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Phytoplankton ecology of Lake Kivu (eastern Africa)

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This article reports a 3-year (2002–04) survey on limnology and phytoplankton of Lake Kivu, a meromictic lake of the East African Rift, with peculiar geophysical and geochemical features. The phytoplankton survey combined high-performance liquid chromatography (HPLC) analysis of marker pigments, flow cytometry and epifluorescence and electron microscopy. Availability of similar data from a parallel study on Lake Tanganyika allowed a detailed comparison of phytoplankton composition and ecology in these two lakes. Lake Kivu combines a relatively shallow euphotic layer, usually smaller than its mixed layer, with relatively low nutrient content of the mixolimnion and with unstable thermal stratification of the surface waters. With an annual average chlorophyll a (Chl a) in the mixed layer of 2.2 mg m^{-3} *and low nutrient levels in the euphotic zone, the lake is clearly oligotrophic. As in other large African Rift lakes, seasonal variations of algal biomass and composition occurred, with substantial interannual variations, mainly related to variability of wind pattern and water column stability. Contrary to earlier reports that described Lake Kivu phytoplankton as dominated by cyanobacteria and green algae, we found that diatoms were the dominant group in the lake, particularly during the dry season (DS) episodes of deep mixing. During the rainy season (RS), the stratified water column, with high light and lower nutrient availability, favoured dominance of filamentous, of diazotrophic cyanobacteria and of picocyanobacteria, which represented a substantial fraction of autotrophic biomass. Different phytoplankton functional groups were identified in Lake Kivu, which place it in an intermediate position between the oligotrophic lakes Tanganyika and Malawi and the more eutrophic Lake Victoria. However, the dominant diatoms of Lake Kivu (Urosolenia sp. and the needle-like Nitzschia bacata Hust. and Fragilaria danica Lange-Bert.) are known from oligotrophic, P-deficient African lakes, and do not seem to be adequately included in the current functional classifications of freshwater phytoplankton.*

INTRODUCTION

Lake Kivu, located between Rwanda and the Kivu Province (Democratic Republic of Congo), is the smallest of the East African Great Lakes. It is a deep (maximum 489 m), meromictic lake, with an oxic mixolimnion up to 70 m, and a deep monimolimnion rich in dissolved gases, particularly methane (Tietze *et al.*, 1980; Schmid *et al.*, 2005). Lake Kivu has unique limnological characteristics, with temperature and salinity increasing in the deep water layers, due to the input of geothermal sources at the bottom of the lake (Degens *et al.*, 1973; Spigel and Coulter, 1996). As a consequence of high altitude (1463 m), the surface waters are slightly cooler than in other East African Great Lakes (24.9 versus 26.8°C in Lake Tanganyika). At present, the fish community of Lake Kivu comprises not >28 species, probably as a result of intense volcanic and tectonic activity in this region during the late Pleistocene and Holocene (Haberyan and Hecky, 1987).

By contrast with the knowledge of zooplankton (Kaningini *et al.*, 2003; M. Isumbisho *et al.*, submitted for publication) and fish biology (de Iongh *et al.*, 1983; Spliethoff *et al.*, 1983; Marshall, 1991; Snoeks *et al.*, 1997; Isumbisho

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et al., 2004) that was promoted by the development of fisheries, the overall ecology of Lake Kivu is far from well known. In particular, data on phytoplankton, primary production and nutrients are scarce, and long-term surveys were never conducted. Hecky and Kling (Hecky and Kling, 1987) reported phytoplankton fresh weight biomass from 550 up to 2100 mg m^{-3} from March 1972 surface samples. Cyanobacteria and chlorophytes accounted 70–90% of total biomass. The northern part of the lake was rich in peridinians, and diatoms were abundant only in an isolated bay (Kabuno Bay). Therefore, the planktonic assemblage of Lake Kivu at that time appeared to be similar to that of the other East African Great Lakes, i.e. dominated by chlorophytes and cyanobacteria, with diatoms at lower abundances (Hecky and Kling, 1987). Different diatom taxa were reported from the north and the south of the lake and related to the differences in Si : P dissolved ratio (Kilham *et al.*, 1986). In particular, needle-like *Fragilaria* and *Nitzschia*, favoured by high Si : P, dominated in the largest northern basin and in Kabuno Bay, while *Stephanodiscus* sp. was found in the southern Bukavu Bay, where dissolved Si : P was much lower. Another trait of Lake Kivu was its higher algal biomass than in the larger lakes Malawi and Tanganyika (Hecky and Kling, 1987), and a slightly higher primary production: 1.44 g C m^{-2} day^{-1} reported by Beadle (Beadle, 1981), which is actually an estimate based on the few measurements available at the time (Degens *et al.*, 1973; Jannasch, 1975). Based on palaeolimnological studies, Haberyan and Hecky (Haberyan and Hecky, 1987) have reconstructed the past ecology of Lake Kivu and have shown considerable changes in diatom assemblages from the sediment record, related to the volcanic activity in this region for the past few thousand years.

In this article, we present limnology and phytoplankton data from a 3-year survey (2002–04) of Lake Kivu. Phytoplankton biomass and composition were assessed using high-performance liquid chromatography (HPLC) analysis of marker pigments, processed with CHEMTAX. As a parallel study was carried out in Lake Tanganyika using the same techniques and sampling schedule (Descy *et al.*, 2005), we draw a comparison of the present phytoplankton ecology of these two Rift lakes. We conclude with a discussion on the phytoplankton assemblages of other large lakes from this region, in particular Lake Victoria and Lake Malawi.

METHODS

Sampling sites

Samples were collected in the 0–100 m water column, at 10-m intervals, with a 6-L Van Dorn bottle at Ishungu, in the southern basin of Lake Kivu (02°33.94′S, 28°97.65′E), twice a month from February 2002 to February 2005. In addition, four cruises took place: two during the rainy season (RS) (27–31 January 2003 and 23 February to 6 March 2004) and two in the dry season (DS) (26 August to 2 September 2003 and 9–12 September 2004). Cruises sampling points (Fig. 1) were distributed in the different basins: northern basin (01°68.08′S, 29°15.69′E), eastern basin (01°96.17′S, 29°12.26′E) and western basin (02°22.79′S, 28°97.35′E) as well as the two main bays, Kabuno Bay (02°61.62′S, 28°08.22′E) and Bukavu Bay (02°46.63′S, 28°85.71′E). The sampling protocol and equipment were identical to those used at the Ishungu (southern basin) station. Meteorological data were collected only for 2003 and 2004 by a Davis Weather Wizard III station (Davis Inotek Instruments, Baltimore, MD, USA).

Limnological profiles

Limnological profiles using multiparameter data sonde (Hydrolab DS4a, Loveland, CO, USA), transparency measurements (Secchi disk depth) and nutrient analysis [using standard spectrophotometric techniques (A.P.H.A., 1992) or Macherey-Nägel (Düren, Germany) analytical kits] were carried out during regular sampling at the Ishungu site and at all sites during the cruises. Detection limits for nutrients were the following: soluble reactive phosphorus (SRP), 0.16 μM; NH_4^+, 0.29 μM; NO_3^-, 1.43 μM; and NO_2-, 0.14 μM. Euphotic depth (z_{eu}, depth at which light is 1% of subsurface light) was derived from estimates of the vertical light attenuation coefficient from Secchi depth, using a coefficient (k = 1.34/Secchi disk depth) obtained by calibration with measurement of photosynthetically active radition (PAR) downward attenuation with Li-C (Lincoln, Nebraska, USA) quantum sensors at each sampling site (n = 16). Average light in the mixed layer (expressed in μE m^{-2} s^{-1}) was calculated according to Riley (Riley, 1957):

$$I_{z_m} = \frac{I_0\left(1 - e^{(-z_m \bullet K_e)}\right)}{z_m \bullet K_e} \quad (1)$$

where z_m is the depth of the mixed layer, K_e the coefficient of light extinction and I_0 the mean incident light.

Depth of the mixed layer (z_m) was estimated from the depth of the top of the thermocline, as shown by the temperature and oxygen vertical profiles obtained with the multiparameter data sonde. Thermal resistance to mixing (amount of work required to completely mix a water column with different temperatures) was calculated for the 0–100 m layer according to Birge (Birge, 1910, 1916):

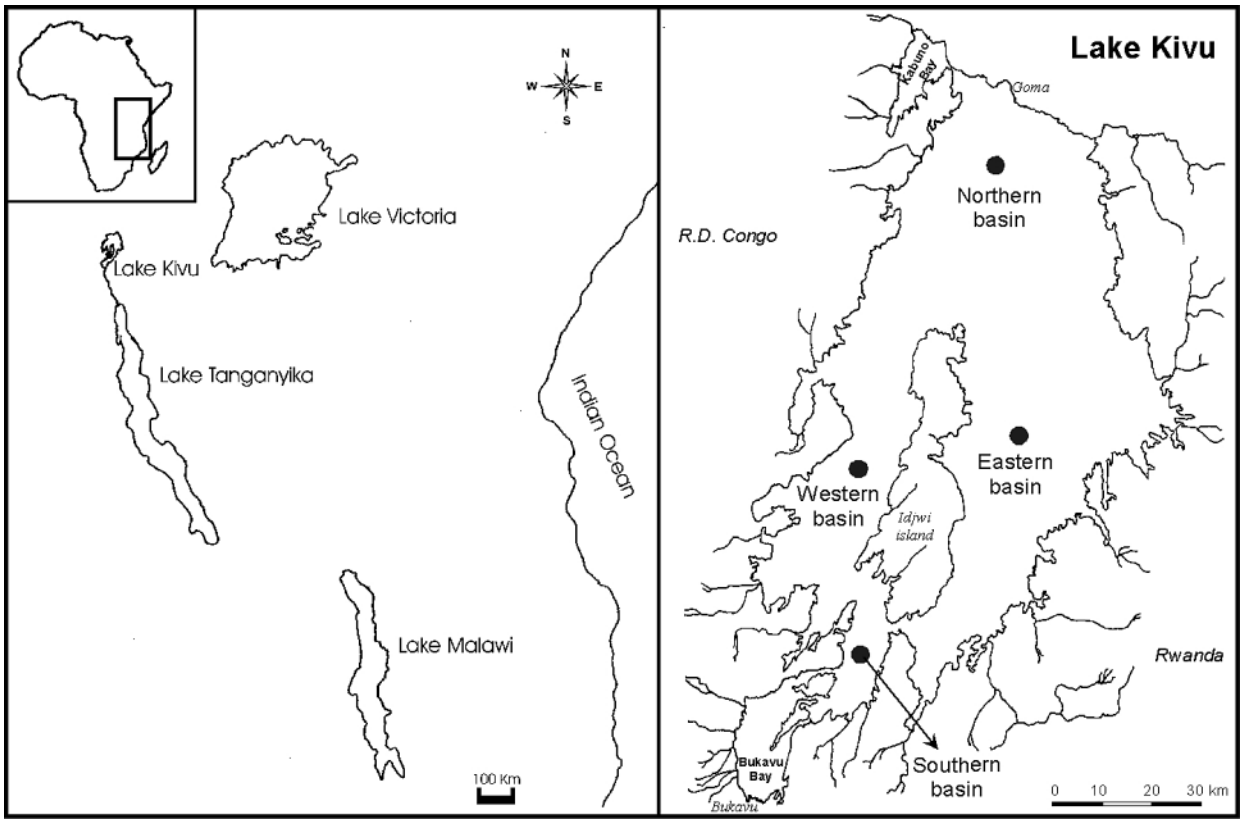

Fig. 1. Geographic situation of Lake Kivu. Black dots are the sampling sites [see text for global positioning system (GPS) coordinates].

$$\text{Work (ergs)} = \frac{AC^2}{12}(\rho_2 - \rho_1) \qquad (2)$$

where A is the area of the water column surface (1 cm^2 in this case), C the height of water column (cm), ρ_2 the water density at the bottom of the water column and ρ_1 the water density at the top of the water column (both in g cm^{-3}).

Pigment analysis

In addition to water column samples every 10 m, occasional additional sampling was done at 5 m, to get a more detailed vertical distribution of the algae. Samples for pigment analysis followed a procedure described in Descy *et al.* (Descy *et al.*, 2000): 3 L was filtered on Whatman GF/F (Maidstone, UK) or Macherey-Nägel GF5 filters of 0.7 μm pore size. Pigment extraction was carried out in 10 mL of 90% HPLC grade acetone. After two 15-min sonications separated by an overnight period at 4°C in the dark, extracts were stored in 2 mL of amber vials in a freezer (at –25°C) for several months (under the regular sampling scheme) or for 2–3 weeks at most (for the cruise samples). Transport to Belgium was carried out on ice in cooler boxes. HPLC analysis was carried out using the Wright *et al.* (Wright *et al.*, 1991) gradient elution method, with a Waters system comprising a PDA detector and a fluorescence detector. Calibration was made using commercial external standards (DHI, Denmark). Carotenoids not present in the standard were quantified against fucoxanthin, using as relative response the ratio of the specific absorbance coefficients at 440 nm (Jeffrey *et al.*, 1997) in methanol. Pigment concentrations were processed with the CHEMTAX software (CSIRO Marine Laboratories, Hobart, Tasmania, Australia) (Mackey *et al.*, 1996) using input ratio matrices adapted for freshwater phytoplankton (Descy *et al.*, 2000). Lake Kivu data processing followed a procedure similar to that of Descy *et al.* (Descy *et al.*, 2005), allowing estimating chlorophyll a (Chl *a*) biomass of chlorophytes, chrysophytes, diatoms, cryptophytes, dinoflagellates and cyanobacteria, taking into account variations of pigment ratios with season and depth.

Picophytoplankton counts (flow cytometry)

Samples for flow cytometry counts were taken during cruises. Four millilitres of water was collected and fixed immediately with cold 10% glutaraldehyde (final concentration 1%), left in the dark for 10 min at room temperature and stored at –20°C. We used a FacsCalibur (Becton Dickinson, USA) flow cytometer equipped with a 15 mW argon-ion laser (488 nm emission). At least 30 000 events were acquired for each subsample (usually 90 000 events). Fluorescent beads (1 μm, Fluoresbrite carboxylate microspheres; Polysciences, Warrington, PA, USA) were added at a known density as an internal standard. The bead standard concentration was determined by epifluorescence microscopy. We identified four different populations of picoautorophic organisms: three picocyanobacteria (one *Synechococcus*-like that alone accounted for >70% of the events and two undetermined picocyanobacteria, probably two- and four-celled *Synechococcus* colonies) and one picoeukaryote. These four groups of algae were easily identified in plots of side scatter (SSC) versus FL3 (red fluorescence) and FL2 (orange fluorescence) versus FL3 (red fluorescence). Data acquisition and analysis were performed with the program Paint-A-Gate (Becton Dickinson). The flow cytometry results for the *Synechococcus*-like population were confirmed by epifluorescence microscopy counts performed in some of the 0–20 m samples (correlation between the results from the two methods was highly significant: $r = 0.99$, $P < 0.05$, $n = 20$, with a 1.01 slope).

RESULTS

Regional climate and water column structure

Seasons, with their large variation in wind speed and precipitation, are the major factor responsible for variability in the water column structure of East African Great Lakes (Beadle, 1981). As in all eastern Africa, the Lake Kivu region is characterized by a windy main DS (long DS, June–September) and a calmer RS (October–May). In the Kivu region, however, there is a short DS around January when the winds can be stronger than in typical RS conditions. During DS, the daily range of air temperature increases and minimum temperatures occur (at night), but the mean air temperature is higher. The rest of the year (RS) temperatures are more stable, ~19°C, thanks to the high air humidity. Another feature of DS in relation to the hydrodynamic regime of Lake Kivu is the southeastern dominant wind that reaches maximum velocity around July every year (Fig. 2).

During the study period, Lake Kivu mean surface water temperature was 24.9°C, while the mean annual air temperature was 19.6°C. Although the highest air temperatures were registered during DS, epilimnion temperature declined throughout this period, mainly due to evaporation and night cooling, attenuating the temperature–density gradient, so that deeper vertical mixing occurs. However, the depth of the mixed layer is limited to 60–70 m (depth of the chemocline), which presents a steep salinity gradient (Fig. 3). Conductivity in the oxic layer oscillates between 950 and 1300 μS, but it

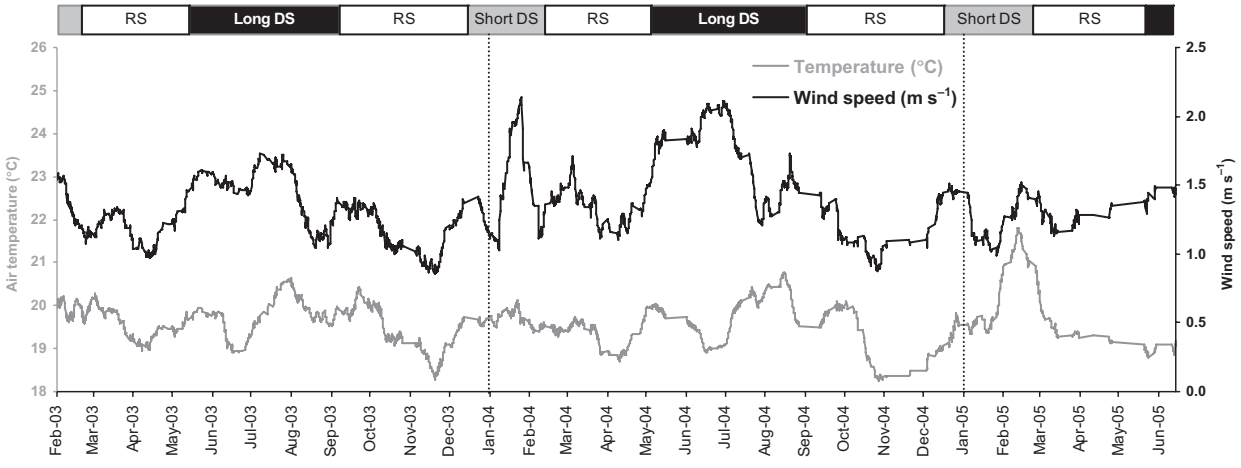

Fig. 2. Wind speed and air temperature in the southern end of Lake Kivu (Bukavu, Democratic Republic of the Congo) and season delimitation in 2003 and 2004. DS, dry season; RS, rainy season.

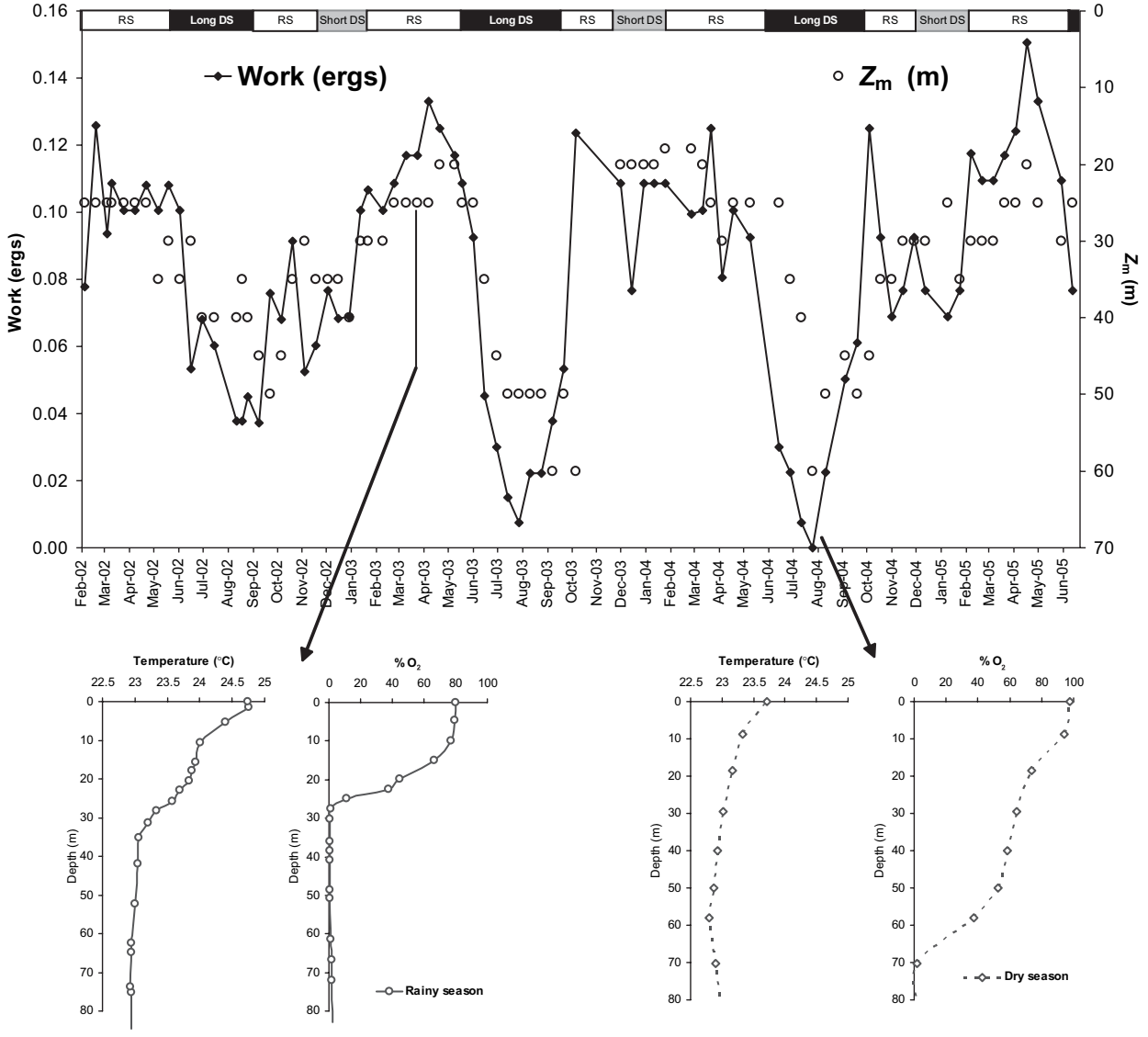

Fig. 3. Mixed layer depth, Z_m (open circles) and thermal resistance to mixing (line) variation along seasons in Lake Kivu in the southern basin during 2002–04. Arrows indicate examples of rainy season (RS) and dry season (DS) temperature and oxygen profiles.

doubles at 100–120 m depth, below the chemocline. The pH is also a good indicator of this chemical gradient, showing an extreme contrast from pH ~9.1 in the oxic layer but dropping to pH 6.5 at 100 m.

Along with weakening of the temperature–density gradient in the mixolimnion, the dominant southeastern winds, more intense during DS, contribute to thickening of the mixed layer. The configuration of Lake Kivu, with a restricted littoral zone and several high mountains surrounding the lake basin, makes the eastern and northern basins more exposed to the DS winds. As a result, seasonal changes in the mixed layer were more diverse in these two basins. At the Ishungu site in the southern basin, the mixed layer depth during RS is usually ~25 m, while in DS it can reach 60 m (Fig. 3).

Bukavu Bay is not meromictic (Tietze *et al.*, 1980). It has a maximum depth of 100 m, and complete mixing could be observed during the DS. On the contrary, Kabuno Bay has a permanent chemocline at 12 m, whatever the wind strength (data not shown). This bay is actually isolated from the rest of the lake; the only connection is a 150 m wide, 16 m deep, channel (Damas, 1937).

By comparison, the vertical mixing regime off Kigoma (northern basin of Lake Tanganyika) is more variable due to internal waves and to the particular

hydrodynamic complexity of this lake, although the depth of the mixed layer varies in a similar range to that of Lake Kivu: 25 m in RS, down to 80 m in DS (Descy *et al.*, 2005).

Nutrient and light conditions

Lake Kivu is less transparent than Lake Tanganyika (Fig. 4): mean Z_{eu} at Ishungu in the southern basin was 18 m, while in Lake Tanganyika off Kigoma it was 39 m during the same period. The transparency tended to increase during DS in Lake Kivu. As a consequence of different degrees of light penetration, the $Z_m : Z_{eu}$ ratio was usually higher in Lake Kivu (range at Ishungu: 0.9–3.8; mean 1.9) than in Lake Tanganyika (range: 0.42–1.88; mean 1.0). The DS mixing pattern is not similar in the two lakes, and the maximum $Z_m : Z_{eu}$ ratio occurs later in Lake Kivu (southern basin) than off Kigoma (Lake Tanganyika) (Fig. 4). Consequently, the average light in the mixed layer was about half in Lake Kivu compared with Lake Tanganyika (Fig. 5), and its temporal variation was different.

Nutrient concentrations in the euphotic zone of Lake Kivu were often below detection limits, but during DS, SRP and dissolved inorganic nitrogen (DIN) mean concentrations reached detectable levels. Figure 6 shows DS vertical profiles of nutrient concentration in Lake Kivu compared with those in Lake Tanganyika. SRP in the euphotic zone of Lake Kivu was on average 0.44 μM in RS and 0.75 μM in DS; mean SRP in the euphotic layer of Lake Tanganyika was from 0.19 (RS) to 0.43 μM (DS) in 2002 off Kigoma, with a DS maximum of 1.22 μM. Average DIN in Lake Kivu was 2.42 and 3.29 μM in RS and DS, respectively. This contrasts with lower DIN in Lake Tanganyika off Kigoma (mean RS DIN: 0.48 μM; mean DS DIN: 0.69 μM). The difference stems from higher concentration of ammonium in the euphotic layer of Lake Kivu, while this nitrogen form was most often below detection level in Lake Tanganyika.

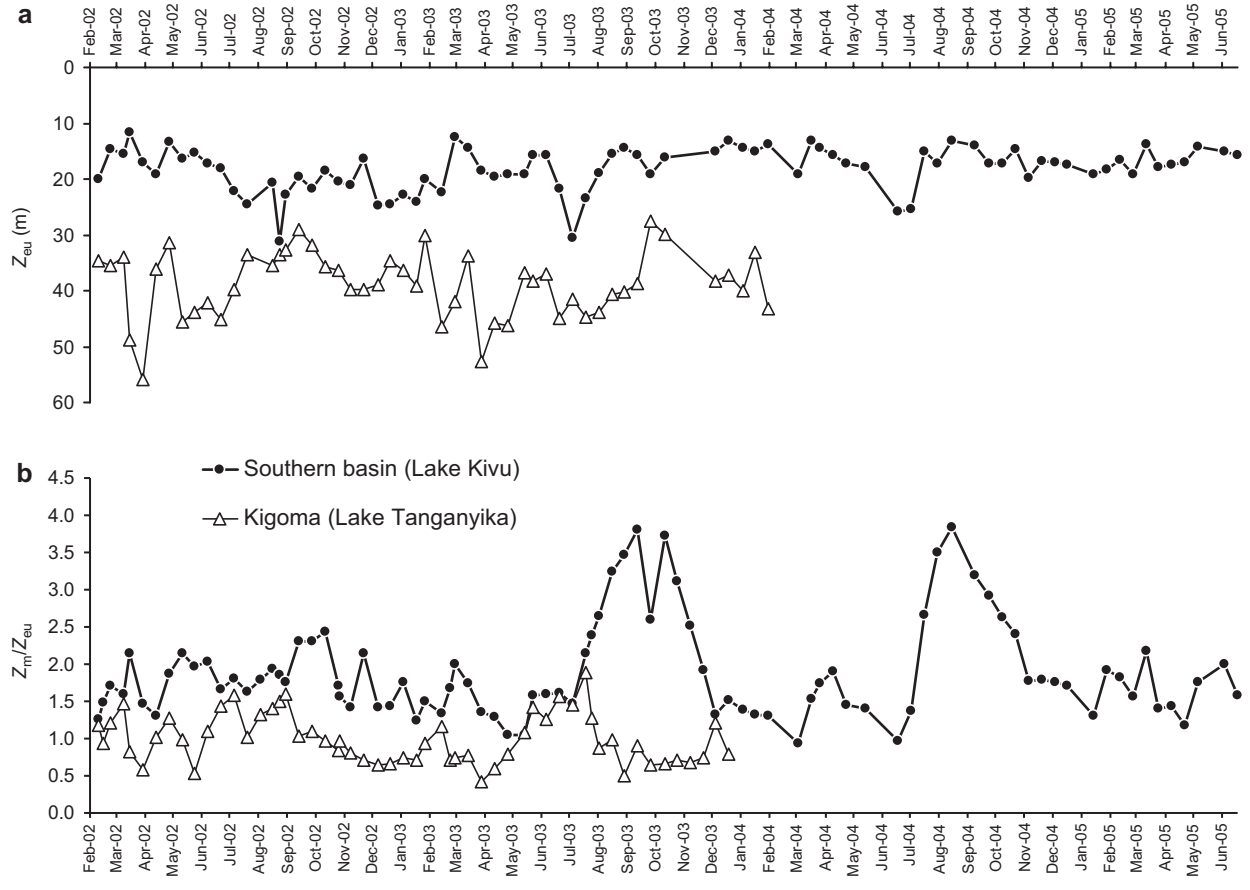

Fig. 4. (**a**) Euphotic depth (Z_{eu}) evolution in Lake Kivu in the southern basin (dots) and Lake Tanganyika off Kigoma (open triangles) during 2002 and 2003. (**b**) Mixed layer depth : euphotic depth ($Z_m : Z_{eu}$) ratio at the same sites during 2002–04.

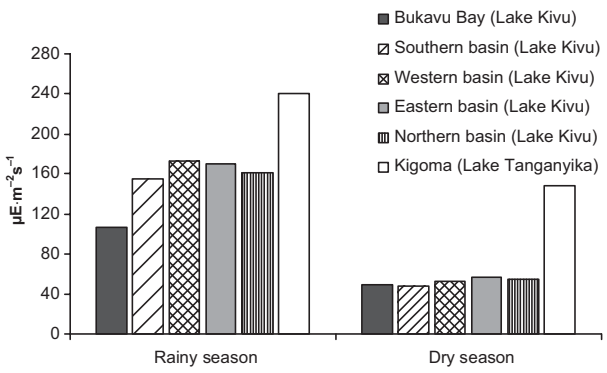

Fig. 5. Average light in the mixed layer in lakes Kivu and Tanganyika off Kigoma for dry and rainy seasons (RSs).

Dissolved reactive silica (DRSi) in the euphotic layer was a major difference between these two lakes: mean DRSi concentration was 100.1 μM in Lake Kivu versus 25.5 in Lake Tanganyika. Naturally, this affects the dissolved Si:P ratios in the euphotic layer, which was 154 in Lake Kivu Si:P versus 103 in Lake Tanganyika.

Phytoplankton biomass and composition

Phytoplankton biomass (Chl *a*) and composition were determined by HPLC pigment analysis, followed by CHEMTAX processing of marker pigment concentrations. The results expressed in Chl *a* mg m^{-2} were determined by multiplying the average Chl *a* concentration (mg m^{-3}) within the 0–60 m layer by 60 m to obtain integrated values of the whole water column in a highly variable productive layer. During 2002–04 (Fig. 7), Chl *a* average concentration was 76.9 mg m^{-2} in Lake Kivu at the southern basin versus 37.4 mg m^{-2} in the 0–100 m layer off Kigoma (Lake Tanganyika) for the 2002–03 period. Large temporal variations occurred in Lake Kivu: a large difference was observed in 2003 and 2004 between seasons but not in 2002. There was a clear annual biomass maximum during DS, reaching 180 mg Chl *a* m^{-2} the 20 August 2003 and the 20 July 2004. In Kigoma (Lake Tanganyika), the DS peak occurred at the very end of DS in 2002 (82 mg Chl *a* m^{-2}) and was lower than the 2003 DS maximum (94 mg Chl *a* m^{-2} on 2 September).

The Chl *a* data collected during the cruises in Lake Kivu showed some season-related spatial variation (Fig. 8): the RS Chl *a* varied little in the four main basins

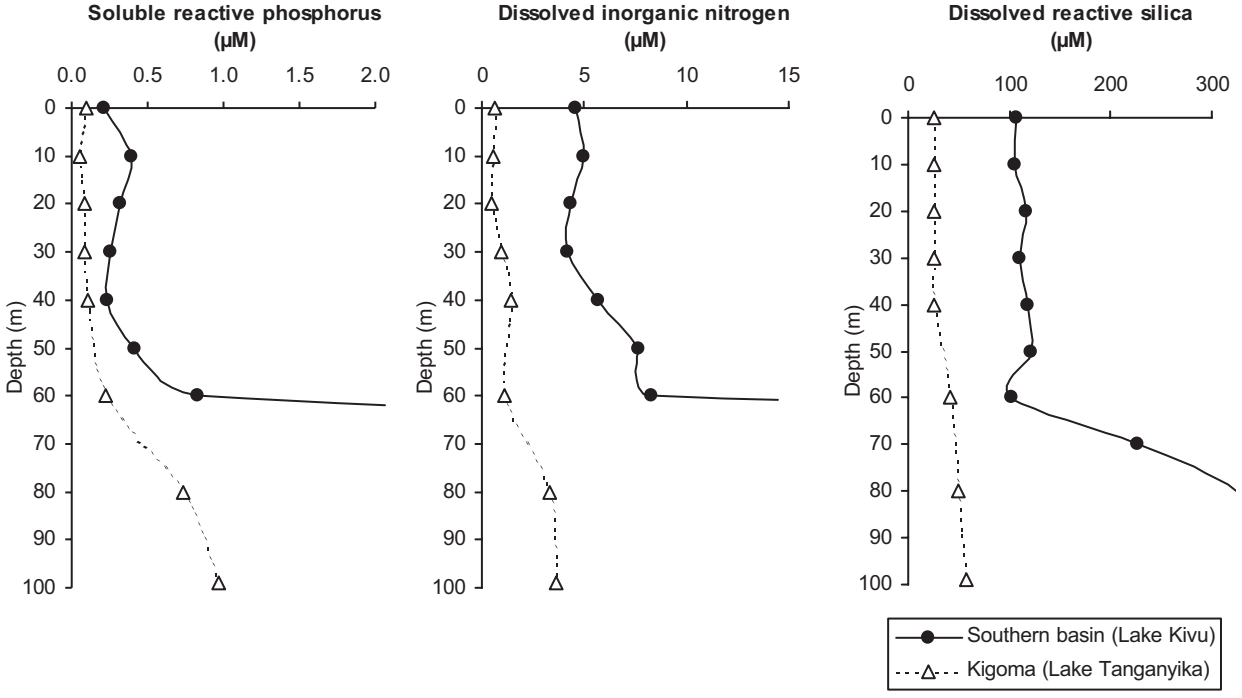

Fig. 6. Main macronutrient profiles in Lake Kivu in the southern basin (dots) and Lake Tanganyika off Kigoma (open triangles). Measurements for depths <60 m in Lake Kivu are not depicted, because values are much higher that the detailed scale permits [>10 μM $P–PO_4$ for soluble reactive phosphorus (SRP) at 70 m, >130 μM N for dissolved inorganic nitrogen (DIN) at 70 m and >320 μM Si for dissolved reactive silica (DRSi) at 80 m].

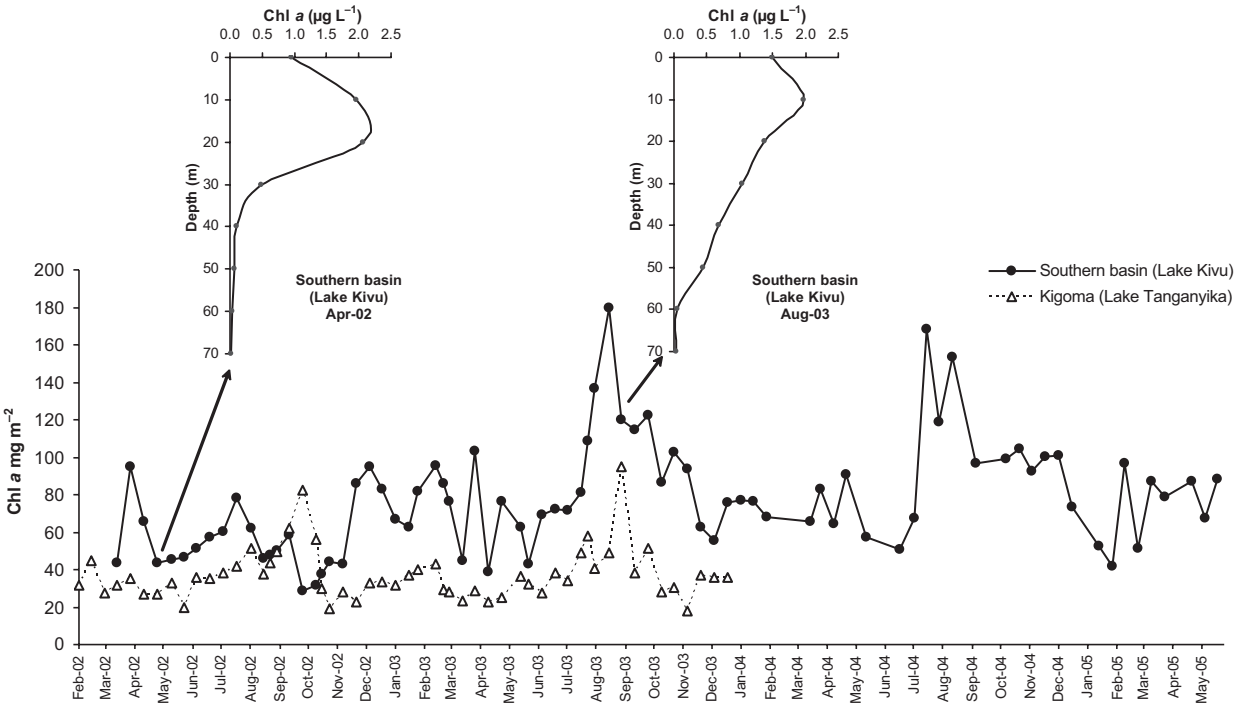

Fig. 7. Chlorophyll *a* (Chl *a*) evolution in Lake Kivu southern basin (dots) and Lake Tanganyika off Kigoma (open triangles) during 2002–04. Arrows indicate examples of rainy season (RS) and dry season (DS) profiles in Lake Kivu (southern basin).

(near 55 mg Chl *a* m^{-2}), while more contrast among basins appeared in DS, with 160 mg Chl *a* m^{-2} in the northern basin. The species composition and variation patterns were generally similar in open lake waters. The results from the survey in the southern basin can then be considered as representative of the whole lake situation. The isolated bays of Bukavu and Kabuno were two exceptional cases because of their very different limnology compared with the rest of the lake: the first showed higher biomass than the rest of the lake, particularly during DS when complete mixing occurred; in Kabuno Bay, the shallow epilimnion harbours low Chl *a* m^{-2} (22.9 in RS and 33.7 in DS cruises), with less seasonal difference than in the open lake.

According to HPLC analysis, the phytoplankton in Lake Kivu was dominated by a diatom–cyanobacteria assemblage (Fig. 9a). The most common species in pelagic Lake Kivu were pennate diatoms (*Nitzschia bacata* Hust. and *Fragilaria danica* Lange-Bert.) and the cyanobacteria *Planktolyngbya limnetica* Lemm. and *Synechococcus* sp. centric diatom *Urosolenia* sp. and various *Microcystis* spp. can also be very abundant. They form mostly distinct near-surface populations under daily stratification conditions. Cryptophytes and chrysophytes presented a similar pattern, without noticeable seasonal variations; cryptophytes tended to occur in greater abundance in the deep epilimnion, close to the thermocline (data not shown). They are motile and have been shown to migrate in the water column. Chrysophytes occurred regularly, with one single identified species, *Paraphysomonas vestita* Stokes. During DS, diatom dominance was even more abundant at all the sampling stations (Fig. 8); this was as conspicuous in the temporal survey at the southern basin as in the cruise samples. Chlorophytes were barely represented. This contrasts sharply with the phytoplankton of Lake Tanganyika off Kigoma in 2002–03 (Fig. 9b), which was characterized by a chlorophyte–cyanobacteria (including picocyanobacteria) assemblage, with a larger contribution of diatoms in DS (Descy *et al.*, 2005).

Finally, the $z_m : z_{eu}$ ratio was significantly correlated (Pearson correlation = 0.76, $P < 0.05$, $n = 118$) with Chl *a* integrated over the 0–60 m layer for Lake Kivu and 0–100 m layer for Lake Tanganyika (Fig. 10a). In the 3-year pigment data series from the southern basin, diatom and cyanobacteria contributions to total Chl *a* were inversely correlated (Pearson correlation = 0.73, $P < 0.05$, $n = 70$), which suggests a prevalence of some well-adapted species of cyanobacteria during stratified RS conditions (Fig. 10b), while diatoms dominated during the DS.

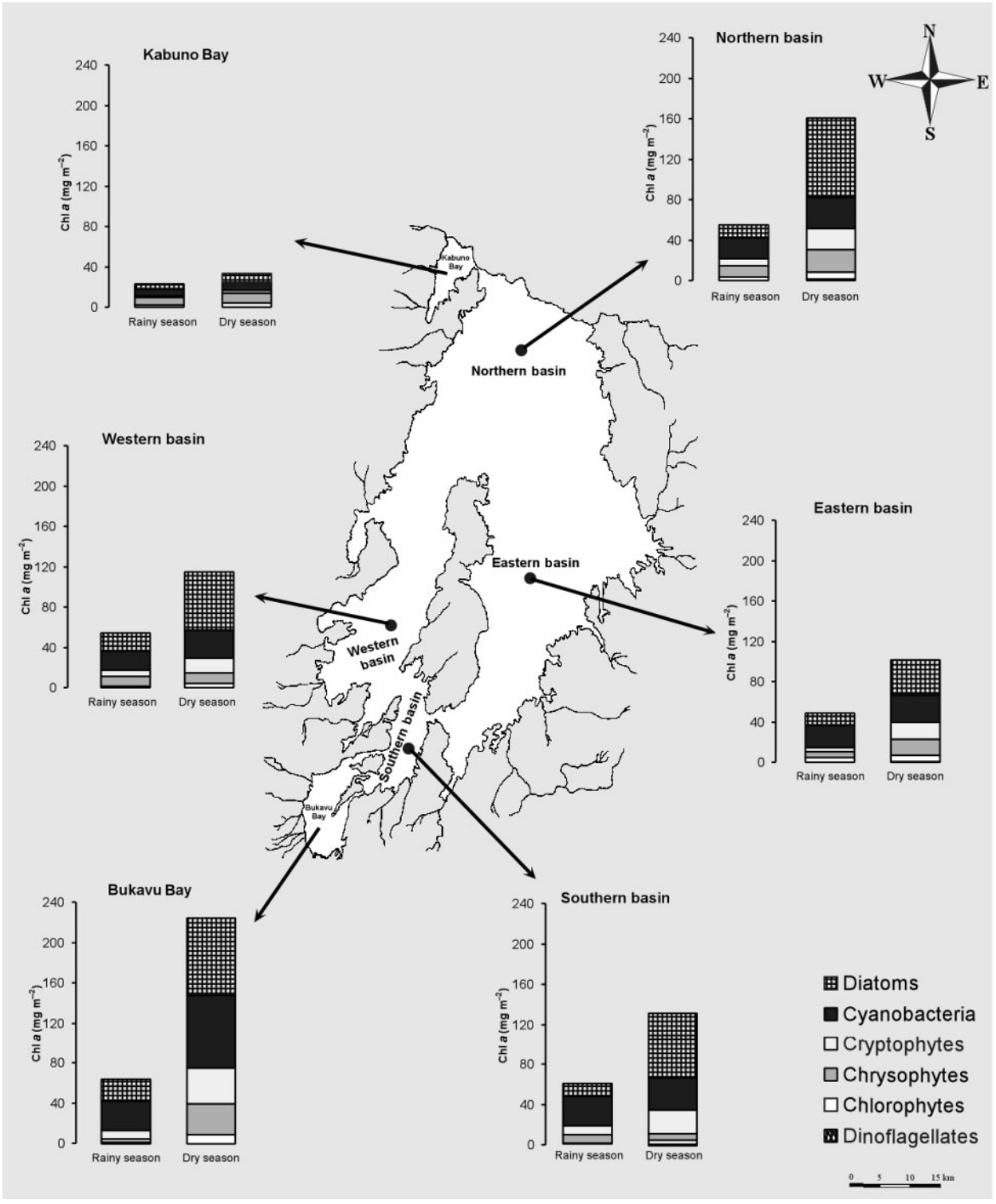

Fig. 8. Spatial variability of phytoplankton biomass and composition from pigment analysis in the four major basins and two isolated bays (Kabuno and Bukavu) of Lake Kivu. The results correspond to epilimnion average observed during different seasonal cruises. Chl *a*, chlorophyll *a*.

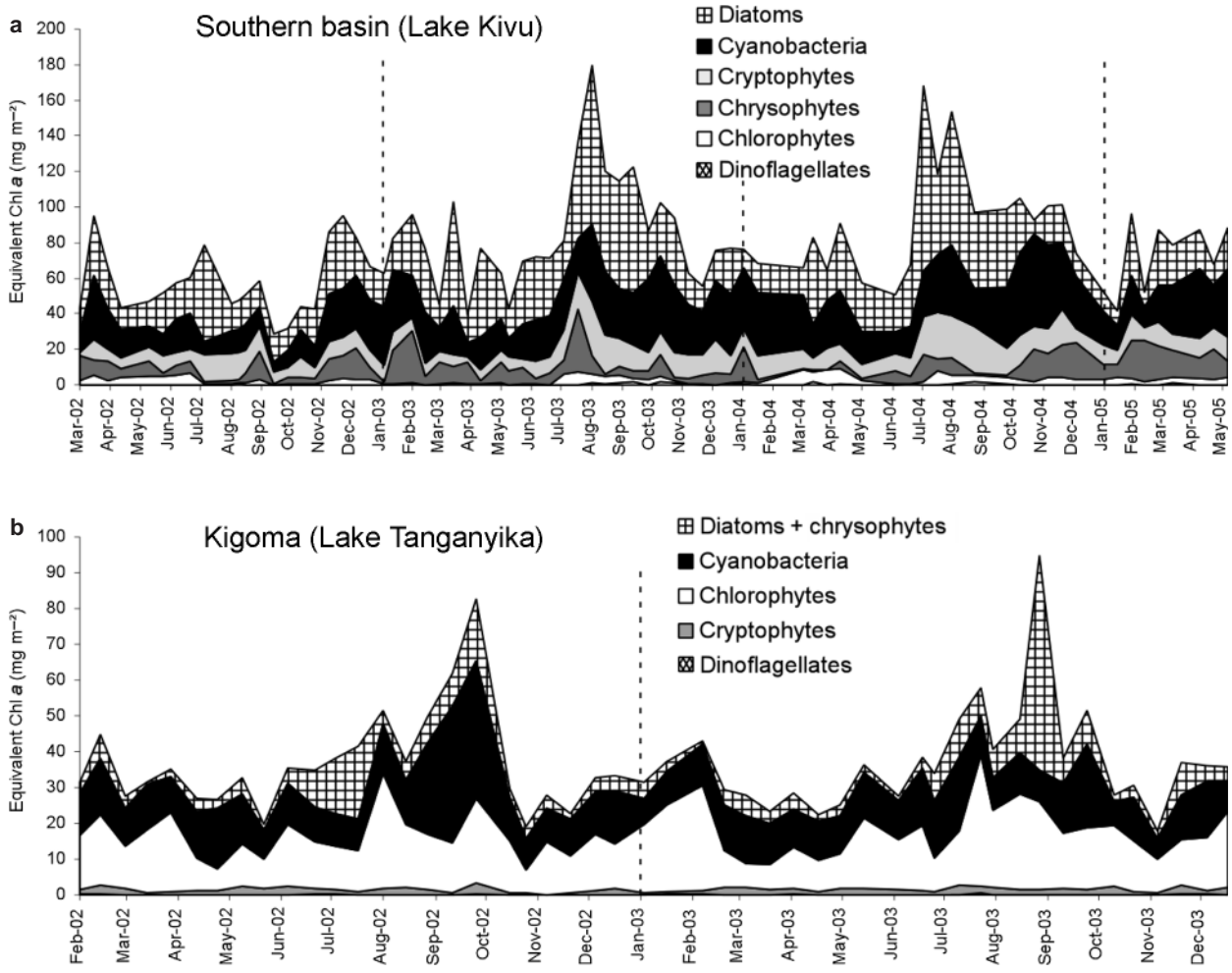

Fig. 9. (**a**) Phytoplankton biomass and composition from pigment analysis in Lake Kivu (southern basin) in the 2002–04. (**b**) Phytoplankton biomass and composition from pigment analysis in Lake Tanganyika off Kigoma in 2002 and 2003 (redrawn from Descy *et al.*, 2005). Chl *a*, chlorophyll *a*.

Picophytoplankton

As expected, contrary to temperate lakes where picophytoplankton has a marked seasonal distribution cycle (Callieri and Stockner, 2002; Belykh and Sorokovikova, 2003), the autotrophic picoplankton (APP) was abundant at all seasons in lakes Tanganyika and Kivu (and probably in other East African oligotrophic lakes). The spatial and temporal variations in those two lakes will be discussed in another article. The flow cytometry counts during cruises showed *Synechococcus*-like densities in the range 1–6 $\times$ 10^5 cells mL^{-1} (Fig. 11). Lake Tanganyika showed higher cell densities, but the average cell biovolume was smaller: 0.37 versus 0.43 μm in Lake Kivu. Therefore, in terms of biomass, the differences were attenuated; using a conversion factor of 0.47 pg C per μm (Verity *et al.*, 1992), mean APP biomass was 1.1 g C m^{-2} for Lake Kivu in the southern basin and 1.8 g C m^{-2} in Lake Tanganyika off Kigoma. The <2 μm fraction at the different cruise sampling points corresponded, in average (n = 15), to 21% of the total Chl *a* within a 10–35% range. In Lake Tanganyika, this fraction was usually higher; Descy *et al.* (Descy *et al.*, 2005) reported a mean APP biomass of 50% in the southern basin.

DISCUSSION

A biweekly limnological and HPLC pigment survey of Lake Kivu in 2002–04 showed an important interannual variability, rarely evaluated before in the East African

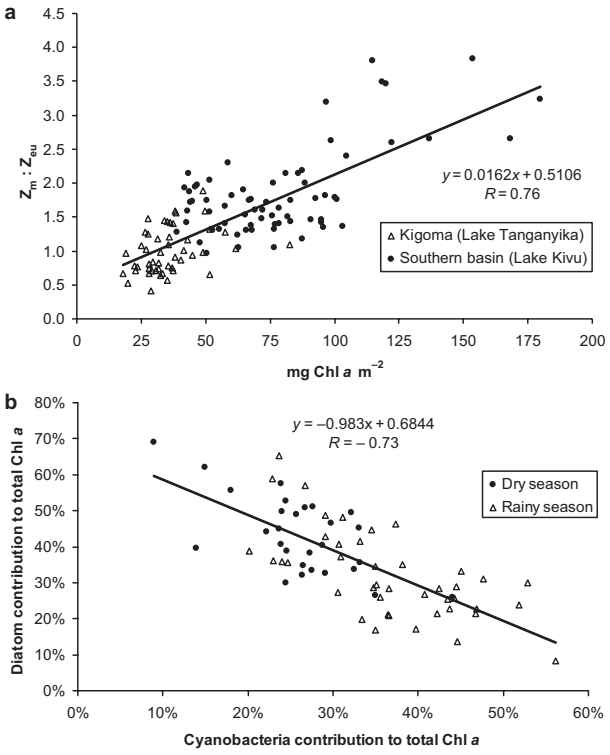

Fig. 10. (**a**) Relationship between phytoplankton biomass and the Z_m : Z_{eu} ratio in lakes Kivu and Tanganyika (Kigoma). (**b**) Relationship between diatoms and cyanobacteria contribution to total chlorophyll *a* (Chl *a*) in Lake Kivu.

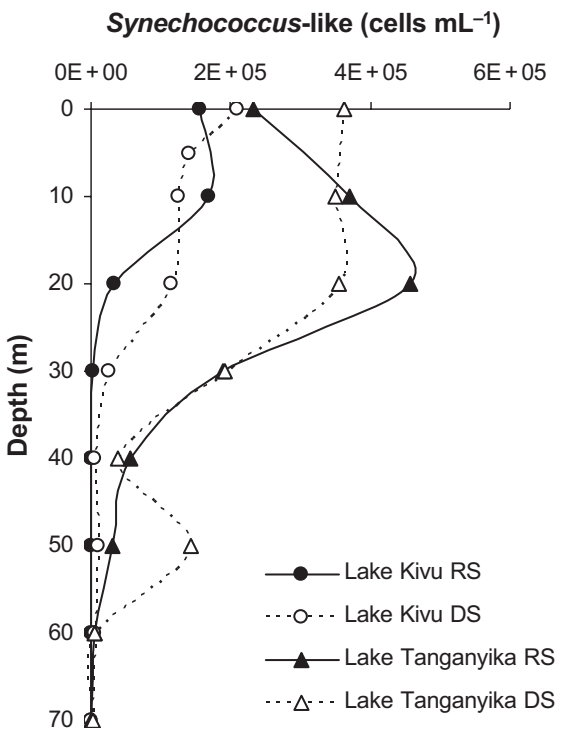

Fig. 11. *Synechococcus*-like abundance profiles (from flow cytometry counts) in Lake Kivu at the southern basin (circles) and Lake Tanganyika off Kigoma (triangles) in the 2004s rainy season (RS) (full lines) and dry season (DS) (dashed lines).

Great Lakes. As expected from differences in wind stress and mixing conditions, Chl *a* was lower under stratified conditions (RS) and rose in DS, but this increase in phytoplankton biomass was much more important in 2003 and 2004 than in 2002. The extent of the mixed layer and the duration of the deep mixing conditions were the main factors driving this interannual variability in algal biomass. Although the meteorological data were not available for 2002, we can hypothesize that 2003 and 2004 DS winds were stronger and that the windy season lasted longer than in 2002. This can be derived from the observed vertical profiles of temperature: the thermal density gradient was weaker during the DS in 2003–04 than in 2002. This again demonstrates the sensitivity of tropical lakes to climate variability, as emphasized by several authors (e.g. Johnson and Odada, 1996) which implies that a survey of several years, with sufficient sampling periodicity, is necessary to assess productivity of tropical lakes. With mean annual Chl *a* concentration of 1.3 mg m^{-3} (average in the 0–60 m layer), Lake Kivu is clearly in the oligotrophic range.

As previous accounts of the phytoplankton of Lake Kivu were based on limited sampling over shorter periods of time than our 3-year monitoring, comparison with other biomass estimates is limited. However, the picture of a more productive Lake Kivu, with phytoplankton biomass 10 times higher than Lake Tanganyika reported by Hecky and Kling (Hecky and Kling, 1987), is certainly to be corrected. Indeed, Chl *a* per unit volume in Lake Kivu was only two to three times higher than in the pelagic zone of Lake Tanganyika off Kigoma, and the difference in algal biomass is even lower when expressed per unit area, owing to the greater extent of the mixed layer in Lake Tanganyika. Moreover, Hecky and Kling (Hecky and Kling, 1987), on the basis of microscope examinations of their few samples, described the phytoplankton assemblage of Lake Kivu as dominated by a cyanobacteria–chlorophyte assemblage. This is a major difference with our study, where, thanks to the combination of optical and electron microscopy (H. Sarmento *et al.*, submitted for publication) and of HPLC analysis of phytoplankton pigments, we found diatoms and cyanobacteria as the dominant groups on average over the 3 years, green algae being a minor component of the algal assemblage.

A review of the most characteristic taxa of the algal assemblages of the large lakes of Eastern Africa is synthesized in Table I. Considering only the dominant algal

Table I: Annual succession of the functional groups (according to Reynolds et al., 2002) and some of the dominant phytoplankton species in the East African Great Lakes

Lake (pelagic)		Functional group	Some of the main species	References
Malawi	Jan–May	Z, F	*Synechococcus* (?), *Planktolyngbya*, *Lobocystis*, *Coenococcus*	Patterson and Kachinjika (1995)
	May–Sept	***... C, T**	*Nitzschia*, *Aulacoseira*... then *Stephanodiscus/Cyclostephanos*, *Mougeotia*	Hecky and Kling, 1987
	Sept–Dec	Z, F (S_N)	As in Jan–May, but *Strombidium* and *Anabaena* can bloom	
Tanganyika	Jan–May	Z, F	*Synechococcus*, *Chroococcus*, *Lobocystis/Dictyosphaerium*, *Oocystis*	Descy *et al.* (2005)
	May–Sept	***... C**	*Nitzschia*... then *Stephanodiscus*	Hecky and Kling, 1987
	Sept–Dec	Z, F (S_N)	As in Jan–May, but more Chrysophyceae, *Strombidium*, *Anabaena* can bloom	
Victoria (1950s)	Jan–May	Z (*****)	*Synechococcus* (?), *Planktolyngbya* (if mixing occurs: *Nitzschia*, *Aulacoseira*, *Stephanodiscus*)	Talling (1957)
	May–Sept	***... C**	*Nitzschia*... then *Aulacoseira*, *Stephanodiscus*	Talling (1987)
	Sept–Dec	Z, S_N	As in Jan–May, *Anabaena* and *Anabaenopsis* can bloom	
Victoria (1990s)	Jan–May	Z, S_N	As in the 1950s, but cyanobacteria persist; when mixing occurs, only *Nitzschia*	Hecky (1993)
	May–Sept	S_N	? Persistence of N_2-fixing cyanobacteria (*Anabaena*, *Cylindrospermopsis*)?	Lehman and Branstrator (1993)
	Sept–Dec	S_N	Persistence of N_2-fixing cyanobacteria (*Anabaena*, *Cylindrospermopsis*, ...)	
Kivu	Jan–May	Z, *****	*Synechococcus*, *Planktolyngbya*, *Nitzschia*	This study
	May–Sept	***, A**	*Nitzschia*, *Fragilaria* (*Synedra*); *Urosolenia* can bloom	
	Sept–Dec	Z, ***** (**M**)	As in Jan–May, but *Microcystis* can bloom	

A short dry season (DS) takes place in the January–May period in lakes Victoria and Kivu. From May to September is the DS in all East Africa. The rest of the year it is rainy season (RS).
*Adequate assemblage not found in the functional classification of Reynolds *et al.* (Reynolds *et al.*, 2002).

classes, phytoplankton of Lake Kivu seems more related to the shallower Lake Victoria (before anthropogenic eutrophication) than to the great, deep, oligotrophic lakes Malawi and Tanganyika. To some extent, this is not unexpected, as the two largest lakes are located farther from the equator. However, a key common feature between Lake Victoria and Lake Kivu is the $Z_m : Z_{eu}$ ratio, usually greater than one which favours algae with high accessory pigment providing improved light-harvesting capabilities. Also, despite the great depth of Lake Kivu, it never mixes vertically <60–70 m, where the permanent chemocline is situated. Lake Victoria is shallower, and vertical mixing involves contact with the sediment, which correlates with the greater nutrient availability and higher productivity of this large lake, even before its anthropogenic eutrophication. A key feature of Lake Kivu, pointed out by Spigel and Coulter (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 lakes. In addition, clear seasonal differences in dominant wind regime and mixing events driven by short but intense winds are likely to occur frequently and alternate with episodes of stratification. To summarize, Lake Kivu combines a relatively shallow euphotic layer, usually smaller than its mixed layer, with relatively low nutrient content of the mixolimnion and with unstable thermally stratified surface waters. To be successful in such an environment, phytoplankton units must be well adapted to low-light regimes and resistant to nutrient stress. An additional advantage to survival would be the ability to achieve vertical migration in the stratified but unstable water column, to optimize nutrient uptake and light harvesting for photosynthesis. These conditions contrast with those of lakes Tanganyika and Malawi, which combine stronger seasonality with complex hydrodynamics, creating sharp contrast between DS (deep mixing, increase of nutrients and reduction of light) and RS (shallow thermocline, low nutrients and high light); hence, the chlorophyte–cyanobacteria-dominated

assemblage reported for these large lakes, with diatoms developing during deep mixing events.

The taxonomic composition of the diatom assemblages of East African Great Lakes deserves more scrutiny and reveals important differences among lakes. In most of these lakes, needle-like or colonial *Nitzschia* appear first and are often followed by centrics like *Stephanodiscus* and *Aulacoseira*, when Si inputs decrease at advanced stages of the DS (Hecky and Kling, 1987). In Lake Kivu, long pennate diatoms, known to be good competitors at high Si : P ratio (i.e. at very low P availability), are always dominant, and centrics that develop at lower Si : P are very rare. This is a specific trait of Lake Kivu as DRSi is relatively high in all seasons; we never measured DRSi <70 μM in the euphotic zone, and the 3-year average was 100 μM, whereas average DRSi concentrations in the other lakes are much lower (Table II). With such a large amount of DRSi and low P in the euphotic zone, the diatom assemblage of Lake Kivu never shifts to centric *Stephanodiscus*- or *Aulacoseira*-like during the DS, contrarily to the rest of the cited lakes. Moreover, the surface waters of Lake Kivu support a population of *Urosolenia* sp., a genus that is well known for its oligotrophic affinities (see discussion, para 6) and tolerance to high light.

A very convenient and commonly used approach to synthesize the ecology of lacustrine phytoplankton is the functional classification of algal assemblages proposed by Reynolds *et al.* (Reynolds *et al.*, 2002). In Lake Kivu, in stratified conditions (RS), the low nutrient and higher available light favour specialized cyanobacteria, and a coexistence of assemblages Z (*Synechococcus*) and M (*Microcystis*) is often observed. However, we could not find an adequate functional group for the DS assemblages. From our results and from other studies in the East African Lakes (Table I), the assemblages found during the DS (usually needle-like or centric diatoms) seem to be a very particular feature from this region not found in other tropical lakes. Moreover, the dominant taxa are often specific to tropical regions or even strictly African (as *N. bacata* Hust. in Lake Kivu or *Nitzschia asterionelloides* O. Müll. in lakes Tanganyika and Malawi). For this reason, the DS assemblages are not quoted in the Table I.

Table II: Overview of silica concentrations in the epilimnion of some East African Great Lakes

Lake	Epilimnion Si (μM)	References
Malawi	20	Haberyan and Hecky, 1987
	14.2	Patterson and Kachinjika (1995)
	16	Branchu (2001)
Tanganyika	1.2	Degens *et al.* (1973)
	15	Branchu (2001)
	25.5	Descy *et al.* (2005)
Victoria	>45	Talling and Talling (1965)
	2.3	Lehman and Branstrator (1993)
Kivu	231	Degens *et al.* (1973)
	100	This study

Daily stratification in tropical lakes is very common and well known since Worthington (Worthington, 1930). A secondary thermocline can form in the surface water during the day and is broken down when the sun sets. In Lake Kivu, this phenomenon was frequently observed and could be part of the reason for the recurrent high surface biomass observed recurrently (up to 8 mg Chl *a* m^{-3}), accompanied by a high abundance of the centric diatom *Urosolenia* (A assemblage), tolerant to nutrient depletion and high light intensity. The real abundance of *Urosolenia* could be overlooked when using optical microscopy. Not only the valves are very thin and delicate, which render observation more difficult, but fixation with formaldehyde seems to destroy them further (E. Rott, personal communication). Otherwise, it could be that these organisms simply do not settle and are consequently absent from microscopic counts at the inverted microscope. In our study, HPLC pigment analysis coupled with scanning electronic microscopy allowed detection of these diatoms. Although this genus is frequently listed in taxonomical works in tropical freshwaters, very little is known about their abundance and ecology. Instead of proliferation in a specific layer, other possible explanation for these surface accumulations of *Urosolenia* cells would be the migration upwards the water column, as described in several works for marine *Rhizosolenia* spp. (Villareal and Lipschultz, 1995; Villareal *et al.*, 1996, 1999; Heather and Villareal, 2005). As *Urosolenia* plastids occupy a small proportion of the entire valve, the large cells surrounded by a thin silica wall could have a similar function as colony mucilage in *Microcystis aeruginosa* (Walsby and Reynolds, 1980), i.e. reducing their sinking rate, by reducing the overall cell density. Moreover, the same authors stated that *Urosolenia* long spines contributed to form resistance to sedimentation.

Another group of organisms that was completely missed in classical microscopic counts is APP, which represents around one fourth of total Chl *a* in Lake Kivu. Flow cytometry and epifluorescence have confirmed that *Synechococcus* biomass in both lakes Tanganyika and Kivu was in the same order of magnitude, even if it corresponds to higher relative abundance in Lake Tanganyika. This means that the Chl *a* differences between these two lakes fit exclusively for the >2

μm fraction, which could be a result of different top-down control related to two different trophic structure. In Lake Kivu, the planktivorous sardine *Limnothrissa miodon* Boulenger, introduced from Lake Tanganyika 45 years ago, has no natural predators. Zooplankton, dominated by copepods, has lower biomass than other East African Great Lakes (M. Isumbisho *et al.*, submitted for publication). A reduction of the top-down control of edible phytoplankton may have resulted from grazer control after the sardine introduction, which could explain why phytoplankton biomass is comparatively high in Lake Kivu.

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REFERENCES

American Public Health Association (A.P.H.A.) (1992) *Standard Methods for the Examination of Water and Wastewater*. A.P.H.A., New York.

Beadle, L. C. (1981) *The Inland Waters of Tropical Africa – An Introduction to Tropical Limnology*. Longman, New York.

Belykh, O. I. and Sorokovikova, E. G. (2003) Autotrophic picoplankton in Lake Baikal: Abundance, dynamics, and distribution. *Aquat. Ecosyst. Health Manage.*, **6**(3), 251–261.

Birge, E. A. (1910) An unregarded factor in lake temperatures. *Trans. Wiss. Acad. Sci. Arts Lett.*, **16**, 989–1004.

Birge, E. A. (1916) The work of the wind in warming a lake. *Trans. Wiss. Acad. Sci. Arts Lett.*, **18**(2), 341–391.

Branchu, P. (2001) Cycle des éléments majeurs et traces dans les grands lacs de rift tropicaux (lacs Tanganyika et Malawi). PhD Thesis. *Annales – Sciences Géologiques*. Vol. 106. Musée Royal de l'Afrique Centrale, Tervuren.

Callieri, C. and Stockner, J. G. (2002) Freshwater autotrophic picoplankton: a review. *J. Limnol.*, **61**(1), 1–14.

Damas, H. (1937) Quelques caractères écologiques de trois lacs équatoriaux: Kivu, Edouard, Ndalaga. *Ann. Soc. R. Zool. Belg.*, **68**(3), 121–135.

Degens, E., Herzen, R. P., Wong, H.-K. *et al.* (1973) Lake Kivu: Structure, chemistry and biology of an East African Rift lake. *Geol. Rundsch.*, **62**, 245–277.

Descy, J.-P., Hardy, M.-A., Sténuite, S. *et al.* (2005) Phytoplankton pigments and community composition in Lake Tanganyika. *Freshw. Biol.*, **50**, 668–684.

Descy, J.-P., Higgins, H. W., Mackey, D. J. *et al.* (2000) Pigment ratios and phytoplankton assessment in northern Wisconsin lakes. *J. Phycol.*, **36**, 274–286.

Haberyan, K. A. and Hecky, R. E. (1987) The late pleistocene and holocene stratigraphy and paleolimnology of lakes Kivu and Tanganyika. *Paleogeogr. Paleoclimatol. Paleoecol.*, **61**, 169–197.

Heather, R. S. and Villareal, T. A. (2005) Nitrogen inputs into the euphotic zone by vertically migrating *Rhizosolenia* mats. *J. Plankton Res.*, **27**, 545–556.

Hecky, R. E. (1993) The eutrophication of Lake Victoria. *Verh. Internat. Verein. Limnol.*, **25**, 39–48.

Hecky, R. E. and Kling, H. J. (1987) Phytoplankton ecology of the great lakes in the rift valleys of Central Africa. *Arch. Hydrobiol. Beih. Ergebn. Limnol.*, **25**, 197–228.

de Iongh, H., Spliethoff, P. and Frank, V. (1983) Feeding habits of the clupeid *Limnothrissa miodon* (Boulenger), in Lake Kivu. *Hydrobiologia*, **102**(2), 113–122.

Isumbisho, M., Kaningini, M., Descy, J.-P. and Baras, E. (2004) Seasonal and diel variations in diet of the young stages of *Limnothrissa miodon* in lake Kivu, Eastern Africa. *J. Trop. Ecol.*, **20**, 73–83.

Jannasch, H. W. (1975) Methane oxidation in Lake Kivu (central Africa). *Limnol. Oceanogr.*, **20**, 860–864.

Jeffrey, S. W., Vesk, M. and Mantoura, R. F. C. (1997) Phytoplankton pigments: windows into the pastures of the sea. *Nat. Resour.*, **33**(2), 14–29.

Johnson, T. C. and Odada, E. O. (1996) *The Limnology, Climatology and Paleoclimatology of the East African Lakes*. Gordon and Breach Publishers, Amsterdam.

Kaningini, B., Isumbisho, M., Ndayike, N. and Micha, J.-C. (2003) Etude du zooplancton du lac Kivu: composition, variations d'abondance et distribution. *Bull. Séanc. Acad. R. Sci. Outre-Mer*, **49**(2), 145–160.

Kilham, P., Kilham, S. S. and Hecky, R. E. (1986) Hypothesized resource relationships among African planktonic diatoms. *Limnol. Oceanogr.*, **31**, 1169–1181.

Lehman, J. and Branstrator, D. (1993) Effects of nutrients and grazing on the phytoplankton of Lake Victoria. *Verh. Internat. Verein. Limnol.*, **25**, 850–855.

Mackey, M. D., Mackey, D. J., Higgins, H. W. and Wright, S. W. (1996) CHEMTAX – a program for estimating class abundances from chemical markers: application to HPLC measurements of phytoplankton. *Mar. Ecol. Prog. Ser.*, **144**, 265–283.

Marshall, B. E. (1991) Seasonal and annual variations in the abundance of the clupeid *Limnothrissa miodon* in lake Kivu. *J. Fish Biol.*, **39**, 641–648.

Patterson, G. and Kachinjika, O. (1995) Limnology and phytoplankton ecology. In Menz, A. (ed.), *The Fishery Potential and Productivity of the Pelagic Zone of Lake Malawi/Niassa- Scientific Report of the UK/SADC Pelagic Fish Resource Assessment Project*. Natural Resources Institute, Overseas Development Administration, pp. 1–67.

Reynolds, C., Huszar, V., Kruk, C. *et al.* (2002) Towards a functional classification of the freshwater phytoplankton. *J. Plankton Res.*, **24**(5), 417–428.

Riley, G. A. (1957) Phytoplankton of the north Central Sargasso Sea, 1950–52. *Limnol. Oceanogr.*, **2**, 252–270.

Schmid, M., Halbwachs, M., Wehrli, B. and Wüest, A. (2005) Weak mixing in Lake Kivu: New insights indicate increasing risk of uncontrolled gas eruption. *Geochem. Geophys. Geosyst.*, **6**(1), 1–11.

Snoeks, J., De Vos, L. and Thys van den Audenaerde, D. (1997) The ichthyogeography of Lake Kivu. S. *Afr. J. Sci.*, **93**, 579–584.

Spigel, R. H. and Coulter, G. W. (1996) Comparison of hydrology and physical limnology of the East African Great Lakes: Tanganyika, Malawi, Victoria, Kivu and Turkana (with references to some North American great lakes). In Johnson, T. C. and Odada, E. O. (eds), *The Limnology, Climatology and Paleoclimatology of the East African Lakes*. Gordon and Breach Publishers, Amsterdam, pp. 103–140.

Spliethoff, P. C., de Iongh, H. H. and Frank, V. G. (1983) Success of the introduction of the fresh water Clupeid *Limnothrissa miodon* (Boulenger) in Lake Kivu. *Fish. Manage.*, **14**, 17–31.

Talling, J. F. (1957) Some observations on the stratification of Lake Victoria. *Limnol. Oceanogr.*, **2**, 213–221.

Talling, J. F. (1987) The phytoplankton of Lake Victoria (East Africa). *Arch. Hydrobiol. Beih. Ergebn. Limnol.*, **25**, 229–256.

Talling, J. F. and Talling, I. B. (1965) The chemical composition of African lake waters. *Int. Rev. Gesamten Hydrobiol.*, **50**, 421–463.

Tietze, K., Geyh, M., Müller, H. *et al.* (1980) The genesis of the methane in the Lake Kivu (Central Africa). *Geol. Rundsch.*, **69**, 452–472.

Verity, P. G., Robertson, C. Y., Tronzo, C. R. *et al.* (1992) Relationships between cell Volume and the carbon and nitrogen content of marine photosynthetic nanoplankton. *Limnol. Oceanogr.*, **37**, 1434–1446.

Villareal, T. A. and Lipschultz, F. (1995) Internal nitrate concentrations in single cells of large phytoplankton from the Sargasso Sea. *J. Phycol.*, **31**, 689–696.

Villareal, T. A., Pilskaln, C., Brzezinski, M. *et al.* (1999) Upward transport of oceanic nitrate by migrating diatom mats. *Nature*, **397**, 423–425.

Villareal, T. A., Woods, S., Moore, J. K. *et al.* (1996) Vertical migration of *Rhizosolenia* mats and their significance to NO_3– fluxes in the central North Pacific gyre. *J. Plankton Res.*, **18**, 1103–1121.

Walsby, A. E. and Reynolds, C. S. (1980) Sinking and floating. In Morris, I. (ed.), *The Physiological Ecology of Phytoplankton*. Vol. 7. Blackwell Scientific Publications, Oxford, pp. 371–412.

Worthington, M. A. (1930) Observations on the temperature, Hydrogen-ion concentration, and other physical conditions of the Victoria and Albert Nyanzas. *Int. Rev. Gesamten Hydrobiol. Hydrogr.*, **24**, 328–357.

Wright, S. W., Jeffrey, S. W., Mantoura, R. F. C. *et al.* (1991) Improved HPLC method for the analysis of chlorophylls and carotenoids in marine phytoplankton. *Mar. Ecol. Prog. Ser.*, **77**, 183–196.