Article

Microorganisms of the East African Great Lakes and their response to environmental changes

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Abstract

We have reviewed the phytoplankton composition and succession in the East African Great Lakes, their response to environmental changes, and the communities of microorganisms of the microbial food web. Recent studies in some great lakes, as well as progress in understanding phytoplankton succession and response to environmental factors, enable us to update knowledge of the phytoplankton ecology of these lakes. In particular, we present information indicating that phytoplankton composition in lakes Tanganyika and Kivu may reflect recent changes as a result of global warming or species introduction. We also stress the importance of microbes (at the base of the food web) in these systems and suggest that the microbial food web, which has been mostly overlooked until recently, may play a very large role in determining productivity and nutrient cycling in these large lakes.

Keywords: Phytoplankton; tropical lakes; microbial food web; community changes; Tanganyika; Malawi; Kivu; Victoria; Edward; Albert.

Introduction

In a context of increased evidence of human-induced climate change and its negative impacts on the world's ecosystems, the productivity of the East African Great Lakes (Fig. 1) has attracted much attention from limnologists, fisheries experts, geochemists and paleolimnologists. Despite the fact that the impact of climate on these ecosystems is still a matter of debate (Sarvala et al., 2006; Verburg et al., 2006), evidence has been accumulating that environmental changes have adversely affected these lakes in recent decades, even though the stories may differ among lakes. Lake Tanganyika and Lake Malawi are threatened by many anthropogenic influences: global warming (Verburg et al., 2003; Verschuren, 2003), fisheries overexploitation (Sarvala et al., 2006), watershed erosion and wastewater discharge (Oguto-Ohwayo & Hecky, 1991; Lehman, 1996), affecting both the littoral and pelagic ecosystems. In Lake Victoria and Lake Kivu, in addition to these pressures, ecosystem changes have been driven by alien species introduction, with spectacular consequences on ecosystem function, geochemistry, biodiversity, fisheries and socio-economics (Oguto-Ohwayo & Hecky, 1991; Odada et al., 2003). Recent reports have attempted

Fig. 1. Map of the East African Rift region, indicating the large lakes and surrounding countries.

to evaluate the present situation in each lake and have stressed the measures to be taken for preserving and restoring these lakes (Odada et al., 2004).

Even though each of these large lakes has unique characteristics, they share some common features:

- They are among the largest and/or deepest lakes in the world; some of them are very old, and their sediments are invaluable archives for paleolimnology and offer opportunities for reconstruction of past climates;
- They are located in the tropics, and they enjoy 'endless summer' (Kilham & Kilham, 1990); consequently the deepest lakes remain stratified all year round, although there is substantial variation in mixed-layer depth depending on seasonal factors (surface temperature, winds);
- They support a large biodiversity (particularly well known for fishes and some other animal groups);
- The fishery is still an important food resource for local populations: for instance, Lake Tanganyika has a

highly productive fishery (Hecky et al., 1981; Coulter, 1991), based on a few, mostly pelagic, species;

- Due to their large size, ecosystem function is dominated by pelagic processes; hence bacteria, phytoplankton and protozoans are a key component of the aquatic community, responding to various factors driven by physical forcing, and whose production and structure determine consumer production and fisheries yield.

The overwhelming importance of phytoplankton in ecosystem processes in large lakes has been emphasised by many authors (e.g. Reynolds et al., 2000), yet the phytoplankton of tropical lakes has received comparatively little attention. In these lakes, the focus of most studies has been on fisheries and animal biodiversity (e.g. Lévêque, 1995), on geochemistry (Craig et al., 1974; Edmond et al., 1993) and on paleolimnology (Haberyan & Hecky, 1987; Johnson, 1996; Cohen et al., 2005). This is why a review, starting from some key papers on phytoplankton ecology in tropical lakes and incorporating recent data, may be of special interest.

In this paper, we review phytoplankton composition and succession in the East African Great Lakes, their response to environmental changes, and the communities of microorganisms and the microbial food web. The last aspect is fairly new and refers to very recent studies, as studies on microbes in these large lakes were scarce until the 1990s. In particular, we believe that possible changes in food web structure need to be addressed, as they may have large consequences on lake productivity.

Phytoplankton diversity and succession in the East African Great Lakes

Margalef's differentiation between *biodiversity*, as the total genetic information present in the ecosystem, and *diversity*, as the set of core species, responsible for carbon and energy flow in the ecosystem at a particular time (Margalef, 1994, 1997; see also Pedrós-Alió, 2006), fits perfectly well with the history of phytoplankton research in the East African Rift region. The first scientific expeditions basically consisted of taxonomical studies and led to the description of many

species, some of them new to science (in Lake Tanganyika: e.g. West, 1907; Van Meel, 1954; in Lake Kivu: Hustedt, 1949; Frémy et al., 1949; in Lake Malawi: e.g. Schmidle, 1898, 1902; Iles, 1960; in Lake Victoria: e.g. West, 1907; Woloszynska, 1914; Bachman, 1933; Fish, 1952; Evans, 1962a, b). A complete reference list and a floristic inventory of the pelagic and benthic algae of the East African Great Lakes can be found in Cocquyt et al. (1993) and Cocquyt & Vyverman (1994). In a second stage, a number of studies were published addressing the dynamics of the dominant phytoplankton species, to increase understanding of the ecology of these pelagic algal communities. In this review we will attempt to update the review by Talling (1986) and the comparative study by Hecky & Kling (1987), with an analysis at the *diversity* level (*sensu* Margalef) focusing on the functional aspects of the dominant assemblages of phytoplankton in the East African Great Lakes.

Contrary to the common assumption that in tropical regions the 'endless summer' dictates very constant conditions with only subtle contrasts between seasons, it has been demonstrated that the algal succession in the East African Great Lakes is largely influenced by meteorological conditions and by the physical constraints that differ during a year cycle (e.g. Lemoalle et al., 1981; Talling, 1986; Hecky & Kling, 1987; Sarmento et al., 2006). The East African region is characterised by a dry season with south-eastern dominant winds (from June to September), and a calmer and warmer rainy season (October to May). Near the equator (Lakes Kivu and Victoria) a short dry season might be defined around January, when the winds can be stronger than in typical rainy season conditions (Talling, 1966; Sarmento et al., 2006), which will obviously influence the seasonal variations of phytoplankton abundance and composition.

Hecky & Kling (1981) published a seasonal cycle of the phytoplankton (and protozooplankton) species composition, biomass and chlorophyll *a* in Lake Tanganyika. A chlorophyte (Chroococcales) assemblage was described as characteristic of the wet season (October to April), with high light and poor nutrient availability in the shallow epilimnion. In the dry season (May to 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* spp.) developed at the end of the dry season, when the water column re-stratified. The Tanganyika phytoplankton record was completed by cruise samples that allowed spatial variation to be determined (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, 2000). More recently, both algal pigment (Descy et al., 2005) and microscopy (Cocquyt & Vyverman, 2005) surveys have provided current data on algal biomass, composition and dynamics in the pelagic waters of Lake Tanganyika, and have underlined the Cyanobacteria–chlorophyte dominance during the primary portion of the annual cycle, showing a particular prominence of the picocyanobacteria *Synechococcus* spp. (Vuorio et al., 2003; Descy et al., 2005; Sarmento et al., 2008). 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. In contrast, in the southern basin, where the temperature density gradient is usually weaker, diatom development does not follow a clear seasonal pattern, and picocyanobacteria tend to dominate at all times (Descy et al., 2005). Another *Nitzschia* species, identified as *N. fonticola* Grun., is more characteristic of the stratified conditions of the rainy season (Cocquyt & Vyverman, 2005), particularly in the southern part of the lake. These same recent investigations (Descy et al., 2005), indicate that green algae are far more abundant and diverse in the region of Kigoma (northern basin) than off Mpulungu (southern basin). *Lobocystis planctonica* Tiffany et Ahlstrom was often found to be the dominant green alga; also worth mentioning are the endosymbionts in ciliates, previously referred to as 'zoochlorellae' by Hecky & Kling (1981), and identified as *Siderocelis irregularis* Hindák, by Stoyneva et al. (2008). Several floristic differences in the green algal assemblages of these two lake areas have also been shown

(Stoyneva et al., 2007a), with taxonomic updates and new species descriptions (Stoyneva et al., 2005, 2006, 2007b).

Farther from the equator, Lake Malawi has a weaker thermal gradient and the dry season mixing has a greater extent than in other East African Great Lakes: Patterson & Kachinjika (1995) reported a mixed layer reaching 230 m in the central part of the lake (Nkhotakota) in August/ September 1992/1993. In an analogous region of Lake Tanganyika (Kigoma), Descy et al. (2006) never observed a mixed layer deeper than 80 m during a three-year survey (2002–2004). The rainy season algal assemblages in Lake Malawi are fairly comparable to those described for Lake Tanganyika, with chlorophytes (Chlorococcales such as *Coenococcus* spp. or *Lobocystis* spp.) and some Cyanobacteria (such as *Planktolyngbya* spp.), but diatom prominence during the dry season seems more marked (Hecky & Kling, 1987; Haberyan & Mhone, 1991; Bootsma, 1993; Patterson & Kachinjika, 1995). Within the dry season, a diatom-dominated community comprising various *Nitzschia* taxa usually develops first, followed by centric diatoms, such as *Stephanodiscus* spp. and *Cyclostephanos* spp., that co-dominate the algal community along with the chlorophyte *Mougeotia* spp. The diatom assemblage shift may well indicate a change in resource ratios driven by the deeper mixing and nutrient uptake by phytoplankton: the diatom succession is consistent with a decrease in the Si:P ratio, in agreement with the hypothesis of Kilham et al. (1986), who classified planktonic diatoms according to their probable
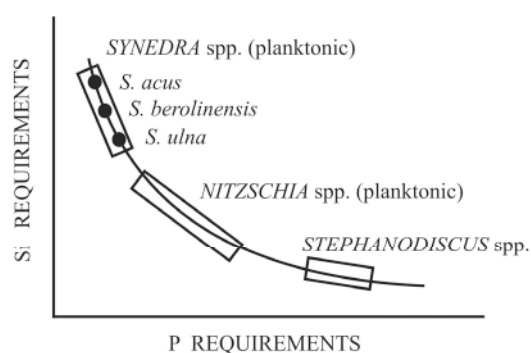

Fig. 2. Hypothetical growth relationship for planktonic diatoms from Africa as a function of phosphorus and silica requirements. *Synedra* refers to *Fragilaria*, according to current taxonomy. (Redrawn from Kilham et al., 1986).

Si and P requirements (Fig. 2). It is interesting to note here that, according to published records, *Stephanodiscus*, *Cyclostephanos* and *Aulacoseira* are not found in the Lake Tanganyika phytoplankton off Kigoma (Cocquyt & Vyverman, 2005); this would be consistent with differences in patterns of vertical mixing between both lakes.

For Lake Kivu, a smaller rift lake located north of Lake Tanganyika, Hecky & Kling (1987) reported a Cyanobacteria–chlorophyte dominated phytoplankton at that time similar to that in the larger Rift lakes. This description of Lake Kivu phytoplankton was, however, based on few samples collected in the 1970s. Kilham et al. (1986) reported a dominance (within the diatom population) of needle-like *Fragilaria* and *Nitzschia* in the largest northern basin and in Kabuno Bay, in agreement with the high dissolved Si:P ratio reported for these lake parts, while *Stephanodiscus* was more abundant in the southern, holomictic, Bukavu Bay, where dissolved Si:P was much lower. A more complete study, based on microscopy and marker pigments, by Sarmento et al. (2006, 2007) showed that, more recently (2002–2005), the phytoplankton in Lake Kivu was dominated by diatoms (*Urosolenia* spp., *Nitzschia bacata* Hust. and *Fragilaria danica* Lange-Bert.), particularly during the dry season episodes of deep mixing. During the rainy season, the stratified water column favoured dominance of filamentous Cyanobacteria (namely *Planktolyngbya limnetica* Lemm.) and of picocyanobacteria (*Synechococcus* spp.; Sarmento et al., 2008). Green algae were found to be always a minor plankton component at several sample locations on Lake Kivu, well below diatoms, Cyanobacteria, cryptophytes and chrysophytes. This peculiar phytoplankton assemblage points to substantial differences in water column structure and transparency between Lake Kivu and its larger neighbours, despite a similar range of primary production and nutrient concentrations (Sarmento, 2006; Sarmento et al., 2006).

The situation in Lake Victoria, which can be described from historical data prior to the eutrophication of this lake, is substantially different from that of the other East African lakes. Talling's detailed records from the 1950s (Talling, 1957, 1966, 1987) enable observations of the eutrophication

process which started in the early 1960s following the introduction of the Nile perch (*Lates niloticus* Lin.) and the Nile tilapia (*Oreochromis niloticus* Sci.) into this lake, and the increasing human population along its shores (Hecky, 1993; Mugidde, 1993; Hecky et al., 1994; Gophen et al., 1995; Kling et al., 2001; Verschuren et al., 2002; Silsbe et al., 2006). The abundant literature on recent changes emphasises an increasing persistency of a reduced number of Cyanobacteria taxa (namely *Cylindrospermopsis* and *Anabaena*) along with a decrease of species number in diatoms.

The amount of data found in the literature concerning phytoplankton in Lakes Edward and Albert is, comparatively, very restricted. In the same study cited above for other East African lakes, Hecky & Kling (1987) reported some results from a sampling campaign in March 1972. At that time, Lake Edward had a relatively high biomass, dominated by Cyanobacteria (*Microcystis* spp., *Chroococcus* spp. and *Merismopedia*) and chlorophytes (*Planktonema lauterborni* Skuja, *Tetraedron* spp., *Oocystis* spp., *Scenedesmus* spp. and *Lagerheimia subsalsa* Lemm.). Algal biovolume in Lake Albert was low, in the same order of magnitude as Lakes Malawi and Tanganyika, and the dominant taxa were *Stephanodiscus* (now *Cyclostephanos*) spp. (largely dominant), *Ochromonas*, *Chromulina* and *Bisocoeca*, along with a few chlorophytes such as *Ankyra paradoxoides* Cirile and *Schroederia setigera* (Schröder) Lem. One, almost complete, year-cycle on phytoplankton biomass and composition in Lake Albert was published by Evans (1997), but the samples were taken in 1961–1962. At that time the phytoplankton was dominated by diatoms and Cyanobacteria. Evans confirmed the *Stephanodiscus* spp. dominance, but also highlighted the considerable abundance of *Nitzschia* spp. and *Anabaena flos-aquae* (Bréb.) Bornet et Flah. in other periods of the year.

Phytoplankton structure as an indicator of ecological changes

Changes in Lake Victoria brought about by food web alterations and increasing human pressure on its watershed have been well documented, due to the existence of detailed past and present phytoplankton data (Talling, 1966; Hecky, 1993) and the availability of diatom records in the sediment (Haberyan & Hecky, 1987). The recent phytoplankton studies in Lake Tanganyika and Lake Kivu provide other examples of how phytoplankton assemblages may reflect geochemical and ecological changes which have been related to environmental changes.

Verburg et al. (2003) presented a strong case for a significant global warming impact and reduction of primary production in Lake Tanganyika, based on rise of temperature in the surface waters, increase in transparency associated with a decrease in phytoplankton biovolume, and change in Si concentration in the euphotic layer. Although some arguments can be challenged (see Descy et al., 2005 and Sarvala et al., 2006), evidence from the observed increase in Si concentration relates well to a reduction in diatom abundance and a change in diatom composition in the phytoplankton. Silica measurements over several decades indicate that Si in the upper 50 m has tripled, while no change has occurred below 100 m. According to Verburg et al. (2003), '*The increase in silica in the mixed layer is a result of decreased diatom production, driven by a lower availability of nutrients such as phosphorus. Nutrient limitation lowers diatom sedimentation rates, and silica accumulates in the mixed layer*'. Alleman et al. (2005) confirmed the increasing Si trend, with current concentrations of surface dissolved Si of 32 ± 8 μmol L^{-1} compared to the 1938–1975 period (9.5 ± 4.6 μmol L^{-1}), and estimated an increase rate of about 70 mmol m^{-2} yr^{-1} over the last 28 years (1975–2003), with no corresponding change in Si loading from the tributaries of the lake. In the same period of time, a change in composition occurred in the lake diatom assemblage. Hecky & Kling (1987) clearly mentioned peaks of *Stephanodiscus* (now *Cyclostephanos*) spp. occurring in the dry season, followed by a peak of *Nitzschia* spp. These data from the 1970s are confirmed by the abundance of *Cyclostephanos*., as well as of *Nitzschia* spp. (gr. *lanceolatae*) and even of *Aulacoseira granulata* (Ehrenberg) Simonsen in the sediment (Haberyan & Hecky, 1987). In contrast, recent studies showed dominance of the dry season peaks by *Nitzschia asterionelloides* O.Müll. (Cocquyt & Vyverman, 2005), and the absence of other planktonic diatom taxa. This compositional change fits very well

with the observed increase of Si:P ratio in the surface water of Lake Tanganyika, as a result of the warming trend, which strengthened stratification and reduced P supply to the euphotic layer, reducing primary production and affecting particularly the dry season diatom development. Indeed, we may infer from *N. asterionelloides* morphology that it is a better competitor for P, due to its narrow and elongated shape, and that it should therefore be located in the medium part of the Si:P gradient and better adapted to the changed conditions in Lake Tanganyika, while *Cyclostephanos* was virtually excluded as a result of its higher P requirements. Also, *Nitzschia asterionelloides* is a colonial form, with settling properties which allow it to concentrate in the lower part of the euphotic zone under stratified conditions (Descy et al., 2005); accordingly, these diatoms have a remarkably low concentration of the photoprotective xanthophyll diadinoxanthin (Descy et al., 2005). This taxon, therefore, appears to be better adapted to the strengthened stratification of Lake Tanganyika (shallower mixed layer during a longer stratification period) that occurs as a result of surface warming and to the decreased strength of the prevailing trade winds. Possibly, higher specific settling velocities might have contributed to the exclusion of the *Stephanodiscus* taxa.

Recent and important geochemical changes relating to biological processes may also have occurred in Lake Kivu, with a possible response at the phytoplankton level. Surprisingly at first glance, the chemical changes in Lake Kivu appear to be opposite to those in Lake Tanganyika: surface Si concentrations have decreased since the 1970s (100 μmol L^{-1} now vs. 290 μmol L^{-1}; Sarmento et al., 2006) whereas Si and P concentrations below the chemocline have increased (25–30 % for Si and by a factor of 3 for P; Schmid et al., 2005). During the same period of time, substantial changes in gas concentrations have occurred in the deep waters of the lake. Compared to previous measurements in the 1970s (Tietze et al., 1980), the measured CH$_4$ concentrations in the deep waters have increased by 15–20 % and CO$_2$ concentrations by about 10 % (Schmid et al., 2005). Given that this gas increase has required an increased input of organic carbon to the monimolimnion, it would be tempting to hypothesise

that the lake underwent anthropogenic eutrophication and that a part of the increased planktonic production was exported to the sediment, where most of the methane formation occurs. Indeed, human population density has increased around Lake Kivu in recent decades, which as a result increased nutrient input from the watershed. However, measurements of primary production using ^{14}C incubations have not shown a substantial change in the range of values compared to those measured in the 1970s (Sarmento, 2006). An alternative explanation may be that a larger part of the primary production, consisting of diatoms, has been exported from the surface to the deep waters; this would be consistent with Si, P and CH$_4$ increases in these layers, while primary production did not change substantially. The hypothesis of an increased C vertical flux is supported by a few facts. First, Lake Kivu chlorophyll *a* concentration is two to three times higher than that in the northern part of Lake Tanganyika, with similar climate and nutrient conditions, and with a similar range of depth-integrated primary production. Second, a key feature of Lake Kivu is its food web, without control of the planktivores by predation: the top consumer in Lake Kivu is the zooplanktivorous clupeid *Limnothrissa miodon* Boulanger (the Tanganyika sardine), an endemic from Lake Tanganyika introduced in the 1950s to develop a pelagic fishery. This introduction, which has been successful as far as the fishery is concerned, has had dramatic effects on the zooplankton, resulting in the disappearance of the largest and most efficient grazer (Dumont, 1986; Isumbisho et al., 2006) and probably a substantial reduction of copepod abundance. The lower grazing pressure which has resulted from reduction in zooplankton structure and abundance may explain why the present phytoplankton biomass is higher in Lake Kivu than in Lakes Tanganyika and Malawi, having a similar level of primary production.

Although few data are available from past studies, the phytoplankton community structure in Lake Kivu may also have changed. Hecky & Kling (1987), while also noticing greater phytoplankton abundance in Lake Kivu than in Malawi and Tanganyika, mentioned dominance by Cyanobacteria and chlorophytes, more significant dinoflagellate development than in other lakes, and

diatoms only in an isolated bay. Today, diatoms are the most abundant phytoplankton group in Lake Kivu, and cryptophytes are well developed, whereas chlorophytes are much less represented (Sarmento et al., 2006). These changes are consistent with lower light availability as a result of decreased water transparency, due to increased chlorophyll a. Furthermore, the diatom assemblage of Lake Kivu comprises large slower growing, inedible, pennate diatoms (chiefly *Fragilaria danica* and *Nitzschia bacata*), which may have contributed, by their sedimentation, to the increase in export flux of C, Si and P from the surface to the deep layers, and thus to the geochemical changes mentioned above. In summary, the introduction of the Tanganyika sardine, through a trophic cascade effect which ultimately favoured diatom production, may have had the unexpected consequence of enhancing methane formation in the monimolimnion, with a possible hazardous outcome for the local populations (Bellanger, 2007).

Do changes in phytoplankton composition affect zooplankton abundance and fish yields?

There has been rising concern about the changes in fisheries in the African Great Lakes, starting with the dramatic changes that occurred in Lake Victoria as a result of eutrophication, invasive species (the water hyacinth in particular), and the Nile perch and Nile tilapia introductions with the associated species loss (Oguto-Ohwayo & Hecky, 1991). Climate change may also have contributed to greater stratification, which promoted changes in the phytoplankton, with loss of diatoms and success of Cyanobacteria, deoxygenation of the hypolimnion and loss of habitat (Lehman, 1996). Dumont (1986) speculated that the developing fishery in Lake Kivu was doomed by the adverse effect of the introduced sardine on zooplankton, its main resource. More recently, evidence has accumulated that other Rift lakes are threatened, most notably Lake Tanganyika, with reports of declining primary production related to global warming (O'Reilly et al., 2003; Verburg et al., 2003) and overexploitation (Sarvala et al., 2006). Other problems have been identified

in several studies, summarised in general reviews such as those by Odada et al. (2003, 2004). Fisheries are of course of primary importance for the local populations, with annual catches of 30 000 metric tonnes for Lake Malawi, and up to 100 000 metric tonnes for Lake Tanganyika (Bootsma & Hecky, 2003).

As classic models based on statistical relationships between primary production and fish yield have shown (Melack, 1976), one may expect that reduced phytoplankton production in pelagic systems will result in decreased fish production. This has been observed in Lake Tanganyika, for which Plisnier (2004) has shown correlations between ENSO (El Niño-Southern Oscillation) indices and the catches (CPUE, catch per unit effort) of the main species exploited by the fishery. Although an impact of the fishing effort is still probable, as a decline in the industrial fishery was more than compensated by a rise in artisanal catches (Sarvala et al., 2006), the evidence for a climate-driven productivity change, affecting primary production with an expected impact on pelagic fish production, is fairly strong (Verburg et al., 2006; Stenuite et al., 2007).

In this debate, the efficiency of carbon transfer through the food web has not been explicitly considered, despite the fact that there are signs of substantial changes in the structure of planktonic assemblages in Lake Tanganyika which have not been documented yet for other Great African lakes.

Recent studies (Pirlot et al., 2005) have shown that a substantial fraction of producer biomass in Lake Tanganyika is represented by picoplankton (Fig. 3), comprising heterotrophic bacteria and picocyanobacteria, later identified as *Synechococcus* (Stéphane Stenuite, personal communication). In the southern part of the lake, the proportion of picoplankton biomass may reach 80 % of the total phytoplankton biomass. In a broad comparison of aquatic systems, Sarmento et al. (2008) have shown that picocyanobacteria abundance and biomass in Lake Tanganyika is among the largest known worldwide. Moreover, bacterial production in Lake Tanganyika approaches the range of particulate primary production (Pirlot, 2006), and a major fraction of this production is grazed by heterotrophic nanoflagellates and ciliates (Pirlot
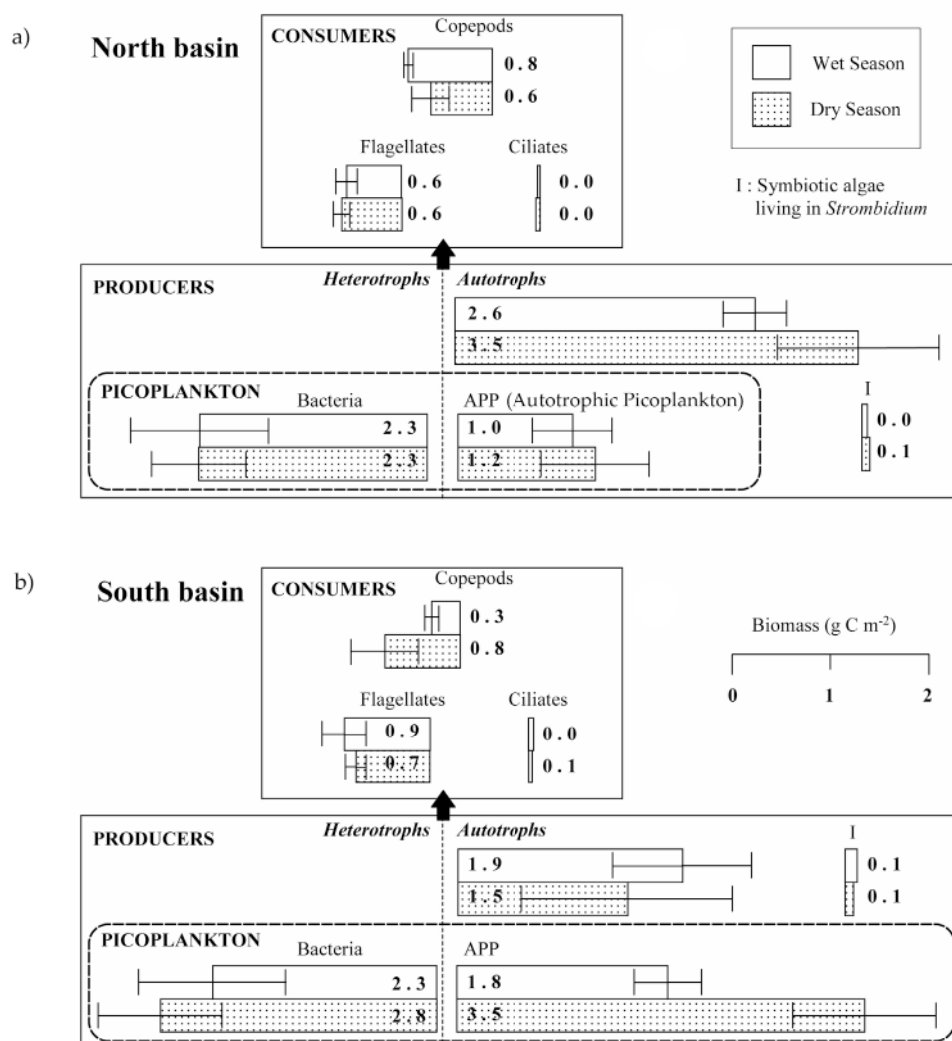
Fig. 3. Biomass of different plankton compartments in Lake Tanganyika, integrated in the 0 m–100 m water column. (a) Northern basin off Kigoma; (b) Southern basin off Mpulungu (data from 2002–2005; redrawn with permission from Pirlot et al., 2005).

et al., 2007). Results from grazing experiments (Stenuite et al., personal communication) have demonstrated that heterotrophic nanoflagellates and ciliates actively graze upon all picoplankton, with a preference by the former, which are the main grazers, for picocyanobacteria. These data clearly reinforce the concept that consumer production in Lake Tanganyika is supported in a substantial way by heterotrophic production, which takes place in the whole oxic layer (down to 100 m depth), while primary production is confined to the euphotic layer (Hecky et al., 1981). In other words, the

microbial food web seems to be well developed in the lake, and plays a key role in organic matter transfer from the primary producers to the metazoans, as well as in nutrient regeneration. In this respect, the Lake Tanganyika pelagic zone appears very close to oligotrophic marine systems in ecological functioning.

But what is the overall trophic efficiency of a system dominated by a microbial food web? Theoretically, one may expect that trophic efficiency would be lower in a system dominated by the microbial loop, where additional steps and high respiration rates contribute to large

organic carbon losses, even if heterotrophic protists are grazed upon by metazooplankton. This hypothesis has been tested experimentally by Berglund et al. (2007) who obtained a 2 % trophic efficiency in a bacteria-based system, compared with 22 % in a phytoplankton-based system, where most phytoplankton production passed directly to the metazoan grazers. One may question to what extent the present Lake Tanganyika, with its longer stratification periods as a result of global warming, its diminished primary production and a high bacterial production, is not analogous to the bacteria-based system. Furthermore, as mentioned above, the phytoplankton community changes may have affected consumer production in Lake Tanganyika. Diatom production, which takes place mostly during deep mixing events, has decreased (Verburg et al., 2003), and species favoured by deep mixing and increased P availability have virtually disappeared. It is likely that both autotrophic and heterotrophic picoplankton have increased as a result of increased stratification and temperature, and lower nutrient availability (Agawin et al., 2000; Cotner & Biddanda, 2002). Among phytoplankters, *Synechococcus* has adaptations suited to the high-light environment of a shallower epilimnion, with its high cell content of photoprotective pigment (Falkowski & Raven, 1997), which fits well with its dominance in the upper mixed layer in Lake Tanganyika in rainy season conditions.

The picture of the present Lake Tanganyika food web which arises from these recent studies, possibly as a result of global warming, is substantially different from what was described from data of the 1970s:

- In the stratified conditions of the rainy season, possibly enhanced in ENSO years, with warmer temperatures and lower wind velocities (Plisnier, 2000), picocyanobacteria dominate, along with green algae (mostly colonial), and with short-lived events of surface *Anabaena* blooms; high light exposure in the shallow mixed layer promotes extracellular DOC (dissolved organic carbon) release by phytoplankton cells which, together with mortality of different phytoplankton components, provides heterotrophic bacteria with labile DOM (dissolved organic matter) and helps increase bacterial production. In such conditions, the system is picoplankton-dominated and most of the production goes to the microbial food web, lowering trophic efficiency but enhancing nutrient cycling in the euphotic zone; when *Anabaena* blooms occur, the collapse by mortality of these Cyanobacteria would probably fuel the microbial loop rather than providing food directly to the metazooplankton.

- In dry-season conditions, deep mixing and improved nutrient availability favour diatom development, as was described by Hecky & Kling (1987); the fast, positive, response of metazooplankton to these diatoms (Kurki, 1999) indicates direct trophic transfer of high-quality food. Internal nutrient loading from the hypolimnion dominates in most of the lake, and upwellings at the southern tip of the lake add substantial amounts of nutrients to the euphotic layer, allowing 'new production' to take place. Most of the lake consumer production, including fish, depends on these wind-driven dry season events and hence is also dependent on climate variability.

A similar impact of climate variability has been described to explain reduced productivity in the ocean from lower trophic efficiency in ENSO years (Karl et al., 2002), and oligotrophication in some European mountain lakes (e.g. Anneville et al., 2005).

Perspectives

The recent studies in some of the East African Great Lakes, mainly on the smaller size compartments of the food web (see above), may have introduced new concepts to tropical limnology. New challenges must be overcome to understand the functioning of these systems and their response to the environmental changes expected, or already taking place, in this century. The study of microbes requires advanced technology, and the application of technologies like flow cytometry, epifluorescence microscopy or molecular techniques in remote African regions is certainly one of these challenges. At present, the simple problem of sample preservation is still an inevitable obstacle for producing good science in most parts of Africa.

A significant amount of work remains to be done in some lakes (for example, Malawi, Victoria, Edward and Albert), in order to obtain such basic information as auto- and heterotrophic picoplankton biomass, diversity, and its importance in the pelagic food webs. Heterotrophic and mixotrophic protists, already identified decades ago as key components of the food web, are virtually unknown in some of the largest lakes, whereas there are indications that they are an important link between producers and consumers, and may be an important component in nutrient recycling.

Research in the past decades has focused on the largest of the Rift lakes (Victoria, Tanganyika and Malawi), which have offered the most fascinating opportunities for science, both because of their outstanding characteristics and also because of the numerous problems they have faced. Attention has been drawn to the need for their conservation. In contrast, the smaller of the Rift lakes have been almost totally ignored, with the exception of Lake Kivu, for which recent results are available. Complete and updated limnological and plankton studies are still missing for some of the lakes (Edward and Albert), which are no less important for the local population.

On the other hand, there are practically no molecular studies on microbes in this part of the world, with the notable exception of Lake Tanganyika (de Wever et al., 2005) and of ongoing studies, still unpublished, on photosynthetic and heterotrophic picoplankton. A major research topic for such ancient lakes would be to examine the microbial food web with molecular methods, despite the fact that we may expect less diversity in microorganisms than in the larger vertebrates or invertebrates, and may look for possible endemism or simply detect forms of life which have gone undetected by other methods.

Another obstacle to improving scientific knowledge and, above all, resources management, is that all these lakes are shared by more than one country (Fig. 1). The organisation of a sampling cruise crossing different countries can easily turn into an enormous task. More alarming is the fact that tropical lakes theoretically show a higher degree of adverse response to eutrophication or organic loading than would occur in temperate lakes (Lewis, 2000). In the case of the East African Great Lakes, with integrated management actions requiring international agreements, the potential problems arising from increasing populations along the lakes shores, species introductions, environmental degradation and global warming therefore take on another dimension.

Finally, when compared to the proportion of surface fresh water in the world, the attention given by the scientific community to this part of the world is rather low, as can be easily seen by a web-based literature search, using simple key words (Fig. 4). Why is this, at a time in which global resources and sustainable development are major concerns for the large international organisations,
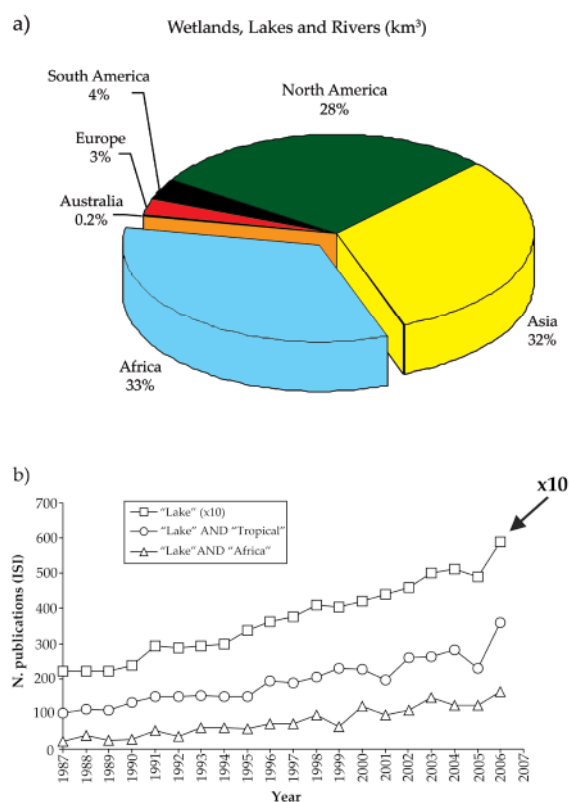

Fig. 4. (a) Distribution of surface fresh water (wetlands, lakes and rivers) among the world continents and subcontinents, highlighting the high proportion found in the African continent. (Source: United Nations Environment Program, *http://www.unep. org/dewa/assessments/ecosystems/water/vitalwater/02.htm*). (b) Number of publications recorded in ISI Web of Knowledge containing the keywords '*Lake*' (squares), '*Lake*' AND '*Tropical*' (circles), '*Lake*' AND '*Africa*' (triangles). (Note that the number of publications for the keyword '*Lake*' was divided by 10 to keep on the same scale).

and for the large proportion of the world population living in developing countries? One of the reasons may be that, among the community of local scientists and technicians, few have received adequate training, not to mention the unattractive salaries and the lack of financial and technical means for undertaking research and sustaining the effort. Fortunately, a generation of African students is emerging which has benefited from the support of well-funded projects and who have become involved in studies of the aquatic ecosystems in their own countries. However, more initiatives of scientific and technical cooperation are still needed, and thanks to them, and to rising awareness of the environmental problems threatening fresh waters, the local scientific communities in Africa will develop the capacity for science-based management of their remarkable natural resources.

Acknowledgements

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Hugo Sarmento comes from Portugal and holds a PhD in aquatic sciences from the University of Namur (Belgium), where he researched the ecology of phytoplankton of the East African Great Lakes (especially lakes Kivu and Tanganyika). At present, he has a post-doctoral research grant from the Spanish Government to study the interactions between phytoplankton and heterotrophic bacteria in marine systems, mainly the bacterial assemblage responses to the dissolved organic carbon released by different phytoplankton species. He is also developing the application of MAR-FISH (Micro Autoradiography coupled with Fluorescent In Situ Hybridation) with labelled organic carbon excreted from algae.