

Drivers of phytoplankton diversity in Lake Tanganyika

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Abstract In keeping with the theme of this volume, the present article commemorates the 50 years of Hutchinson's (Am Nat 93:145–159, 1959) famous publication on the 'very general question of animal diversity', which obviously leads to the more important question regarding the driving forces of biodiversity and their limitation in various habitats. The study of phytoplankton in large lakes is a challenging task which requires the use of a wide variety of techniques to capture the range of spatial and

temporal variations. The analysis of marker pigments may provide an adequate tool for phytoplankton surveys in large water bodies, thanks to automated analysis for processing numerous individual samples, and by achieving sufficient taxonomic resolution for ecological studies. Chlorophylls and carotenoids were analysed by HPLC in water column samples of Lake Tanganyika from 2002 through 2006, at two study sites, off Kigoma (north basin) and off Mpulungu (south basin). Using the CHEMTAX software for calculating contributions of the main algal groups to chlorophyll *a*, variations of phytoplankton composition and biomass were determined. We also investigated selected samples according to standard taxonomic techniques for elucidating the dominant species composition. Most of the phytoplankton biomass was located in the 0–40 m layer, with maxima at 0 or 20 m, and more rarely at 40 m. Deep chlorophyll maxima (DCM) and surface 'blooms' were occasionally observed. The phytoplankton assemblage was essentially dominated by chlorophytes and cyanobacteria, with diatoms developing mainly in the dry season. The dominant cyanobacteria were very small unicells (mostly *Synechococcus*), which were much more abundant in the southern basin, whereas green algae dominated on average at the northern site. A canonical correspondence analysis (CCA) including the main limnological variables, dissolved nutrients and zooplankton abundance was run to explore environment–phytoplankton relations. The CCA points to physical factors, site and

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season as key determinants of the phytoplankton assemblage, but also indicates a significant role, depending on the studied site, of calanoid copepods and of nauplii stages. Our data suggest that the factors allowing coexistence of several phytoplankton taxa in the pelagic zone of Lake Tanganyika are likely differential vertical distribution in the water column, which allows spatial partitioning of light and nutrients, and temporal variability (occurring at time scales preventing long-term dominance by a single taxon), along with effects of predation by grazers.

Keywords Phytoplankton · Chemotaxonomy · Large tropical lake · Grazing

Introduction

The simple initial, question ‘why are there so many kinds of animals?’ proposed in the Hutchinson’s (1959) famous seminal paper, became a challenge, which has fuelled experimental and theoretical research to the present. In spite of the fact that Hutchinson (1959) himself discussed several possible answers and submitted interesting general ideas, followed by considerable scientific efforts on the topic, no universally accepted answer has been forthcoming. However, as a result of the work done, the question of Hutchinson’s paradigm has progressed far beyond and, paraphrasing Finlay & Esteban (2001), could be extended by adding ‘and why they live where they do?’ Therefore, still many points with respect to phytoplankton diversity, as well as finding explanations for the alliance of certain phytoplankters with certain water bodies coupled with their environmental constraints, are in the forefront of many limnological studies.

Interestingly, there was in Hutchinson’s Santa Rosalia paper a statement about the relation between diversity and size of animals: ‘small size ... clearly makes possible a degree of diversity quite unknown among groups of larger organisms’. Although we have today clear evidence that the overall diversity of microbes stems from their evolutionary history (Falkowski & Raven, 2007), Hutchinson’s conclusions, based the varied environmental mosaic at the microscopic scale, still provide a widely accepted explanation as to why many microbe species may coexist in the same environment. We may suppose

that this led the ‘plankton paradox’ (Hutchinson, 1961), which raised questions about species coexistence in an apparently homogeneous water column habitat, that have been addressed by many ecologists and planktologists, with the proposal of various explanations (e.g. Wilson, 1990). Among these explanations, environmental variability and heterogeneity have often been retained (Sommer et al., 1993), as well as variability induced by complex interactions between multiple species (e.g. Scheffer et al., 2003). Large and deep tropical lakes may be, at first sight, a good example of aquatic homogeneous environments: they enjoy ‘endless summer’ (Kilham & Kilham, 1990), remaining stratified all year round, unlike their temperate equivalents, which are submitted to very large seasonal variations. Therefore, large tropical lakes offer a good opportunity to study the factors which drive phytoplankton diversity in those presumably ‘stable’ environments.

Lake Tanganyika, the second deepest freshwater lake on Earth, is well known for presenting large spatial heterogeneity, related to its great size and to its complex hydrodynamics (Spigel & Coulter, 1996). Depending on seasonal variation of surface temperature and wind direction and velocity, substantial variation in mixed layer depth occurs (Coulter, 1991). Spatial differences of water column physical structure and hydrodynamics also appear at different scales (Naithani et al., 2002, 2003). They are conspicuous between the northern and southern basin, particularly in the dry season, whereas the rainy season conditions are more homogeneous, resulting in similar physical and limnological conditions over the whole lake. In addition, a seasonal upwelling occurs at the southern end of the lake during the dry season (Coulter, 1991), bringing up nutrients from the deep waters and generating a burst of primary production in that part of the lake. Apart from this distinct seasonal event, wind-driven thermocline oscillations (Naithani et al., 2003), which enhances diffusion of nutrients from the hypolimnion to the mixed layer, occur at all times (Plisnier et al., 1999; Plisnier & Coenen, 2001).

Hecky & Kling (1981) published a seasonal cycle of the phytoplankton (and protozooplankton) species composition, biomass and chlorophyll *a* in Lake Tanganyika, covering a relatively wide spatial and temporal distribution. A chlorophytes–Chroococcales assemblage was described as characteristic of the wet

season (October–April), with high light and poor nutrient availability in the shallow epilimnion. In the dry season (May–September), when deep mixing occurred, diatom (mostly *Nitzschia* spp.) dominance was explained by the lower light levels and higher nutrient availability. Surface blooms of filamentous cyanobacteria (*Anabaena* sp.) developed frequently at the end of the dry season, when the water column re-stratified. The Tanganyika phytoplankton record was completed by cruise samples that allowed addressing spatial variation (Hecky & Fee, 1981; Hecky & Kling, 1987). At least three other papers were published on the seasonal dynamics of phytoplankton in the following years, but oriented to a specific algal group (diatoms) or restricted to littoral areas (Cocquyt et al., 1991; Cocquyt, 1999; Cocquyt, 2000). More recently, both algal pigment (Descy et al., 2005) and microscopy (Cocquyt & Vyverman, 2005) surveys updated the data on algal biomass, composition and dynamics in the pelagic waters of Lake Tanganyika, and underlined the cyanobacteria–chlorophyte dominance in the most part of the year cycle, with particular prominence of the picocyanobacteria *Synechococcus* sp. (Vuorio et al., 2003; Descy et al., 2005; Sarmiento et al., 2008; Stenuite et al., 2009). There is, however, significant spatial variation in Lake Tanganyika: the dry season diatom peak (comprising the colonial *Nitzschia* cf. *asterionelloides* O. Müll.), coinciding with the chlorophyll *a* maximum in the water column (Cocquyt & Vyverman, 2005), is clearly visible in the northern part of the lake. By contrast, in the southern basin, where the temperature–density gradient is usually weaker, diatom maxima do not fit as well as in the northern basin with the seasonal pattern, and picocyanobacteria tend to dominate at all times (Descy et al., 2005). Another *Nitzschia* species, *N. fonticola* Grun., more characteristic of the stratified conditions of the rainy season, becomes the more abundant diatom (Cocquyt & Vyverman, 2005), particularly in the southern part of the lake. According to the same recent investigations (Descy et al., 2005), green algae are far more abundant and diverse off Kigoma (northern basin) than off Mpulungu (southern basin). Several floristic differences in the green algal assemblages of these two sites have also been shown (Stoyneva et al., 2007a), and taxonomic updates, with new species description, have been made (Stoyneva et al., 2005, 2006, 2007b).

The switch from ‘nutrient depletion—high light’ to ‘higher nutrient–low light’ has been described as a trade-off in the requirements for algal growth, and as a major driver of phytoplankton community changes in large tropical lakes (Hecky & Kling, 1981, 1987). Besides these physically driven changes, little attention has been paid so far to other factors, such as zooplankton grazing, partly due to the lack of simultaneous sampling of zooplankton and phytoplankton. Zooplankton abundance in Lake Tanganyika varies greatly throughout the year (Burgis, 1984; Coulter, 1991; Kurki et al., 1999) and so one can expect significant differences in grazing pressure on the phytoplankton whose size is within the major copepods’ food spectrum. There are also differences in metazooplankton composition in Lake Tanganyika, with more cyclopoids in the northern regions of the lake, and more calanoids in the southern part (Kurki et al., 1999), which may affect grazing pressure, depending on different diet and food selectivity among copepods. Moreover, microzooplankton feeding on small phytoplankton may also present large variations in abundance, both spatially and temporally (Tarbe, 2010). It is thus likely that phytoplankton structure and abundance are affected by biotic interactions.

Here, we use the data of a 4–5 year survey of Lake Tanganyika phytoplankton, for addressing the issue of phytoplankton diversity in a large tropical lake. We studied phytoplankton composition over vertical profiles in the 0–100 m water column, at two distant sites located in the north and in the south basin of the lake, using marker pigments of various phytoplankton classes. Phytoplankton marker pigments have been used widely for assessing biomass at the class level, with many applications in marine, estuarine and freshwater environments (see, e.g. Sarmiento & Descy, 2008). The method is based on the large pigment diversity among the different phyla that constitutes phytoplankton assemblages in surface waters (Falkowski & Raven, 2007). From concentrations of chlorophylls and carotenoids determined by HPLC, algal abundance—or rather biomass in chlorophyll *a* units—can be estimated using different techniques, involving ratios of marker pigment to chlorophyll *a* (Chl *a*) (Mackey et al., 1996). Chemotaxonomy is commonly accepted as a standard method in oceanographic studies and monitoring programs (Jeffrey et al., 1997). The ‘pigment approach’ is less

widespread in the freshwater scientific community; however, it has been used extensively in large lakes surveys (Fietz & Nicklisch, 2004; Descy et al., 2005; Fietz et al., 2005; Sarmiento et al., 2006). In this study, we also investigated selected samples according to standard taxonomic techniques for elucidating the dominant species composition and allocating them to broad classic morphological groups and to the ecological ‘buoyancy’ groups of Reynolds (2006). We demonstrate that, despite the reduced taxonomical resolution of the pigment technique, changes in the phytoplankton assemblage can be detected and can indicate contrasting conditions at two distant monitoring sites. We also investigate, using multivariate analysis (CCA), which environmental factors have a major influence on the phytoplankton assemblage.

Materials and methods

Study sites and limnological measurements

From February 2002 to February or August 2006, water column samples were taken fortnightly from two offshore stations of Lake Tanganyika: Kigoma (Tanzania) in the north (04°51.26'S, 29°35.54'E) and Mpulungu (Zambia), in the south (08°43.98'S, 31°02.43'E). Both sampling sites were located several km away from the shore. Water column samples were collected with Hydrobios (5 l) or Go-Flo (up to 12 l) sampling bottles, every 20 m from the surface down to 100 m, by the local teams of TAFIRI (Tanzanian Fisheries Research Institute, Tanzania) and of DOF (Department of Fisheries, Zambia). Additional sampling at 10 and 30 m was carried out during the Belgian team's seasonal missions. Limnological profiles were usually obtained using CTDs (Seabird 19 in Kigoma, Hydrolab DS4 in Mpulungu). Transparency measurements (Secchi disk depth) and analyses of dissolved nutrients (dissolved inorganic nitrogen, DIN; soluble reactive phosphorus, SRP; dissolved reactive silica, SRSi) were carried out during regular sampling at the two stations. Nutrient analyses were done using standard spectrophotometric techniques (APHA, 2005) or Macherey-Nägel[®] analytical kits; for inorganic N and P forms, absorbance of coloured samples was measured in 40 or 50 mm cells. Euphotic depth (depth at which light is 1% of subsurface light) was derived from Secchi depth (SD) by calculating

the vertical light attenuation coefficient ($k = 1.57/SD$). The conversion coefficient was obtained by calibration with measurement of PAR downwards attenuation with LICOR quantum sensors. Depth of the mixed layer was estimated from the depth of the top of the thermocline, as shown by the temperature and oxygen vertical profiles obtained with the CTDs.

The sampling period started in February 2002 and went through the beginning of 2006 at Kigoma (95 sampling series), and to August 2006 in Mpulungu (123 sampling series). Samples were missing in Kigoma from September 2004 through December 2004. Air temperature, wind speed and rainfall were collected from Kigoma and Mpulungu weather stations. As an assessment of water column thermal stability in upper water, we calculated the potential energy anomaly (PEA, Simpson et al., 1982) from the CTD temperature profiles from 0 to 100 m depth.

Phytoplankton pigment analysis and processing of data

Samples for HPLC analysis were obtained from filtration of 3–4 l on Whatman GF/F or Macherey-Nägel GF5 filters and of 0.7 µm nominal pore size. The subsequent procedure for pigment extraction and analysis followed Descy et al. (2005). Extracts in 90% acetone were then stored in 2 ml amber vials in a freezer (at –25°C) for several months (under the regular sampling scheme) or for 2–3 weeks (for the seasonal sampling missions), and transported to Belgium on ice in cooler boxes. Pigment concentrations were obtained by reverse-phase HPLC using Wright et al.'s method (1991) and a Waters analytical system, with detection in absorbance of 436 nm with a photodiode array detector and with a fluorescence detector set up for optimising detection of chlorophylls and their degradation products. Pigment data processing used the CHEMTAX software (Mackey et al., 1996). CHEMTAX (for CHEmical TAXonomy) is a computer program that allows to allocate Chl *a* among different algal groups defined by a suite of pigment 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: chl *a* ratios and generates the fraction of the total chl *a* pool belonging to each pigment-determined group.

Details of the processing method are given in Descy et al. (2005). The following algal classes were quantified, using several marker pigments: chlorophytes (neoxanthin, violaxanthin, lutein, zeaxanthin, chlorophyll *b*), chrysophytes (fucoxanthin, violaxanthin), diatoms (fucoxanthin, diadinoxanthin, diatoxanthin), cryptophytes (alloxanthin, α -carotene), cyanobacteria type 1 (zeaxanthin), cyanobacteria type 2 (zeaxanthin, echinenone), and dinoflagellates (peridinin, diadinoxanthin, diatoxanthin). Euglenophytes, poorly represented in Lake Tanganyika, were not included in the analysis. When a marker pigment was shared among several classes, the input ratio matrix contained different marker/Chl *a* ratios. Chrysophytes and diatoms were not systematically distinguished in this study, due to uncertainties related to low concentration of some of their diagnostic pigments. However, diatoms were the most important fucoxanthin-containing phytoplankton group in recent Lake Tanganyika samples (Cocquyt & Vyverman, 2005). Total phytoplankton biomass (Chl *a*) and biomass of algal groups were measured at all sampling depths (at least from 0 to 100 m every 20 m).

Zooplankton sampling and data acquisition

The water column was sampled with a 100 μm mesh plankton net in the 0–100 m layer. The samples were concentrated by settling in a 250 ml PVC cylinder for 48 h; after removal of the supernatant, the final volume was adjusted to 100 ml, with lake water added with formaline. Zooplankton counts were carried out with a Leica DIML inverted microscope, at a maximal enlargement of 400 \times , most of the time on subsamples. Four species of copepods were identified: *Microcyclops cunningtonii*, *Tropocyclops tenellus*, *Mesocyclops aequatorialis aequatorialis* and *Tropodiaptomus simplex*. Zooplankton numbers were expressed as mean abundance in the water column (numbers m^{-3}) or biomass per unit area (mg C m^{-2}), taking into account net opening size and the sampling over a 100 m water column. For converting numbers to biomass, we used the following estimates of zooplankton carbon: 2.25 $\mu\text{g C}$ for adult calanoids, 2 $\mu\text{g C}$ for adult cyclopoids, 1.3 $\mu\text{g C}$ for calanoid copepodites, 0.75 $\mu\text{g C}$ for cyclopoid copepodites and 0.175 $\mu\text{g C}$ for nauplii (Kurki et al., 1999).

Multivariate analysis

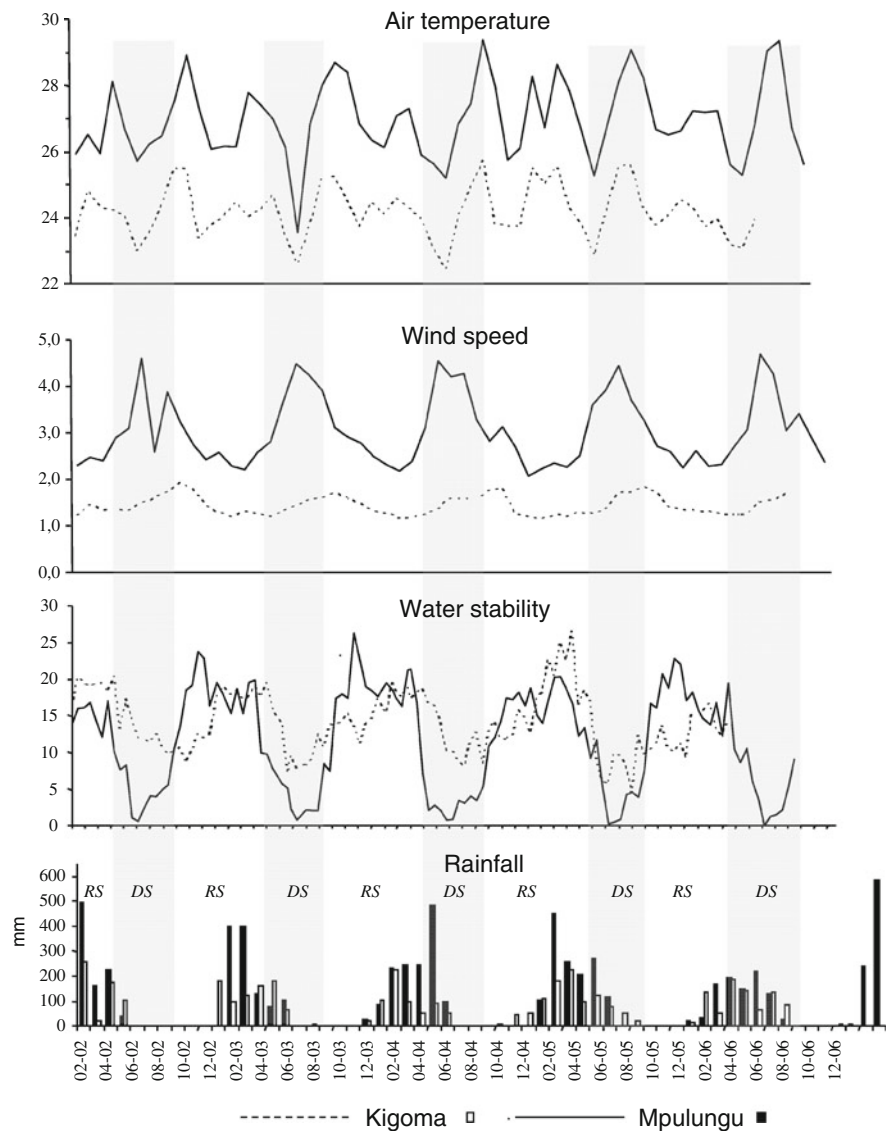
A canonical correspondence analysis, using the CANOCO 4.5 software (ter Braak & Šmilauer, 2002), was run on a database containing the main limnological variables (surface temperature: Tsurf; depth of the mixed layer: Zm; vertical attenuation coefficient of light: *K*; the ratio mixed layer: euphotic layer: Zm:Zeu), SRP and DIN, metazooplankton abundance or biomass, and phytoplankton group biomass and contribution to chlorophyll *a*. As nutrient and zooplankton data were not available for the entire study period, the data analysed covered the period 2002–2004 ($n = 116$). Nutrients, chlorophyll *a* and phytoplankton group biomass were averaged for the euphotic zone (ca. the layer 0–40 m); chlorophyll *a* was also integrated over the whole water column sampled. All data, except surface temperature, euphotic depth, depth of the mixed layer and the Zm:Zeu ratio, were log-transformed before analysis.

Results

Physical and chemical conditions

The meteorological and lake stability data are shown in Fig. 1. A strong annual cycle is well observed, as the seasons are clearly identified: in particular, water column stability varied seasonally as a result of the wind and air temperature regimes. Variations in stability influenced the depth of the mixed layer at both sites, hence the availability of nutrients, water transparency and exposure to light. A synthesis of the available limnological and nutrient data is shown in Table 1. Significant differences (Student *t* test with $P < 0.05$) were found between the two sites for Zeu, Zm, Zm:Zeu, surface temperature, DIN and SRSi, in the dry season. These differences did not appear for the rainy season (except for DIN and SrSi), indicating a greater spatial homogeneity of the lake in this season. At Mpulungu, highly significant differences ($P < 0.005$) were found between seasons for all variables, except SRSi. Such strong seasonal differences did not appear in Kigoma, except for Zm, surface temperature and SRP, showing that deep mixing, resulting from a weaker thermal density gradient combined with increased wind stress, does affect P availability to phytoplankton.

Fig. 1 Air temperature, wind speed, water column stability (as potential energy anomaly over 0–100 m depth) and rainfall at Kigoma and Mpulungu from 2002 to 2006. *RS* rainy season, *DS* dry season



Phytoplankton diversity

As expected from earlier studies (see “[Introduction](#)” section), the phytoplankton of Lake Tanganyika was essentially a chlorophytes–cyanobacteria assemblage, with some diatoms (and chrysophytes, not separated from diatoms, see above). Other groups (cryptophytes, dinoflagellates), had much lower importance, even though some local developments of short duration can be occasionally observed, usually as surface blooms (dinoflagellates) or deep chlorophyll maxima (cryptophytes). The dominant cyanobacteria were coccal unicells and colonies (mostly

Synechococcus sp., *Aphanocapsa* spp., *Gloeotheca hindakii* and *Chroococcus* spp.), or filaments (mainly *Anabaena* spp. and *Anabaenopsis tanganyikae*). The chlorophytes were of coccal type, represented by unicells, colonies and coenobia (*Oocystis lacustris*, *Lobocystis planctonica*, *Closteriopsis petkovii*, *Coelastrum reticulatum*, *Palmelocystis planctonica*, *Eutetmemorus* sp., *Coenocystis subcylindrica*, *Nephrocystium agardhianum*), some of them with strikingly large dimensions (*Eremosphaera tanganyikae*).

Diatoms mostly belonged to the genus *Nitzschia*, with two main taxa, *N. asterionelloides* and *N. cf. fonticola*. More detail can be found in Cocquyt &

Table 1 Summary of the physical and chemical data in Lake Tanganyika, 2002–2006

	K (m^{-1})	Z_{eu} (m)	Z_m (m)	$Z_m: Z_{eu}$	T_{surf} ($^{\circ}C$)	SRP ($\mu g\ l^{-1}$)	DIN ($\mu g\ l^{-1}$)	SRSi ($mg\ l^{-1}$)
<i>Kigoma</i>								
DS								
Average	0.12	39	49	1.3	26.5	14.7	30.1	0.82
Minimum	0.09	24	18	0.5	25.6	0.1	0.6	0.49
Maximum	0.19	53	95	4.0	27.6	54.8	166.0	1.37
n	35	35	36	35	36	26	27	22
RS								
Average	0.13	36	39	1.1	26.9	5.9	28.3	0.77
Minimum	0.08	24	22	0.4	25.8	0.0	0.4	0.50
Maximum	0.19	56	60	1.7	28.0	31.9	81.4	0.99
n	42	42	40	40	41	26	26	22
<i>Mpulungu</i>								
DS								
Average	0.16	31	61	2.2	25.3	17.0	57.4	1.03
Minimum	0.08	14	17	0.4	23.9	2.2	21.9	0.41
Maximum	0.33	55	100	6.6	27.2	46.8	101.1	1.73
n	44	44	42	42	44	25	25	25
RS								
Average	0.13	40	35	1.0	27.5	6.4	42.7	0.96
Minimum	0.07	17	13	0.3	24.9	1.2	9.8	0.65
Maximum	0.27	67	100	5.7	28.8	16.3	122.8	1.71
n	73	73	72	72	74	47	47	47

DS dry season, RS rainy season, K vertical attenuation coefficient of light, Z_{eu} euphotic depth, Z_m depth of the mixed layer, T_{surf} surface temperature, SRP soluble reactive phosphate, DIN dissolved inorganic nitrogen, SRSi soluble reactive silica, n number of observation per season, considering the May–September period as the dry season, and the rest of the year as the rainy season. Nutrient concentrations were averaged on the euphotic layer, 0–40 m

Vyverman (2005), Plisnier & Descy (2005), Stoyneva et al. (2005, 2006, 2007a, b, 2008, 2009).

Vertical distribution of phytoplankton

Most of the phytoplankton biomass was located in the 0–40 m layer, with maxima at 0 or 20 m, and more rarely at 40 m. DCM could be occasionally observed (Fig. 2), but they were relatively rare: they occurred essentially in the rainy season, when the thermocline was located within the euphotic zone, i.e. for thermocline depth <40 m. However, depending on the state of the water column and on the phytoplankton present, the vertical distribution of the phytoplankton groups may be very different, as illustrated in Descy et al. (2005). It is obviously in the rainy season, with a stratified water column, that the most variable vertical distribution was observed. Figure 2 shows one of the DCM observed in the study period.

These events were short-lived, as far as it could be observed with the 2-week sampling interval used most of the time in this study.

Temporal variations of Chl *a* and biomass of the main phytoplankton groups

In Fig. 3, we present Chl *a* integrated over the 100 m surface layer and average total zooplankton abundance in the same layer. The range of Chl *a* was 5–155 $mg\ m^{-2}$ off Mpulungu and 8–95 $mg\ m^{-2}$ off Kigoma, which may be a result of higher phytoplankton production in the south of the lake. Off Kigoma, zooplankton maxima tended to occur after the dry season chlorophyll *a* peaks, whereas a clear pattern cannot be observed in the Mpulungu data. Changes in phytoplankton composition can be examined with depth–time diagrams (Figs. 4, 5, 6, 7).

Fig. 2 Examples of deep chlorophyll maximum (DCM) in Lake Tanganyika, observed in the south basin, in February 2006. Note that diatoms were essentially responsible of this DCM

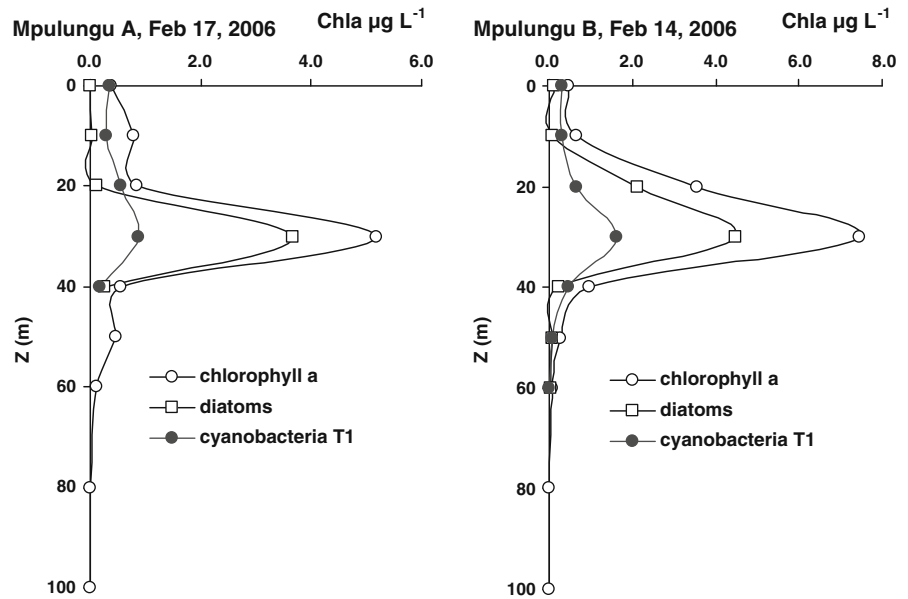
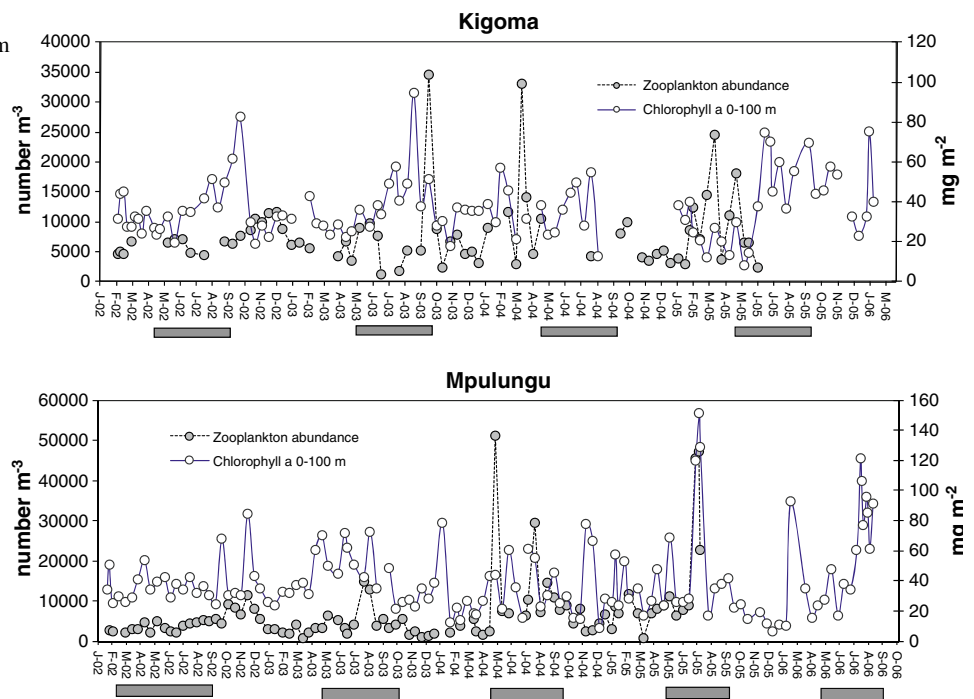


Fig. 3 Chlorophyll *a* integrated over the 0–100 m water column in Lake Tanganyika, from the HPLC analysis of the phytoplankton samples collected from February 2002 to February/August 2006, at Kigoma (northern site) and Mpulungu (southern site), and total zooplankton abundance (number m⁻³), when available. Grey bars indicate the dry season periods



Cyanobacteria T1 (pigment type 1, or *Synechococcus* pigment type, Jeffrey et al., 1997) were clearly more abundant in the south than in the north (Fig. 4). In the water column, they were located essentially in the 0–20 m layer, but were distributed throughout the mixed layer when deep mixing occurred (as, for instance in August 2005 at both

sites). These cyanobacteria increased in the dry seasons at both stations.

Cyanobacteria T2 (pigment type 2, having echinone) are, in Lake Tanganyika, filamentous forms with gas vesicles, which can adjust their buoyancy and therefore are mostly successful in well stratified water columns. These cyanobacteria are also efficient

Fig. 4 Chlorophyll *a* biomass of cyanobacteria T1 (mostly *Synechococcus* spp.) at both stations in Lake Tanganyika for the study period (February 2002–February 2006)

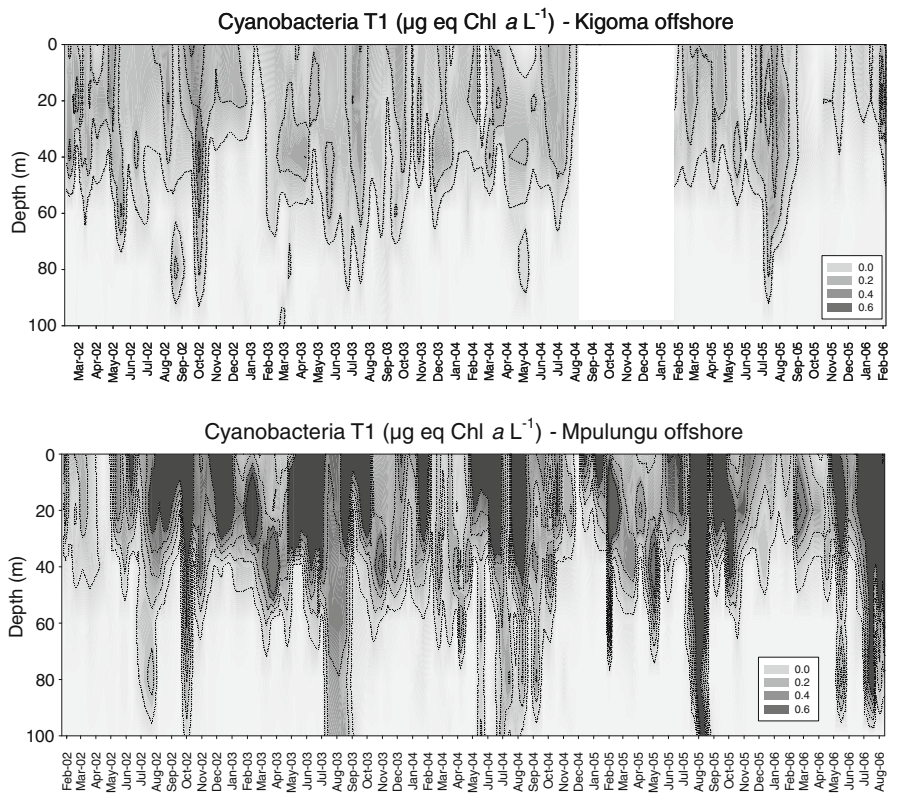


Fig. 5 Chlorophyll *a* biomass of cyanobacteria T2 at both stations in Lake Tanganyika for the study period (February 2002–February 2006)

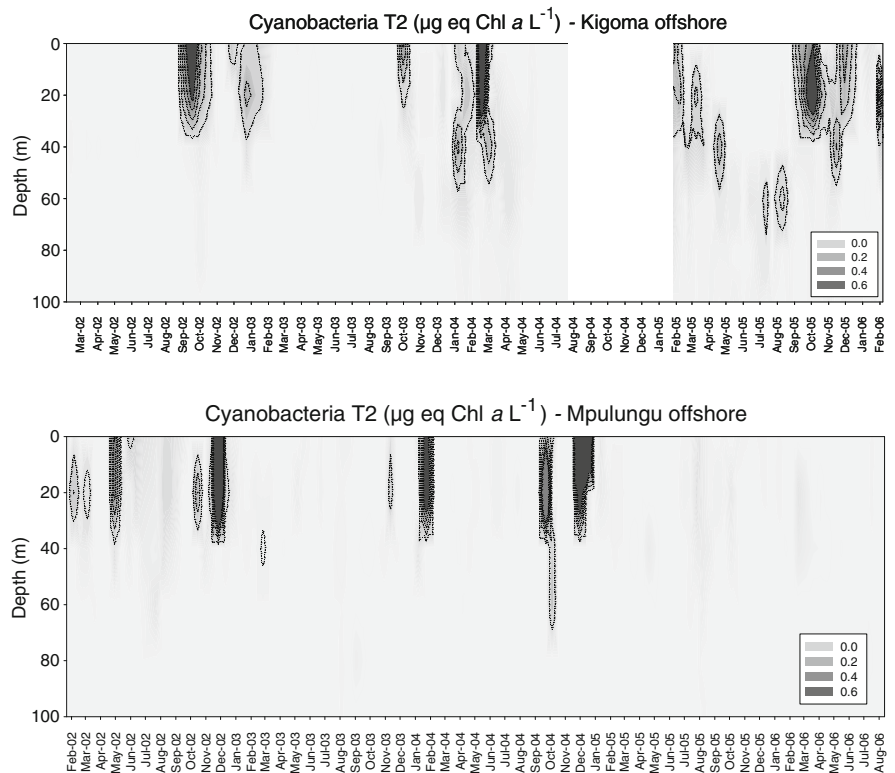


Fig. 6 Chlorophyll *a* biomass of green algae at both stations in Lake Tanganyika for the study period (February 2002–February 2006)

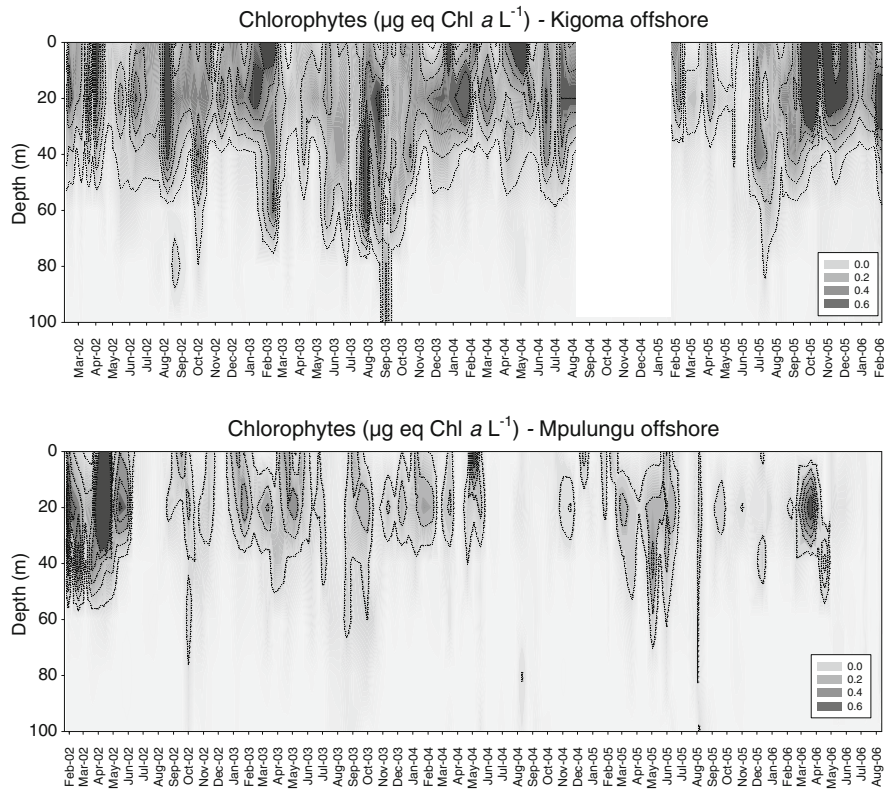
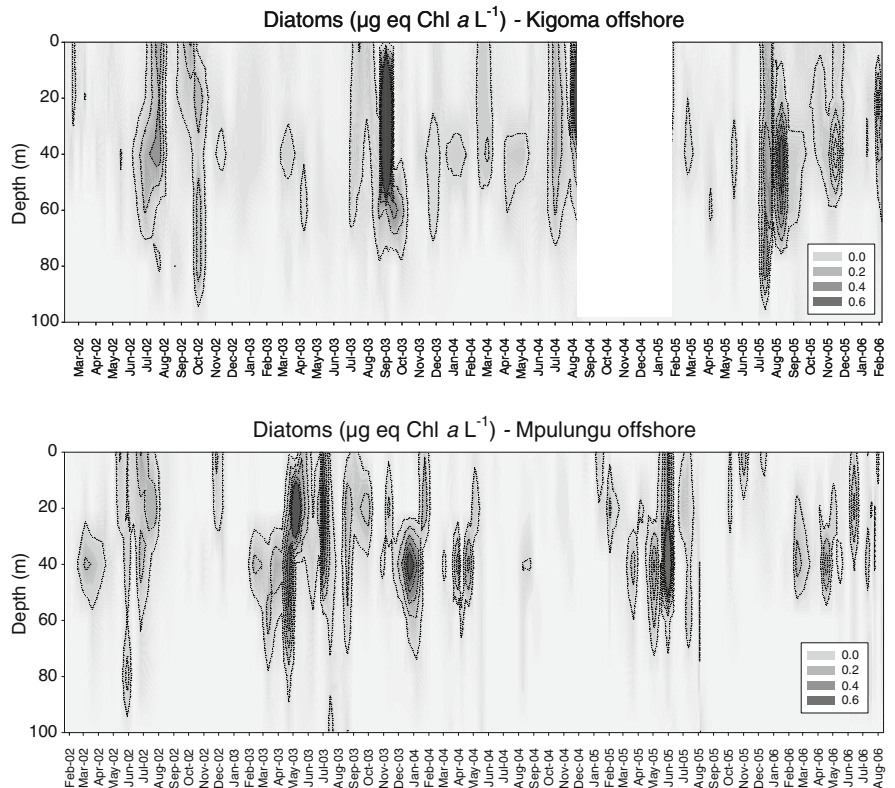


Fig. 7 Chlorophyll *a* biomass of diatoms at both stations in Lake Tanganyika for the study period (February 2002–February 2006)



N-fixers, and maybe favoured when N supply is low relative to P supply (low N:P ratio). These surface ‘blooms’ may have been responsible of surface chlorophyll *a* peaks detected by remote sensing (Plisnier et al., 2009; Horion et al., 2010). Accordingly, Fig. 5 shows scattered development of these cyanobacteria off both survey sites, with similar or different timing in surface bloom development. For instance, while they occurred throughout the lake in the beginning of 2004, they were observed only in the north at the end of 2005. This again reflects large differences in physical status of the mixolimnion in both lake regions.

In Lake Tanganyika, green algae (Fig. 6) were mostly located in the 0–20 m layer, with often distinct peaks at 20-m depth, and tended to be more abundant in the rainy season conditions, i.e. in a well stratified water column, at high irradiance. Almost all well-developed chlorophytes were mucilage-encased, belonging to the neutrally buoyant type (as defined by Reynolds, 2006)—e.g. *Closteriopsis*, *Oocystis*, *Lobocystis*, *Coenocystis*, *Palmelocystis*, *Eutetmemorus* and *Nephrocystium*. They were mostly well developed in the northern station (Stoyneva et al., 2007a, b). Exceptions were *Eremosphaera tanganyikae* and the non-motile, negatively buoyant coenobia of *Pediastrum* spp. and *Scenedesmus* spp., which were better developed predominately in the transitional months of May and September in the southern lake basin.

Diatoms (Fig. 7) were typically located at greater depth than the other main phytoplankton classes: they tended to form maxima, around 40 m, and occasionally lower. They clearly increased in the northern part of the lake during deeper mixing events, and therefore could be good markers of the dry season period. They possessed a strong seasonality off Kigoma, but less so off Mpulungu, where they were less abundant and did not systematically develop in the dry season. Moreover, we observed a rainy season peak (in January 2004), most probably made of another taxon (presumably *Nitzschia fonticola* Grun.) than the one developing in the dry seasons (mostly *N. asterionelloides* O. Müll.).

Canonical correspondence analysis results

The canonical correspondence analysis (CCA) of the data from both sites (Fig. 8) yielded relatively strong relations between chlorophyll *a* biomass of

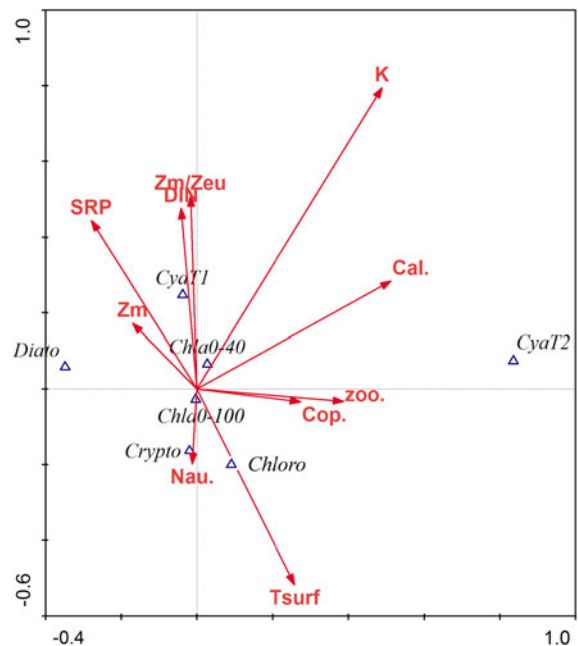


Fig. 8 CCA biplot of phytoplankton groups (triangles) and environmental variables (arrows). SRP soluble reactive phosphorus, DIN dissolved inorganic nitrogen, Zm depth of the mixed layer, K vertical light attenuation coefficient, Zm/Zeu ratio depth of the mixed layer: euphotic layer, Tsurf lake surface temperature, zoo total metazooplankton abundance, Cal. calanoid copepod abundance, Cop. cyclopoid copepod abundance, Nau. nauplii abundance. Phytoplankton: Diato diatoms + chrysophytes, Crypto cryptophytes, Chloro chlorophytes, cyaT1 cyanobacteria pigment type 1, cyaT2 cyanobacteria pigment type 2, Chla0–40 average chlorophyll *a* in the euphotic layer, Chla0–100 chlorophyll *a* integrated over the upper 100 m. Phytoplankton biomass was expressed as log₁₀ (chlorophyll *a* biomass)

phytoplankton groups and environmental data: ‘species–environment’ correlations were 0.502 and 0.599, for the first and second variable, respectively. The cumulated variance explained by the two-first canonical variables was 85.6% (56.2% for the first variable and 29.4% for the second). The forward selection of environmental variables identified the vertical light attenuation coefficient and surface temperature in first and second position, calanoid abundance in the third position, and then Zm, Zm:Zeu and SRP and DIN. This suggests that light and the thermal density gradient were key factors explaining phytoplankton structure, but also that herbivorous zooplankton abundance had a significant effect. The analyses carried out using zooplankton biomass instead of zooplankton abundance yielded similar results, but

with lower levels of significance. The plots of the phytoplankton groups (Fig. 8) clearly oppose diatoms (favoured by high Zm and SRP, and low zooplankton numbers) and cyanobacteria T2 (favoured by low Zm, low DIN and SRP, and by high zooplankton numbers). As expected, chlorophytes were favoured by high surface temperature and low nutrients and low Zm:Zeu (i.e. stratified conditions). As for cyanobacteria T1, they best developed at low surface temperature, high Zm (particularly at the Mpulungu site) and high nutrients, especially DIN, and were not influenced by adult copepods.

Data were also processed separately for the two sites, with broadly similar results. At Kigoma ($n = 45$), the forward selection identified the environmental factors almost in the same order as for the complete data set (but with surface temperature as the major factor). At Mpulungu ($n = 71$), however, SRP came out as the primary environmental variable, followed by light attenuation and, interestingly, by nauplii abundance, while adult copepods were selected after Zm and Zm:Zeu. This points to significant differences either in the composition of the data sets (more records from the rainy season in Mpulungu) or in actual differences in the variables determining the phytoplankton assemblage the two sites.

Discussion

All the aforementioned data and observations lead again to the questions, which emerge in the plankton ecology theory when Hutchinson (1959) wrote his famous paper on the diversity patterns and limitations group various driving forces in different kind of communities. Even now, half-a-century after its publication, this seminal article obviously shapes many of the experimental and theoretical research practices. In limnology many studies have been made for testing a wide range of explanations for high species diversity and coexistence in the plankton. These have focused on abiotic factors and biotic interactions, spatial heterogeneity, non-equilibrium dynamics, etc. But how these different forces apply may depend on the specific aquatic systems and there is still much to learn from the conclusions drawn from many ecological studies of different types of communities.

Here, we recorded variations of phytoplankton groups, identified and quantified by analysis of

marker pigments at two distant offshore sites of a large tropical lake, Lake Tanganyika. The pigment approach allowed a fortnightly phytoplankton survey for several years, based on vertical profiles over the 0–100 m water column. This study essentially based on pigments may have been sufficient to capture the main temporal variations of the phytoplankton assemblages at the two sites. Even though the sampling design and methods for phytoplankton examination were different, our results broadly match those from other studies, as far as the dynamics of the classes are concerned (Hecky & Kling, 1981; Cocquyt & Vyverman, 2005). Slight differences may stem from the fact that the studies using microscopy dealt with samples from 20-m depth and with phytoplankton $>5 \mu\text{m}$, which is about the lower resolution of microscope studies. Moreover, as we identified the most abundant taxa in selected samples, we improved the taxonomic resolution of our study: this combination of a pigment survey with identification of the main taxa may be sufficient in ecological studies of lake phytoplankton (Sarmiento & Descy, 2008), and is able to offset the shortcomings of microscope studies, which may, for instance, miss some significant microorganisms, such as picoplankton or photosynthetic flagellates, poorly preserved in fixed material.

For instance, among particular patterns of vertical distribution, we detected surface blooms of filamentous cyanobacteria by their pigment signature, and these surface blooms match with surface chlorophyll *a* estimated by remote sensing (Bergamino et al., 2010). Another example is the location of biomass maxima near the thermocline, mostly due to diatoms and cryptophytes. Some phytoplankton groups, in particular green algae and diatoms, presented a rather clear seasonal development, indicating transitions from the calm, stratified conditions of the rainy season, to the dry season situation, characterised by deeper mixed layer and better nutrient supply from the internal loading. We have reported elsewhere (Stenuite et al., 2007) the corresponding changes in chlorophyll *a*, particulate organic carbon and seston C:N and C:P ratios at both study sites. In accordance with nutrient supply variability from internal loading, C:P tended to be higher during the stratified conditions of the rainy season than in the dry season. C:N ratios followed a similar seasonal trend, but indicated a possible greater N limitation at times in the northern station than in the southern one (Stenuite et al., 2007).

Although some constancy of the assemblages could be expected given the ‘endless summer’ in this type of lake, large variations of different phytoplankton groups were observed. We believe that these variations resulted from the large spatial and temporal heterogeneity in Lake Tanganyika. As for spatial variation, from our data as well from data from cruises as those reported by Hecky & Kling (1981), it clearly appears that phytoplankton composition and dynamics differ strongly in different lake parts. This was recently confirmed by chlorophyll *a* surface concentrations estimated from satellite images collected mostly in parallel with our pigment survey: Bergamino et al. (2010) identified 13 different sub-regions in Lake Tanganyika, from the pattern of chlorophyll *a* concentration. As for temporal variations, the variability of phytoplankton composition at the class level was conspicuously very large, and the degree of variability differed according to the lake region. In our study, the factors determining this variability were approached through the analysis of the phytoplankton response to several environmental variables, and to mesozooplankton abundance. In accordance with previous publications on phytoplankton studies in this lake (Hecky & Kling, 1981; Salonen et al., 1999; Langenberg et al., 2002; Cocquyt & Vyverman, 2005), the CCA identified physical variables as light availability and mixed layer depth as key drivers of phytoplankton biomass or abundance. Macronutrient concentrations were also identified in the forward selection process of the CCA, but calanoid abundance came out before. This provides clear evidence of grazing pressure by herbivorous zooplankton being a significant determinant of phytoplankton biomass and composition in Lake Tanganyika, as correctly hypothesised by Hecky & Kling (1981). In addition, the CCA reveals differential sensitivity to grazers among phytoplankton groups.

Four major phytoplankton groups deserve more detailed discussion.

Cyanobacteria type 2 in Lake Tanganyika are filamentous forms (*Anabaena* spp., *Anabaenopsis tanganyikae*), which are grazing-resistant: this may be one of the keys to their success at the dry-rainy season transition in October–November (Hecky & Kling, 1981; Salonen et al., 1999). As explained in former studies, they have the advantage of buoyancy due to their gas vesicles and of efficient N fixation

with their heterocytes, and exploit the SRP-rich conditions of the end of the dry season. However, reduction of grazing losses related to large size may be necessary to survival and surface bloom formation in conditions in which zooplankton are at their maximal abundance. The mucilaginous colonies of the positively buoyant *Gloeothece hindakii* equipped with aerotopes were also more abundant in the well stratified lake waters in the rainy season, when the species often appears in dominant phytoplankton assemblages (sometimes down to 40 m).

The other cyanobacterial group, identified here by their pigment signature, consisted mostly of picocyanobacteria of the genus *Synechococcus* and some other chroococcales, typically embedded in mucilage sheaths. Picocyanobacteria are often dominant in Lake Tanganyika phytoplankton, and the key to their success may be high light in the transparent water column, combined with the depth of the mixed layer, selecting for those microorganisms capable of quick acclimation to a varying light climate (Stenuite et al., 2009). Our CCA analysis confirms that competition for uptake of macronutrients did not appear to play a major role. Whereas one would expect that *Synechococcus* would outcompete other phytoplankton in nutrient-poor conditions (e.g., Raven, 1986; Weisse, 1993), the CCA shows that cyanobacteria type 1 in Lake Tanganyika were positively correlated to high DIN and SRP. Interestingly, the CCA also detects an influence of nauplii on phytoplankton abundance, particularly for the southern study site: this may point to grazing as a potential factor determining abundance of small cyanobacteria in Lake Tanganyika. Their small cell size likely allows them to escape grazing by adult copepods, whereas they are preyed upon by microzooplankton, mainly phagotrophic flagellates (Tarbe, 2010).

Chlorophytes were the next most abundant phytoplankton group in our survey, and were conspicuously more successful in the northern site, where higher surface temperature and the stronger temperature-density gradient maintained stratification throughout the entire year. The multivariate analysis clearly confirms their success in these conditions, associated with low nutrients, shallow mixed layer and high light (low Zm:Zeu ratio). Green algae are the most diverse phytoplankton group in Lake Tanganyika (Cocquyt & Vyverman, 2005), but few taxa achieve high abundance, and those doing so are

mostly coccal unicells, coenobia or colonies, which are more noticeable in the stratified period of the rainy season. Resistance to grazing, due to large size, mucilage envelopes or cell walls with protective thick algaenan layers, might again be an advantage, which our data analysis does not show, but this may result from the low taxonomic resolution of the pigment approach. It is important to stress that endosymbionts in ciliates, identified as *Siderocelis irregularis* (Stoyneva et al., 2008) are not distinguished from the aposymbiotic cells of the same species and the other free-living green algae in our samples; this particular taxon may at times contribute to the biomass of green algae in our records. However, it is likely that these endosymbionts did not represent a large fraction of the green algal biomass: indeed, Pirlot et al. (2006) estimated that the biomass of these endosymbionts was generally about 2–3% of total phytoplankton biomass when the ciliates numbers were about 300 ml⁻¹, which is in the higher range of *Strombidium* abundance reported by Hecky & Kling (1987).

The non-motile, often mucilage-bounded coccal green algae occur widely throughout the world, particularly in relatively clear waters of large lakes. Hutchinson (1967) suggested the term ‘oligotrophic chlorococcal plankton’ to the *Oocystis*-rich phytoplankton, which he had observed in large clear Asian lakes. Later on, it was suggested that the chlorococcal association with large oligotrophic lakes is ‘in consequence of the clarity of their mixed layers’ (Reynolds, 1997).

Given the rarity of Chrysophytes in the recent samples of Lake Tanganyika (Cocquyt & Vyverman, 2005), and the few dominant diatoms, the resolution of our approach is rather good for this group. Planktonic diatoms in Lake Tanganyika mostly comprise two taxa with contrasting phenology: *Nitzschia asterionelloides* and *Nitzschia* cf. *fonticola* (Cocquyt & Vyverman, 2005). The first is a colonial form that was associated with the diatom peaks during the dry season: this taxon alone accounts for the position of diatoms in the CCA diagram, associated with deep mixed layer depth and high SRP. Diatoms are also negatively correlated to zooplankton and adult copepod biomass, most likely because they are heavily grazed, thereby contributing to the zooplankton peaks.

Conclusion

This contribution essentially dealt with ecological diversity of the pelagic phytoplankton of a large tropical lake. We attempted to use information available from a long-term survey for understanding phytoplankton dynamics at the class level, but also, to some extent, at a lower taxonomic level. Despite Lake Tanganyika presents permanently stratified conditions (the ‘endless summer’ of Kilham & Kilham, 1990), with the notable exception of the southern end where the dry season upwelling occurs, it does exhibit large spatial and temporal variability of physical, chemical and biotic factors, which leads to some taxonomic diversity among phytoplankton. However, when looking at the available taxonomic lists (as in Cocquyt & Vyverman, 2005), the diversity does not seem so high, by comparison with temperate lakes. These authors observed 89 taxa in an offshore site of Lake Tanganyika (of which not all are truly planktonic). Still, it is a lot of different taxa for an oligotrophic environment where resources are scarce, with all species competing for them. Our data suggest that the factors allowing coexistence of several phytoplankton taxa are likely differential vertical distribution in the water column, which allows spatial partitioning of light and nutrients, and temporal variability (occurring at time scales preventing long-term dominance by a single taxon), along with effects of predation by grazers.

Finally, it may be useful to stress that our perception of biodiversity depends on the tools we use. For instance, recent studies which have used sequencing of 18S rDNA have allowed uncovering an unexpected diversity of protists in Lake Tanganyika (Tarbe, 2010): among them were several phylotypes of photosynthetic Chrysophyceae, Cryptophytes and Dinophyceae, with some of them possibly new to the lake. Similarly, 16S rDNA studies have identified five strains of *Synechococcus* in Lake Tanganyika (Stenuite, 2009). This suggests that we may soon uncover that the diversity of phytoplankton of tropical lakes is much greater than we thought, and that it can only be explained by non-equilibrium dynamics (Scheffer et al., 2003), resulting from niche specialisation, environmental variability and interactions (competition, predation) among many species.

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