the replacement by several needle-like *Nitzschia*. The authors suggested that the cause of this shift may have been the hydrothermal input of CO_2 into the lake due to high volcanic activity in the region, which would have caused lake turnover and consequent disappearance of the plankton by anoxia, extremely low pH or toxic gases.

In a comparative study of the composition and abundance of phytoplankton from several East African lakes, Hecky and Kling (1987) reported for Lake Kivu an algal assemblage dominated by cyanobacteria and chlorophytes, with higher biomass than in Lake Tanganyika. These authors reported *Lyngbya circumcreta* West, *Cylindrospermopsis*, *Anabaenopsis* and *Rhaphidiopsis* as the dominant algae found in settled samples collected in March 1972. Among the green algae, *Cosmarium laeve* Rab. was the most common species. In the northern basin, *Peridinium inconspicuum* Lemm., *Gymnodinium pulvisculus* Klebs and *Gymnodinium* sp. were considerably abundant, whereas diatoms *Nitzschia* and *Synedra* (now included in *Fragilaria*) were abundant only in the isolated Kabuno Bay.

The pelagic flora of Lake Kivu was recently updated with new samples from a long term monitoring survey (Sarmento et al. 2007), in which the most common species (Fig. 5.2) were the pennate diatoms *Nitzschia bacata* Hust. and *Fragilaria danica* (Kütz.) Lange Bert., and the cyanobacteria *Planktolyngbya limnetica* (Lemm.) Komárková-Legnerová and Cronberg. Additionally, the picocyanobacterium *Synechococcus* sp. was shown to constitute a major compartment of the autotrophic plankton in Lake Kivu, with persistently high abundances (~10^5 cells mL^{-1}) throughout the year (Sarmento et al. 2008).

Another important missed (or not reported) aspect in past studies were the high abundances of the centric diatom *Urosolenia* sp. and the cyanobacterium *Microcystis* sp. near the surface under diel stratification conditions (Sarmento et al. 2007). Typical deep epilimnion/metalimnion populations with species such as *Cryptaulax* sp., *Cryptomonas* sp., *Rhodomonas* sp. and *Merismopedia trolleri* Bach were also described. Vertical stratification at different time scales, from day to season, creates a range of different growing conditions that remain stable long enough to allow the development of these segregated phytoplankton populations in specific layers of the water column. This constitutes an important factor of diversification in Lake Kivu.

5.4 Biomass and Production

Historical data on limnology and planktology parameters of Lake Kivu are scarce, and no long-term surveys had been conducted before the year 2002. Hecky and Kling (1987) reported phytoplankton fresh weight biomass from 550 up to 2,100 mg m^{-3} for March 1972 surface samples. Similar to other East African large

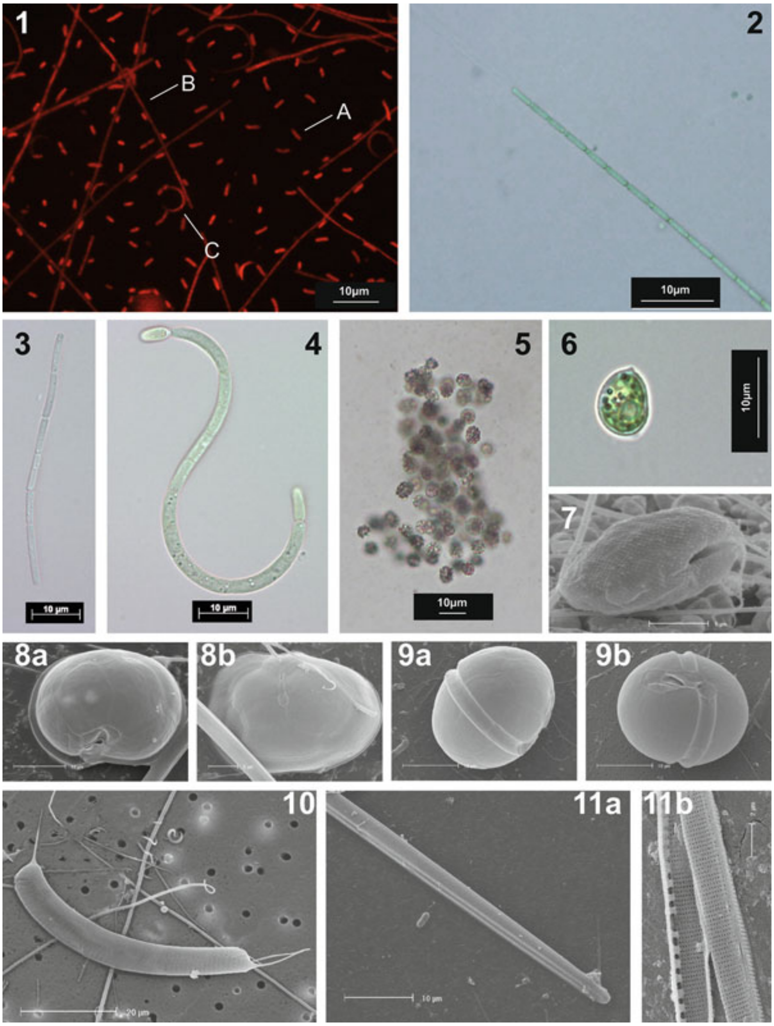

Fig. 5.2 Main phytoplankton taxa present in Lake Kivu. 1. A – *Synechococcus* spp., B – *Planktolyngbya limnetica* (Lemm.) Komárková-Legnerová and Cronberg, C – *Monoraphidium contortum* (Thur.) Kom.-Legn. (epifluorescence microscope); 2. *Planktolyngbya limnetica* (Lemm.) Kom.-Legn. and Cronberg; 3. *Pseudanabaena moniliformis* Kom. and Kling; 4. *Cylindrospermopsis af. curvispora* Wat.; 5. *Microcystis* sp.; 6. *Tetraëdron minimum* (A. Braun) Hansg.; 7. *Cryptomonas* sp.; 8a, b. *Peridinium umbonatum* Stein; 9a, b. *Peridinium* sp.; 10. *Urosolenia* sp.; 11a. *Nitzschia bacata* Hust. (11b. detail of fibulae median interruption). Each scale bar is 10 µm

lakes, the planktonic assemblage of Lake Kivu at that time appeared to be dominated to 70–90% by chlorophytes and cyanobacteria, with diatoms at lower abundances (Hecky and Kling 1987). Another trait of Lake Kivu revealed in that study was its higher algal biomass than in the larger Lakes Malawi and Tanganyika, and a slightly higher primary production: 1.44 g C m^{-2} day^{-1} reported by Beadle (1981), which is an estimate based on few measurements carried out in the 1970s by geochemists (Degens et al. 1973; Jannasch 1975).

In a more complete limnological survey carried out in 2002–2004 (Isumbisho 2006; Isumbisho et al. 2006; Sarmento 2006; Sarmento et al. 2006) phytoplankton biomass and composition were assessed combining diverse complementary techniques such as HPLC analysis of marker pigments and CHEMTAX processing, flow cytometry, and epifluorescence and electron microscopy. Annual average chlorophyll *a* (Chl *a*) in the mixed layer was 2.16 mg m^{-3} and the nutrient levels in the euphotic zone were low, placing Lake Kivu clearly in the oligotrophic range. Seasonal variations of algal biomass and composition were related to variability of wind pattern and water column stability. Contrary to earlier reports, diatoms were the dominant group, particularly during the dry season episodes of deep mixing. During the rainy season, the stratified water column, with high light and lower nutrient availability, favoured dominance of filamentous, diazotrophic cyanobacteria and of picocyanobacteria.

Additional data collected in the framework of a cooperation project (ECOSYKI, 2004–2009) extended the record to the year 2008, thus providing a long-term survey (2002–2008) of Lake Kivu phytoplankton (Fig. 5.3). The first striking aspect is the amplitude of the inter-annual variability of phytoplankton biomass peaks. Apparently, phytoplankton usually peaked during the dry season, but not systematically every year. In Ishungu basin, a phytoplankton bloom with a biomass higher than 100 mg Chl *a* m^{-2} was observed at the end of the dry season (July–August) in 2003, in 2004 and more spectacularly in 2008. A lower dry season peak was observed in 2006 and in 2007, but not in 2002 and in 2005. The variable intensity of the dry season mixing (see Chap. 2) may explain this variation in the phytoplankton biomass peaks.

Grouping the data by station and by season (dry season arbitrarily defined as the period comprised between 1st of June and 30th of September), we can estimate the degree of variance of the total phytoplankton biomass (Chl *a*) and the principal algal groups: diatoms, cyanobacteria and cryptophytes (Fig. 5.4). The dry season Chl *a* values are distributed in a more scattered way than the rainy season values, indicating that extreme and more variable events usually occurred during the dry season. Mean seasonal total biomass was higher during the dry season than during the rainy season in both the main basin and Ishungu basin (Table 5.1, Fig. 5.4). A closer analysis of the phytoplankton community structure indicates a clear seasonal signal: diatoms and cryptophytes were more abundant during the dry season, with a scattered distribution in the box plots, indicating the formation of high biomass peaks during short periods of time, while cyanobacteria showed a more even distribution with slightly lower values during the dry season (Table 5.1, Fig. 5.4). There were no significant differences in the total biomass between the sampling stations, but diatoms and cryptophytes were more abundant in Ishungu basin, while cyanobacteria represented a higher proportion of the biomass in the main basin (Table 5.1, Fig. 5.4).

The vertical distribution of Chl *a* and the major groups of phytoplankton show the typical dominance of cyanobacteria during the stratified conditions of the

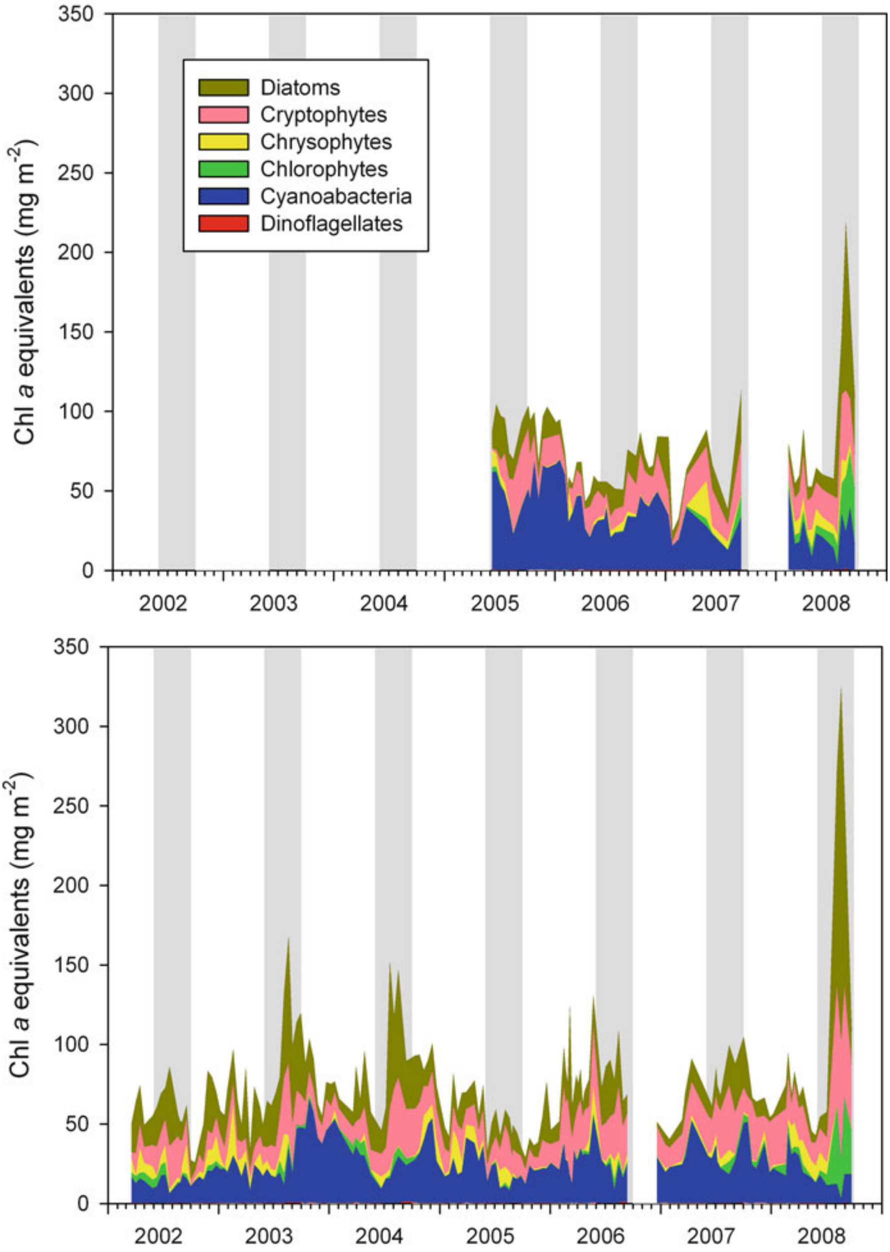

Fig. 5.3 Phytoplankton biomass (chlorophyll *a*, mg m^{-2}) and composition from pigment analysis in Lake Kivu integrated in the upper 70 m layer (2002–2008 period in Ishungu basin; 2005–2008 period in the main basin off Kibuye). Grey areas indicate the annual dry season (from June to September)

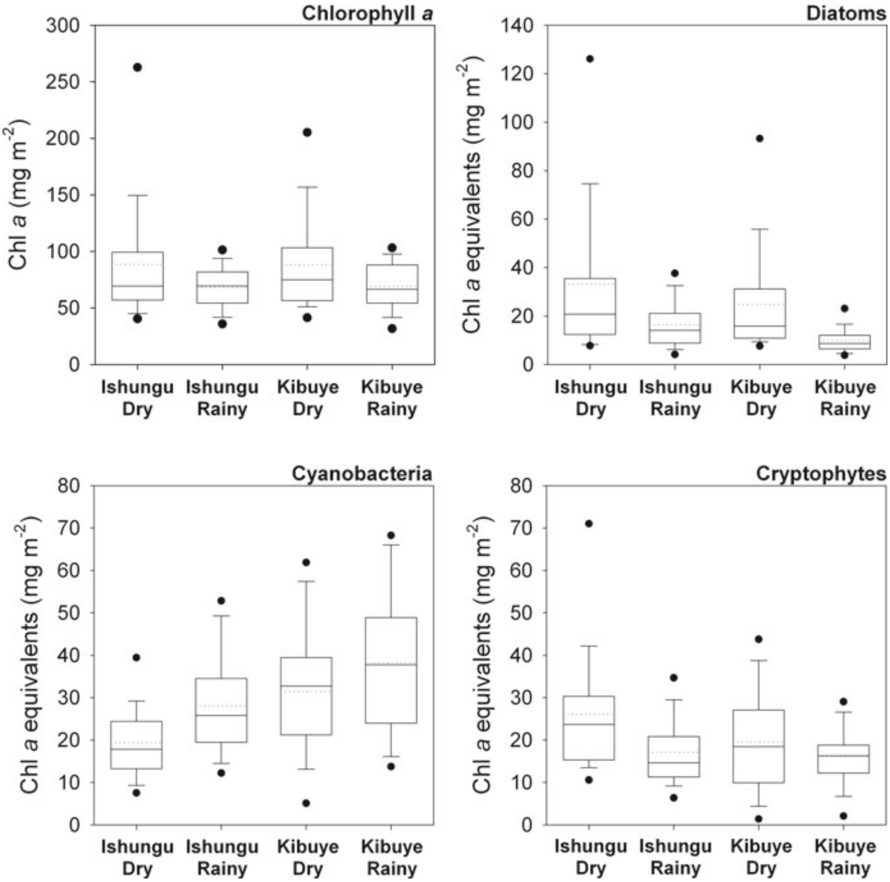

Fig. 5.4 Box plots of the total biomass (chlorophyll *a*, mg m^{-2}) and the major groups of phytoplankton in Lake Kivu. Data from two sampling stations (located in Ishungu basin and in the main basin off Kibuye) and two seasons (rainy vs. dry) are compared. The central full line indicates the median value, the middle dotted line indicates the arithmetic mean value, the box indicates the lower and upper quartiles, the error bars indicate the 10th and 90th percentiles, and the dots represent the 5th and 95th percentiles

Table 5.1 Statistical significance (*p* values of full factorial ANOVA tests with log-transformed data) of the comparison between basins (main vs. Ishungu) and seasons (rainy vs. dry) of the biomass (integrated values over the upper 70 m) of the main phytoplankton groups in Lake Kivu estimated from pigments

Effect	Chlorophyll *a*	Diatoms	Cyanobacteria	Cryptophytes
Basin	0.641	**0.003**	**<0.001**	**0.006**
Season	**0.002**	**<0.001**	**<0.001**	**0.008**
Basin × Season	0.796	0.192	0.321	0.082

Significant values at the 0.05 confidence level are highlighted

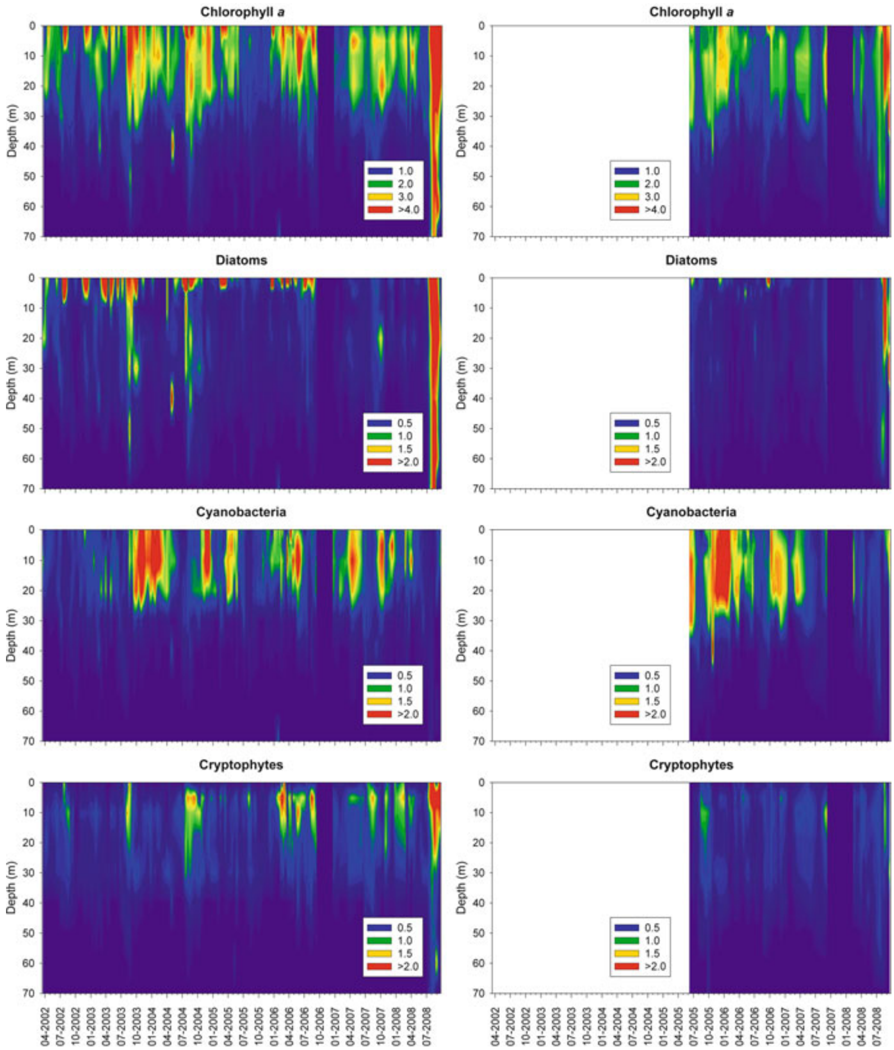

Fig. 5.5 Vertical distribution of the total biomass (chlorophyll *a* , mg m^{-3}) and the major groups of phytoplankton in Ishungu basin during the 2002–2008 period (left column) and the main basin off Kibuye during the 2005–2008 period (right column) in Lake Kivu. Clear areas correspond to missing data

rainy season on the top 20–30 m of the water column (Fig. 5.5). Regularly, during the dry season, lower air temperature (notably night cooling) induced deep mixing, which brought up additional nutrients into the euphotic layer, enhancing phytoplankton and especially diatom growth (Sarmento et al. 2006). The persistence and intensity of these seasonal mixing events may determine the productivity of the lake for the whole year, and most likely affect consumer production and ultimately fisheries yield.

The recent analysis of 96 field photosynthesis-irradiance incubations carried out over the 6 year survey allowed a completion of the planktonic primary production data set of Sarmento et al. (2009), and to design a model for prediction of phytoplankton photosynthesis parameters. The irradiance at the onset of light saturation (Ik) ranged between 91 and 752 μE $m^{-2} s^{-1}$ (mean, 318) and was linearly correlated with the mean irradiance in the mixed layer. The maximum photosynthetic rate (Pmax) ranged between 1.15 and 7.21 gC g Chl $a^{-1} h^{-1}$ (mean, 3.57). The mean observed daily primary production was equal to 0.62 gC $m^{-2} day^{-1}$ (range, 0.14–1.92), and annual primary production, calculated using modeled values of photosynthetic parameters, varied between 138 g C $m^{-2} year^{-1}$ in 2005 and 258 g C $m^{-2} year^{-1}$ in 2003. The mean annual primary production from 2002 to 2008 was 211 gC $m^{-2} year^{-1}$. These data clearly show that the inter-annual variation of phytoplankton production in Lake Kivu was important. This large range of variation and the few historic observations, 1.03–1.44 gC $m^{-2} day^{-1}$ by Degens et al. (1973), 0.66–1.03 g C $m^{-2} day^{-1}$ by Jannasch (1975) and 0.33 g C $m^{-2} day^{-1}$ by Descy (1990), preclude to detect any significant changes of planktonic primary production during the last 30 years.

A comparison of phytoplankton production data from East African Great Lakes (Table 5.2) shows that primary production in Lake Kivu is not greater than that in Lakes Tanganyika or Malawi, taking into account the differences in methodologies, as well as spatial heterogeneity as revealed by analysis of satellite images (Bergamino et al. 2010). This contrasts with expectations from Chl *a* concentration: mean Chl *a* in the euphotic zone of Lake Kivu (2.16 mg m^{-3}) is at least twice as high as in Lake Tanganyika – 1.07 mg m^{-3} (2003) – and in Lake Malawi – 0.86 mg m^{-3} (Guildford and Hecky 2000). This observation holds even when taking into account the great interannual variation, with a minimum mean annual Chl *a* of 1.59 mg m^{-3} in the least productive year (2005) and a maximum of 2.94 mg m^{-3} in the most productive year (2008).

5.5 Nutrient Limitation

The seston elemental ratios in the mixolimnion of Lake Kivu always remain well above the Redfield ratio and follow a clear seasonal pattern (Fig. 5.6). Significantly lower mean values of C:N, C:P and N:P ratios were observed during the dry season (arbitrarily defined as the period comprised between 1st of June and 30th of September) than during the rainy season ($p < 0.05$). Following elemental thresholds defined by Healey and Hendzel (1980) to estimate nutrient deficiency of phytoplankton in lakes (a C:N ratio between 8.3–14.6 indicates a moderate N-deficiency while a C:N ratio > 14.6 indicates an extreme N-deficiency; a C:P ratio between 129–258 or >258 indicates, respectively, a moderate or an extreme P-deficiency), the C:P ratios of seston in Lake Kivu indicated a moderate P-deficiency during the dry, mixing season and a severe P limitation during part of

Table 5.2 Chlorophyll *a* concentration (Chl *a*, average in the euphotic zone, standard deviation in parentheses) and mean annual phytoplankton production (PP) in the East African Great Lakes

	Chl *a* (mg m^{-3})	Chl *a* (mg m^{-2})	PP (g C m^{-2} $year^{-1}$)
L. Kivu (Ishungu basin)			
2002	1.78 (0.63)	59 (17)	223
2003	2.32 (0.78)	80 (30)	258
2004	2.54 (0.77)	86 (28)	241
2005	1.67 (0.63)	53 (15)	138
2006	2.58 (0.70)	79 (21)	223
2007	2.05 (0.44)	71 (18)	144
2008	2.95 (2.09)	112 (92)	252
Mean 2002–2008	2.24 (0.99)	75 (39)	211
L. Kivu (main basin)			
2005	2.11 (0.49)	91 (13)	
2006	1.94 (0.42)	63 (16)	
2007	2.03 (1.04)	65 (25)	
2008	2.10 (1.20)	88 (48)	
Mean 2005–2008	2.03 (0.78)	77 (32)	
L. Tanganyika (2002–2003)[a]			
Off Kigoma – 2002		23.4	123
Off Kigoma – 2003		25.0	130
Off Mpulungu – 2002		21.7	175
Off Mpulungu – 2003		29.9	205
L. Tanganyika (2003)[b]			
Whole-lake, from remote sensing	1.07	42.9	236
L. Malawi (1990s)[c]			
Pelagic (south)	0.86 (0.31)	34.4	169
L. Victoria (2001/2002)			
Lake-wide averages[d]			1061
Three inshore bays[e]	49.53	149.1	2333
Pilkington bay[f]	46.7		
Offshore (Bugaia)	24.5		

[a] Descy et al. (2005), Stenuite et al. (2007)
[b] Bergamino et al. (2010)
[c] Guildford et al. (2007)
[d] Silsbe (2004)
[e] Recalculated from Silsbe et al. (2006)
[f] Mugidde (1993)

the rainy, stratified season. The C:N ratios indicated however a moderate N limitation throughout the year, except at some dates during the dry, mixing season where no N-limitation occurred. A comparison of mean values (Table 5.3) from other East African large lakes suggests a stronger nutrient limitation in Lakes Kivu and Malawi than in Lakes Tanganyika and Victoria. The relatively high C:N and C:P ratios point to co-limitation of the phytoplankton community by N and P in Lake Kivu.

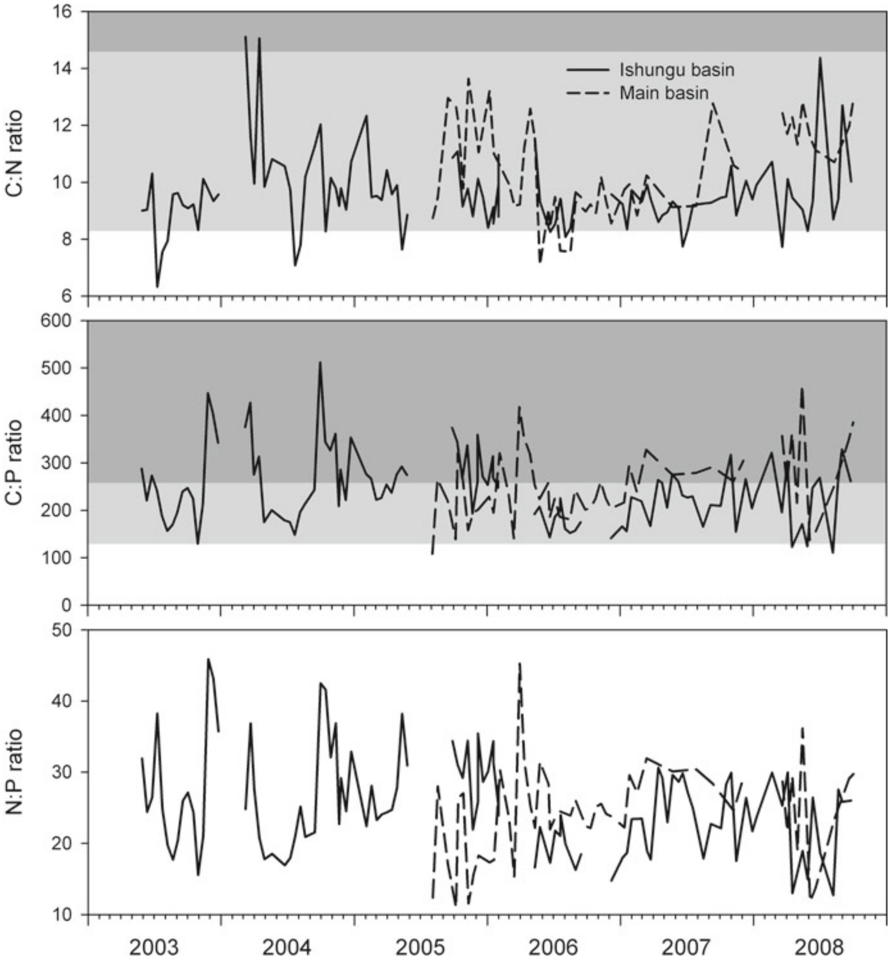

Fig. 5.6 C:N:P elemental ratios (atomic values) of epilimnetic seston in both the main basin and Ishungu basin of Lake Kivu from 2003 to 2008. The light and dark grey areas highlight values indicative of moderate and extreme nutrient limitation, respectively, following Healey and Hendzel (1980)

Table 5.3 C:N:P ratios (elemental values) and chlorophyll *a* (Chl *a*, mg m^{-3}) in the East African Great Lakes (average and standard deviation in the euphotic zone)

	C:P	C:N	N:P	Chl *a* (mg m^{-3})
L. Kivu (Ishungu basin)	243.8 (±73.6)	9.6 (±1.4)	25.4 (±6.8)	2.24 (±0.99)
L. Kivu (main basin)	251.4 (±75.1)	10.5 (±1.7)	24.3 (±6.7)	2.02 (±0.78)
L. Tanganyika[a]	170.8 (±43.3)	8.1 (±1.1)	21.2 (±5.3)	0.67 (±0.25)
L. Malawi[b]	244.3 (±154.4)	12.5 (±3.6)	19.4 (±8.8)	1.40 (±2.00)
L. Victoria[b]	148.5 (±76.4)	8.2 (±1.7)	18.3 (±7.6)	26.50 (±15.90)

[a] Stenuite et al. (2007)

[b] Guildford and Hecky (2000)

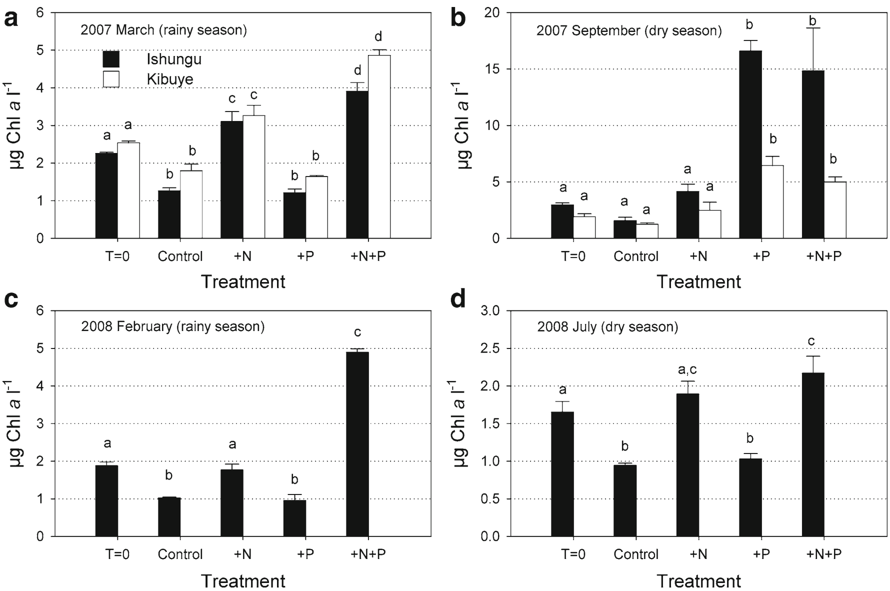

Fig. 5.7 Phytoplankton biomass (chlorophyll *a*, μg Chl *a* l^{-1}) after 4–5 days of incubation at lake temperature in six nutrient addition bioassay experiments carried out during rainy (**a** and **c**) and dry (**b** and **d**) seasons in Lake Kivu. The +N treatment received additional 15 μM NH_4Cl (final concentration), the +P treatment received 5 μM KH_2PO_4 (final concentration), while both N and P supplements were added in the +N+P treatment. All treatments were performed in triplicates. Note the different biomass scales. Identical small letters indicate treatments with no significant difference between biomass at the 0.05 confidence level (Scheffé test)

Nutrient addition assays carried out during rainy and dry seasons in 2007 and 2008 indicated a direct N-limitation and co-limitation by P during rainy seasons (Fig. 5.7a, c) and P or N limitation during dry seasons depending on the year (Fig. 5.7b, d).

5.6 Conclusions

Present Lake Kivu phytoplankton is dominated by diatoms, cyanobacteria and cryptophytes, with substantial seasonal shifts related to variations in depth of the mixed layer, driving contrasting light exposure, and nutrient availability. In this regard, phytoplankton ecology in Lake Kivu does not differ from that of other Rift lakes, where, despite constant irradiance and temperature of the tropical climate, seasonal variations occur and result in a trade-off between low light with high nutrient supply and high light with low nutrient supply. With regard to phytoplankton production, Lake Kivu is also similar to other Rift lakes, despite its greater mean Chl *a* concentration. Phytoplankton growth can be N or P limited, or co-limited by N and P.

Again, such limitations have been shown in Lakes Tanganyika and Malawi, even though the extent of P limitation seems greater in Lake Kivu, giving some indication of less nutrient recycling in the mixolimnion.

However, some features make Lake Kivu different from the other deep East African lakes: a closer look at the phytoplankton composition reveals a peculiar assemblage, with few chlorophytes, but long and slender *Nitzschia* and *Fragilaria* species, thin filamentous cyanobacteria (e.g., *Planktolyngbya limnetica*), picocyanobacteria, and several cryptophytes. In the surface waters, relatively large biomass of *Urosolenia* sp. can be detected at times, and colonies of *Microcystis* make vertical migration, sometimes becoming visible at the lake surface. Therefore, phytoplankton composition suggests affinities with more productive East African Lakes, such as Lakes Edward and Victoria, from a functional group perspective as discussed in Sarmento et al. (2006). As for the higher chlorophyll *a* concentration in Lake Kivu, it may have resulted from the Tanganyika sardine introduction, through a trophic cascade effect: indeed, metazooplankton abundance decreased by a factor of ~3 after the introduction of *Limnothrissa miodon* (see Chap. 7), likely resulting in a proportional decline of the grazing pressure on phytoplankton. This trophic cascade effect, as well as the interaction of phytoplankton with other organisms of the food web, is discussed in Chap. 11. Finally, a key feature of Lake Kivu is the dry season peak of diatoms and cryptophytes, which may determine the productivity for the whole year. However these peaks may vary by a factor of 2 between years, and this variation may determine the productivity of the lake for the whole year, most likely affecting consumer production and ultimately fisheries yield.

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