

New paradigms in tropical limnology: the importance of the microbial food web

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Abstract Limnology has traditionally been a science of temperate regions. Long-term studies are not common in tropical regions despite the number of large tropical lakes that constitute a significant proportion of global freshwater resources. A number of comparative studies have shown that tropical lakes are different from temperate lakes in some fundamental ways. Constantly high temperature and radiation have strong consequences for stratification and biological processes. Previous studies suggested that higher primary production on a given nutrient base in tropical lakes is related to their higher decomposition rates. Moreover, lower efficiency in transforming primary production to higher trophic levels in tropical lakes also has been postulated as a difference. Data on the microbial processes in tropical lakes are scarce, but fail showing any significant difference in epilimnetic decomposition (bacterial) processes between temperate and tropical aquatic systems. The most significant differences found so far are in autotrophic and consumer community composition and body size, which constrain the upper compartments of the food web in a deterministic way. The reconciliation of ecological theory and observations yields a conceptual

framework that illustrates likely structural variations in food webs along the latitudinal gradient.

Keywords Heterotrophic prokaryote · Bacterial production · Phototrophic picoplankton · Latitudinal gradient · Grazing · Nanoflagellates · Metabolic theory of ecology · Food-chain length

Introduction

So far, the most significant advances in limnology were achieved in temperate regions. When compared to the proportion of surface fresh water in the world, the attention given by the scientific community to tropical aquatic systems is low (Descy & Sarmento, 2008). Nevertheless, numerous developing countries cover those latitudes and through regional limnology will improve our knowledge of tropical inland waters. It is likely that anthropogenic pressure on the aquatic systems in tropical countries will increase with economic growth, given that tropical lakes show a higher degree of adverse response to eutrophication or organic loading than temperate ones (Hecky, 2000; Lewis, 2000).

It is difficult to specify differences between temperate and tropical inland waters in a mechanistic way. An example of such work can be found in a few reviews on tropical limnology such as those of Lewis (1987, 1996). In these reviews Lewis describes the main aspects that differentiate tropical lakes and

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many of the mechanisms that drive those differences. In addition to a typology of the deterministic factors that affect the biological processes the latitudinal gradient, Lewis's studies have generated some conclusions: tropical lakes are (1) more efficient in producing phytoplankton biomass on a given nutrient base, (2) inclined to nitrogen rather than phosphorus limitation, (3) inefficient in passing primary production to the highest trophic levels, (4) generally similar to temperate lakes in phytoplankton and zooplankton species composition and (5) typified by strong non-seasonal variation superimposed in most cases on a seasonal cycle.

The importance of the microbial food web in tropical lakes has been hypothesized repeatedly in previous studies (e.g. Hecky & Fee, 1981; Kilham & Kilham, 1990; Lewis, 1996), but very few have been able to put numbers in these compartments (Descy & Sarmento, 2008). The first technical developments to study the microbial communities and metabolism arrived in the late 70s (Hobbie et al., 1977) and were improved thorough the 80s and 90s (e.g. Porter & Feig, 1980; Kirchman et al., 1985; Sherr & Sherr, 1993; Shapiro, 1995). Lately, some of those methods were applied in a comprehensive way in temperate freshwater systems, and only recently in tropical regions (but see Lewis et al., 1986), mostly in South America (e.g. Rejas et al., 2005; Roland et al., 2010) and Eastern Africa (e.g. Pirlot et al., 2007; Sarmento et al., 2008; Stenuite et al., 2009a, b).

In this review, I present a meta-analysis of the available data on standing stocks and fluxes of the microbial food web in tropical lakes to attempt some explanations of an apparent paradox, which is the high efficiency of tropical lakes in producing phytoplankton biomass but a low efficiency in passing primary production to higher trophic levels (Lewis, 1996). I propose several hypotheses based on theoretical concepts and present a compilation of the existing data that are relevant to the hypotheses.

What is a tropical lake?

The tropical region is limited in latitude by the Tropic of Cancer in the northern hemisphere at approximately 23°26'N and the Tropic of Capricorn in the southern hemisphere at 23°26'S. According to the Köppen System (Peel et al., 2007), within the tropical

climate zone there are distinct variations based on precipitation (Fig. 1). Tropical rainforest climate (Af): all 12 months have average precipitation of at least 60 mm; Tropical monsoon climate (Am): this climate has a driest month (which nearly always occurs at or soon after the 'winter' solstice for that side of the equator) with rainfall less than 60 mm, but more than (100 – [total annual precipitation in mm/25]); Tropical wet and dry or savanna climate (Aw): these climates generally have a pronounced dry season, with the driest month having precipitation less than 60 mm and also less than (100 – [total annual precipitation in mm/25]). Although not all the area within this band has tropical climate (Fig. 1), we can safely affirm that all of the lakes between the Tropics of Cancer and Capricorn may be considered as tropical because of their low seasonal amplitude of temperature and irradiance.

Whilst the total area covered by lakes in the tropical region is relatively low (Lehner & Döll, 2004), there are many large lakes in this region (Lewis, 1996). Also, the potential for an increasing interest in tropical limnology is likely because of the rising number of large reservoirs and the green house gas source they represent (especially methane, Tranvik et al., 2009; Barros et al., 2011).

Stratification pattern is one of the most distinctive features of tropical lakes, and is a key to understand the dynamics of the planktonic communities at low latitudes (e.g. Talling & Lemoalle, 1999; Descy et al., 2005; Sarmento et al., 2006). Seasonal stratification is typical but density gradients in tropical lakes are weaker and more susceptible to numerous partial mixing events (Lewis, 1987). Temperature and light regimes are high throughout the year allowing a permanently high biological activity, which gives distinctive chemical and biological features to tropical lakes. Biogeochemical cycling of nutrients are sensitive to biological activity because of utilization, regeneration and the relative availability of critical nutrients that can determine the productivity. In particular, tropical lakes have higher internal nutrient loading (Kilham & Kilham, 1990), and tend to have low nitrogen to phosphorus ratios and anoxic hypolimnion, which often lead to proliferation of nitrogen fixing filamentous cyanobacteria when external nutrient loading increases (Hecky, 2000).

Behind the apparent "endless summer" (Kilham & Kilham, 1990) there is typically one season of low

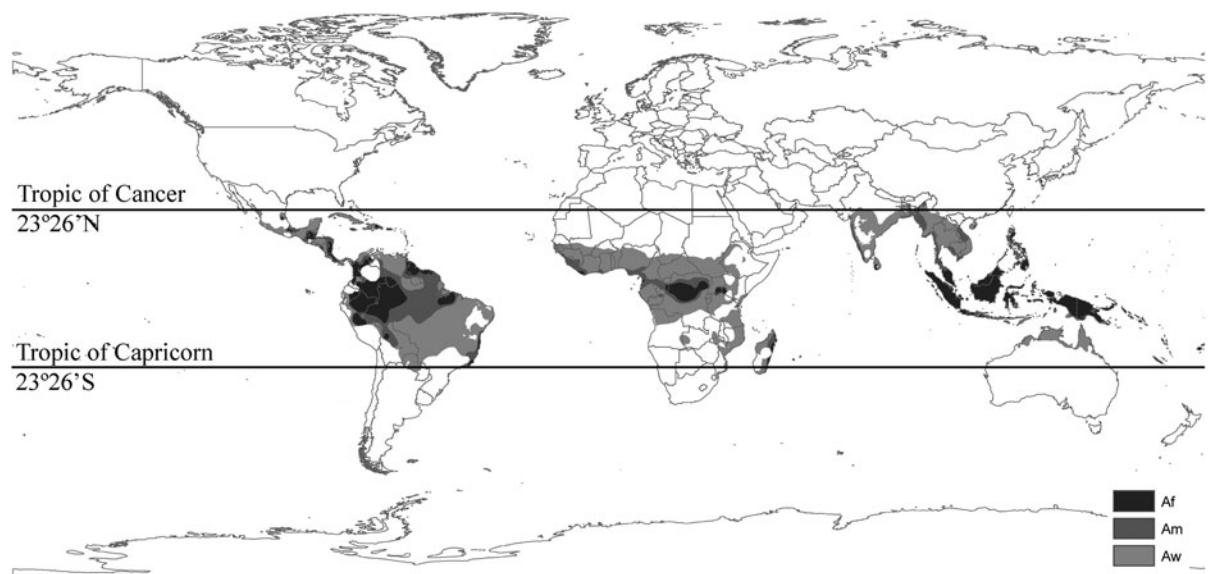


Fig. 1 World distribution of regions with tropical climate according to the Köppen System (see text). Af: tropical rainforest climate; Am: tropical monsoon climate; Aw: tropical wet and dry or savanna climate

stability that allows a seasonal complete mixing of the water column in tropical lakes (Lewis, 1996). Sometimes extended mixing occurs during the dry season and triggers an increase in primary production (Mellack, 1979; Beadle, 1981; Sarmento et al., 2006; Stenuite et al., 2007); in other cases seasonal mixing comes with the hemispheric cool season (Lewis, 1987).

This review focuses on rather large lakes that have seasonal stratification, plankton-based food webs and predominantly pelagic processes. Many of the points discussed here may not apply to small or shallow lakes, which are more susceptible to allochthonous inputs.

The microbial food web

The microbial food web can be presented as functional units, which avoids any need to find a taxonomic definition of microbes and the complexity generated by their high diversity. The two largest functional units in terms of biomass and carbon processing are heterotrophic prokaryotes and phytoplankton. In this review, I give special attention to the small ($<2\text{ }\mu\text{m}$) phototrophic picoplankton because it represents an edible source of food for microzooplankton, in opposition to the larger fraction, which is lost by sedimentation or integrates the classical food

chain (phytoplankton–zooplankton–fish). Phototrophic picoplankton abundance and production increase with increasing eutrophy, but their proportionate contribution to total phytoplankton biomass and production decreases with increasing trophic status in both marine and freshwater ecosystems (reviewed by Callieri, 2008).

Heterotrophic prokaryote and phytoplankton are interconnected by a two-way flux. Phytoplankton excretion and cell lysis are sources of organic matter for heterotrophic prokaryote, and mineralization of this organic matter by heterotrophic prokaryote provides nutrients for primary producers. Phytoplankton excretion of organic carbon may be higher under high light and warm conditions (Zlotnik & Dubinsky, 1989). If so, heterotrophic prokaryote and phytoplankton could be more tightly coupled in tropical systems.

The third functional unit in a simplified view of the microbial food web consists of grazers, comprising protists (flagellates, ciliates, etc.), which can be strictly heterotrophic or mixotrophic and mostly incorporate carbon by ingesting phototrophic picoplankton and heterotrophic prokaryote. These grazers are consumed by larger zooplankton, which allows an energy transfer from the microbial food web into the classic food chain. In this way, the different compartments of the microbial food web are

integrated in the ‘microbial loop’ (Azam et al., 1983). This concept originally proposed for marine systems has been largely applied in freshwater systems (e.g. Weisse et al., 1990; Simek et al., 1995; Pernthaler et al., 1996).

A fourth functional unit is aquatic viruses. There is no information on the influence of latitude on viral abundance or diversity; the environmental factors that trigger viral infection and lysogeny are still poorly understood (but see Maurice et al., 2010; Bouvy et al., 2011).

Do heterotrophic prokaryotes have higher importance in tropical lakes?

At a given rate of primary production, heterotrophic prokaryote activity in tropical lakes is expected to be higher than in temperate lakes (Fig. 2). White et al. (1991) found a significant positive relationship between bacterial specific growth rate and temperature in freshwater and marine habitats. A similar relationship was found using space-for-time substitutions in the global ocean (López-Urrutia et al., 2006; López-Urrutia & Morán, 2007; Sarmento et al., 2010). If this hypothesis (Fig. 2) is validated, it could contribute to the higher efficiency of primary production in tropical lakes (Lewis, 1990, 1996), as mineralization and nutrient recycling rates would be higher.

Heterotrophic prokaryote and phytoplankton have been quantified in surprisingly few studies, especially

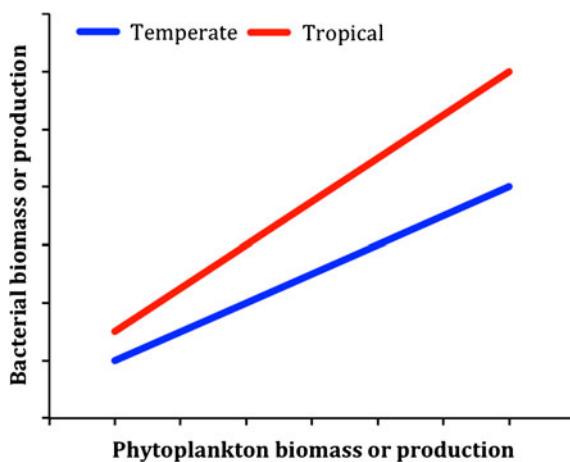


Fig. 2 Hypothetical relationship between bacterial processes and primary producers in temperate and tropical lakes. (Color figure online)

in Asia (but see Lee & Bong, 2008). Several studies of microbial processes deal with the nature and dynamics of dissolved organic matter (e.g. Farjalla et al., 2009) but do not provide data on phytoplankton biomass or production, and could not be included in this review (Table 1).

For a given chlorophyll concentration, heterotrophic prokaryote abundance in tropical lakes may be lower than in temperate lakes (Fig. 3A), in accordance with previous observations drawn from a slightly different data set (Roland et al., 2010) and as predicted by Sarmento et al. (2010). Other results from this meta-analysis are not conclusive (Table 2), but the scatter of points (Fig. 3B, C) suggests that temperate and tropical lakes do not differ in relationship of bacterial production to chlorophyll *a* or primary production, but bacterial production estimates can be strongly influenced by the conversion factors used to transform leucine or thymidine uptake rates to biomass production, especially in oligotrophic systems (Gasol et al., 2008).

Epilimnetic heterotrophic prokaryote may not play such a dominant role as previously supposed in tropical lakes. One possible explanation would be that in tropical waters with low resources (oligotrophy), bacterial production does not scale with temperature, in contrast to bacterial respiration (López-Urrutia & Morán, 2007). Water temperature in tropical lakes is often well above 25°C, UV radiation is high and nutrient limitation is common due to high nutrient uptake potential (related to warm conditions). Phototrophic picoplankton (discussed lower) probably can compete effectively with heterotrophic prokaryote for inorganic nutrients (Morris & Lewis, 1992; Moutin et al., 2002; Tanaka et al., 2004). Bacterial growth efficiency in tropical lakes epilimnion could be affected by these abiotic factors, according to the environmental hostility theory (Carlson et al., 2007). Although more data would be necessary to test this hypothesis in a conclusive way, the available data indicates that epilimnetic heterotrophic prokaryote do not seem to explain the differences in recycling rates suggested previously between tropical and temperate lakes (e.g. Lewis, 1996).

Nevertheless, a consistent solution for this paradox has been suggested (Hecky & Fee, 1981; Hecky, 2000; Lewis, 2010): the loss of nutrients from the epilimnion is a dominant limiting factor for phytoplankton growth in highly stratified water columns;

Table 1 Available published data on microbial metabolism in tropical lakes

Lake	BP ($\mu\text{gC l}^{-1} \text{ day}^{-1}$)	HP abund. ($10^6 \text{ cell ml}^{-1}$)	PP ($\mu\text{gC l}^{-1} \text{ day}^{-1}$)	Chla ($\mu\text{g l}^{-1}$)	HNF abund. (10^3 ind ml^{-1})	Grazing rate (day^{-1})	Reference
Chapala (Mexico)	65.67	20.65	1177.00	11.00			Lind et al. (1997)
Amarela (Brazil)	18.12		979.65	81.80			Petrucio et al. (2006)
Dom Helvécio (Brazil)	5.22		316.05	24.05			Petrucio et al. (2006)
Carioca (Brazil)	11.62		2677.20	45.90			Petrucio et al. (2006)
Palmeirinha (Brazil)	9.06		1199.70	86.50			Petrucio et al. (2006)
Águas Claras (Brazil)	9.44		569.10	49.48			Petrucio et al. (2006)
Jacaré (Brazil)	5.60		584.85	26.08			Petrucio et al. (2006)
Barra (Brazil)	5.90		1009.95	19.50			Petrucio et al. (2006)
Kivu (RD Congo/Rwanda)	13.20	1.25	14.45	2.20	2.50	0.09	Sarmento et al. (2009) and F. Darchambeau (unpublished)
Tanganyika (Zambia/Tanzania)	3.54	2.46	7.25	0.67	2.00	0.12	Pirlot et al. (2007), Stenuite et al. (2007, 2009a) and Tarbe et al. (2011)
Kariba (Zambia/Zimbabwe)	6.41	2.19		2.20			Lindell & Edling (1996)
Mapuey (Venezuela)	6.92	1.37		2.89			Castillo (2000)
Yaru (Venezuela)	5.33	1.04		1.49			Castillo (2000)
Mainstem (Venezuela)	2.12	0.83		0.43			Castillo (2000)
Xolotlán (Nicaragua)	102.00	18.50	2266.67	65.00			Erikson et al. (1998a, b)
Bufeos (Bolivia)		5.80		9.10	1.48	1.31	Rejas et al. (2005)
Nambengué (Ivory Coast)	270.68	7.10	2685.00	41.90			Bouvy et al. (1998)
Brobo (Ivory Coast)	89.64	3.27	1145.40	14.03			Bouvy et al. (1998)
Tiné (Ivory Coast)	112.02	3.00	536.40	18.65			Bouvy et al. (1998)
Batata (Brazil)	49.80	0.47		2.80			Anesio et al. (1997)
382 Reservoirs, floodplain and coastal lakes (Brazil)		0.09–11.92		0.10–437.6			Roland et al. (2010)

BP bacterial production; HP heterotrophic prokaryote; PP primary production; Chla chlorophyll *a*; HNF heterotrophic nanoflagellates

Only the studies having information at least of one parameter concerning both heterotrophic prokaryote (2nd and 3rd columns) and phytoplankton (4th and 5th columns) were selected for this study

hypolimnetic waters of tropical lakes are warm and thus have much higher metabolic potential than hypolimnetic waters of mid-latitude lakes; nutrient resupply from points below the epilimnion through partial mixing can maintain the nutrient availability, much of which otherwise would be lost to deeper water over the long period of stratification in tropical lakes. Thus, biogeochemical cycles in tropical lakes (driven by stratification) should not be interpreted as constant throughout the year, but rather as constantly changing. However, the amplitude of change (in no

matter which variable) in tropical lakes generally fluctuates in a shorter range than in temperate lakes (idea already expressed by Lewis, 1974).

Do phototrophic picoplankton have higher importance in tropical lakes?

A second hypothesis is that the contribution of phototrophic picoplankton to primary production could be higher in tropical lakes. Phototrophic

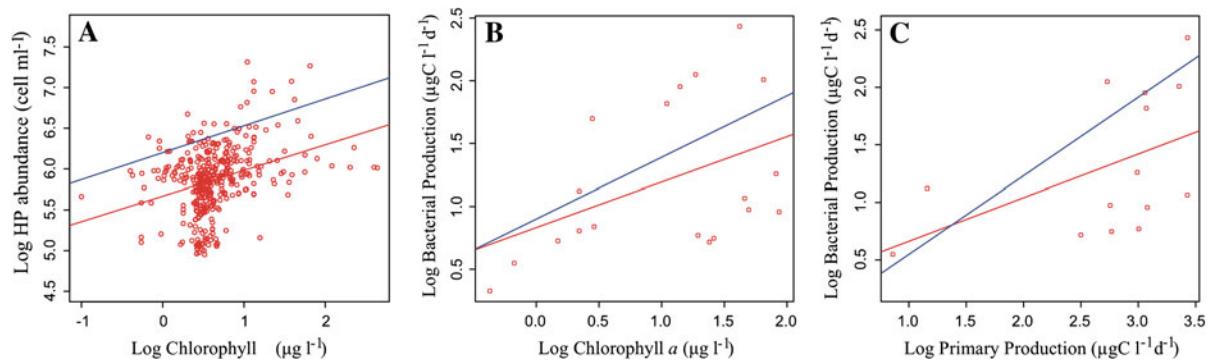


Fig. 3 Relationship between heterotrophic prokaryote abundance (HPA) or production (BP) with phytoplankton production or biomass in tropical lakes (red) in temperate (blue). Data used for tropical lakes listed in Table 1, slopes and intercepts indicated in Table 2. Slope and intercept for

temperate lakes (blue line): **A** $\text{Log HPA} = 0.330 \text{ Log Chla} + 6.200, r^2 = 0.16, n = 361$, Currie (1990); **B** $\text{Log BP} = 0.490 \text{ Log Chla} + 0.900, r^2 = 0.20, n = 219$, White et al. (1991); **C** $\text{Log BP} = 0.683 \text{ Log PP} - 0.135, r^2 = 0.38, n = 24$, Cole et al. (1988). (Color figure online)

Table 2 Logarithmic relationship between heterotrophic prokaryote abundance or production with phytoplankton production or biomass in tropical lakes

Log-log relationship	Slope	Significance	Intercept	Significance	r^2
HPA versus Chla	0.314	$p < 0.001$	5.669	$p < 0.001$	0.11
BP versus Chla	0.361	n.s.	0.832	$p < 0.01$	0.19
BP versus PP	0.378	n.s.	0.284	n.s.	0.23

BP bacterial production; PP primary production; HPA heterotrophic prokaryote abundance; Chla chlorophyll a

picoplankton is mainly constituted by *Synechococcus*-like cyanobacteria (Callieri, 2008), which are typically r-strategists with higher growth rates at high temperatures than larger phytoplankton (Reynolds, 2006) and high surface:volume ratio, a critical factor to be competitive in nutrient depleted environments (Lewis, 1976). Reynolds et al. (2000) reported that phototrophic picoplankton might be most abundant during periods of relatively high insolation in large lakes, and phytoplankton communities may be increasingly composed of cyanobacteria towards the equator.

Annual phototrophic picoplankton abundance is available for temperate lakes Maggiore and Baikal and tropical lakes Tanganyika and Kivu (Fig. 5). Pigment data were available for 3 years for lake Tanganyika and 8 years for lake Kivu (Descy et al., 2005; Sarmento et al., 2006, in press). The cyanobacteria of type-I obtained from HPLC pigment analysis and CHEMTAX processing was almost exclusively *Synechococcus*-like phototrophic picoplankton (Sarmento et al., 2007, 2008; Stenuite et al., 2009b). Cyanobacteria of type-I from pigment

analysis and the 104 samples analyzed by flow cytometry for phototrophic picoplankton abundance (Sarmento et al., 2008; Stenuite et al., 2009b) were highly correlated. The equation derived from this correlation (Fig. 4) was used to estimate phototrophic picoplankton abundance throughout the year (Fig. 5).

The data suggest consistent differences between temperate and tropical phototrophic picoplankton abundance for the four lakes in all seasons (Figs. 5, 6) except during summer (mid-June to mid-September, Fig. 6). The high abundance of phototrophic picoplankton in tropical phytoplankton was probably overlooked in the past due to technical limitations and could explain the higher efficiency of primary producers on a given nutrient base in tropical lakes when compared to temperate ones, as postulated by Lewis (1990, 1996).

Lake size and nutrient availability determine the abundance and contribution of phototrophic picoplankton to total phytoplankton (Callieri & Stockner, 2002), and it is probable that all large lakes of the world have high phototrophic picoplankton abundances as forecast by Reynolds et al. (2000) with the

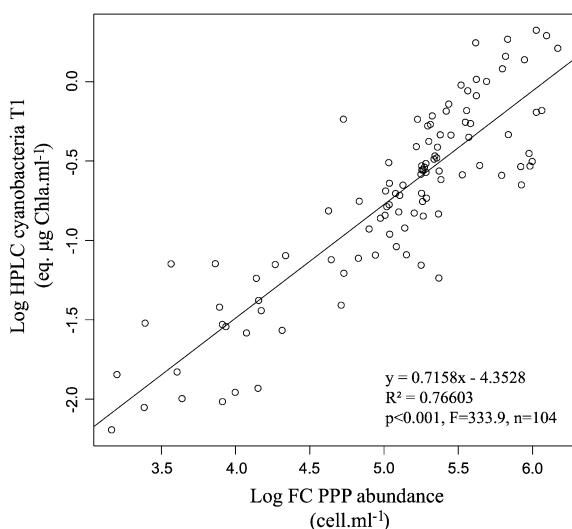


Fig. 4 Relationship between Cyanobacteria Type-I obtained from HPLC pigment analysis and CHEMTAX processing (Descy et al., 2005; Sarmento et al., 2006, in press) and *Synechococcus* abundance determined by flow cytometry (Sarmento et al., 2008; Stenuite et al., 2009b)

following sentence: ‘it seems to be only a matter of time before the prevalence of picoplankton in many more of the world’s great lakes is established’. The meta-analysis presented here (Figs. 5, 6), however, indicates that the main difference is not so much related to the maximum but rather to the persistence of high phototrophic picoplankton abundances.

Fig. 5 Phototrophic picoplankton abundance in temperate (Baikal and Maggiore) and tropical (Kivu and Tanganyika) lakes throughout the year. Data from lake Kivu and Tanganyika were obtained from HPLC pigment analysis and CHEMTAX processing (see text and Fig. 4). Data from lake Baikal include aggregates of cyanobacteria and picoeukaryotes (<5% total phototrophic picoplankton abundance), extracted from Belykh et al. (2006). Data from lake Maggiore were gently provided by Callieri (2010). (Color figure online)

Do nano- and micro-grazers have higher importance in tropical lakes?

A meta-analysis using space-for-time substitution along a latitudinal gradient indicated that protist grazing on heterotrophic bacteria scales with temperature, in marine systems (Sarmento et al., 2010). The corollary to these observations would be that at higher temperatures heterotrophic protist need more energy to fulfill their requirements and grazing rates should be higher in warm waters, as in the epilimnion of tropical lakes. However, systematic differences on food web structure along a latitudinal gradient might challenge this theory.

Low abundance or absence of large cladocerans in tropical lakes determines a particular configuration of the food web (Fig. 7), along with *Chaoborus*, which (if present) can also have a major role in the food web configuration, exerting a massive pressure on herbivore zooplankton (e.g. Saunders & Lewis, 1988). In temperate lakes, the presence of large filter feeding cladocerans reduces abundance of heterotrophic nanoflagellates and ciliates (Gasol et al., 1995; Zöllner et al., 2003), disrupting the microbial food web (Pace et al., 1990; Riemann & Christoffersen, 1993). Tropical lakes are dominated by small-bodied zooplankton (Fernando, 1994), leading to relative higher abundances of rotifers, ciliates and nanoflagellates, which are more efficient consumers of heterotrophic prokaryote and phototrophic picoplankton. Thus, both

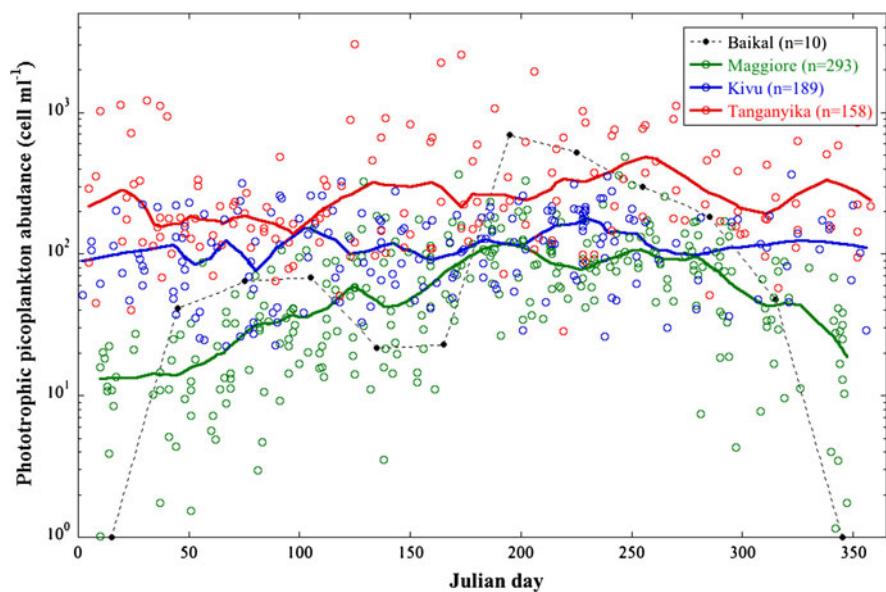
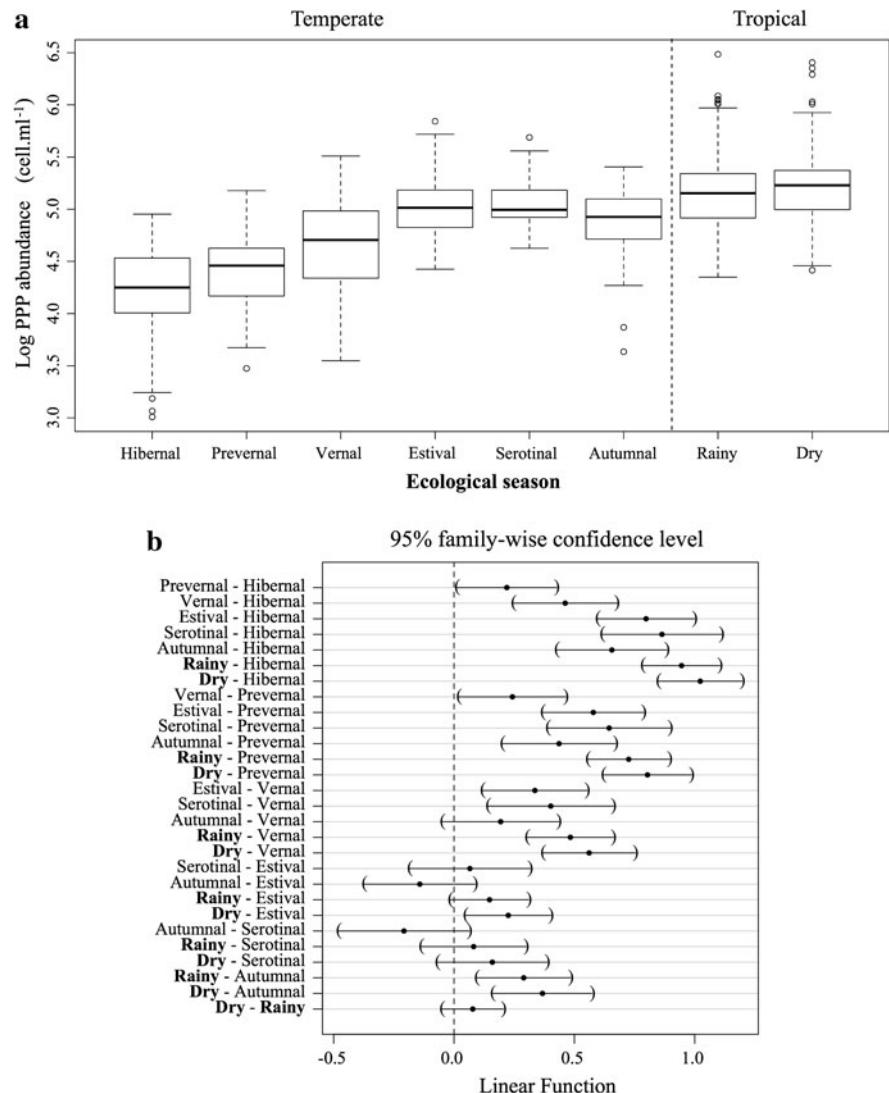


Fig. 6 *Upper panel* boxplot of the phototrophic picoplankton abundance in temperate (Baikal and Maggiore) and tropical (Kivu and Tanganyika) lakes at the different ecological seasons. *Lower panel* graphical representation of multiple comparisons of means (Tukey Contrasts); significant one-way Anova by season ($p < 0.001$). Tropical seasons highlighted in **bold** character



temperature and food web structure concur to the idea of higher grazing rates in the epilimnion of tropical lakes, in accordance to the observations in marine systems (reviewed by Sarmento et al., 2010).

The hypothetically high abundance phototrophic picoplankton in tropical lakes throughout the year (discussed in the upper sections) leads to the question of protist prey preferences, in other words, bacterivory versus herbivory. Tarbe et al. (2011) reported high grazing rates of heterotrophic nanoflagellates on phototrophic picoplankton on tropical lake Tanganyika. In that study, heterotrophic nanoflagellates were the main consumers of primary production (46–74%) and showed a clear preference for herbivory rather than

bacterivory. This is an indication that heterotrophic nanoflagellates might have a major role on the carbon flow in low latitude lakes and establish an additional trophic step, feeding on small primary producers more than on decomposers. In fact, Ngochera & Bootsma (2011), using stable isotope signatures, observed that zooplankton of Lake Malawi were nearly 2 trophic levels above seston implying that adult zooplankton could be consuming other food than phytoplankton, such as heterotrophic nanoflagellates.

The efficiency of carbon transfer from the microbial food web to the classic food web is uncertain. The reports in temperate lakes are rather contradictory, probably because of the importance of

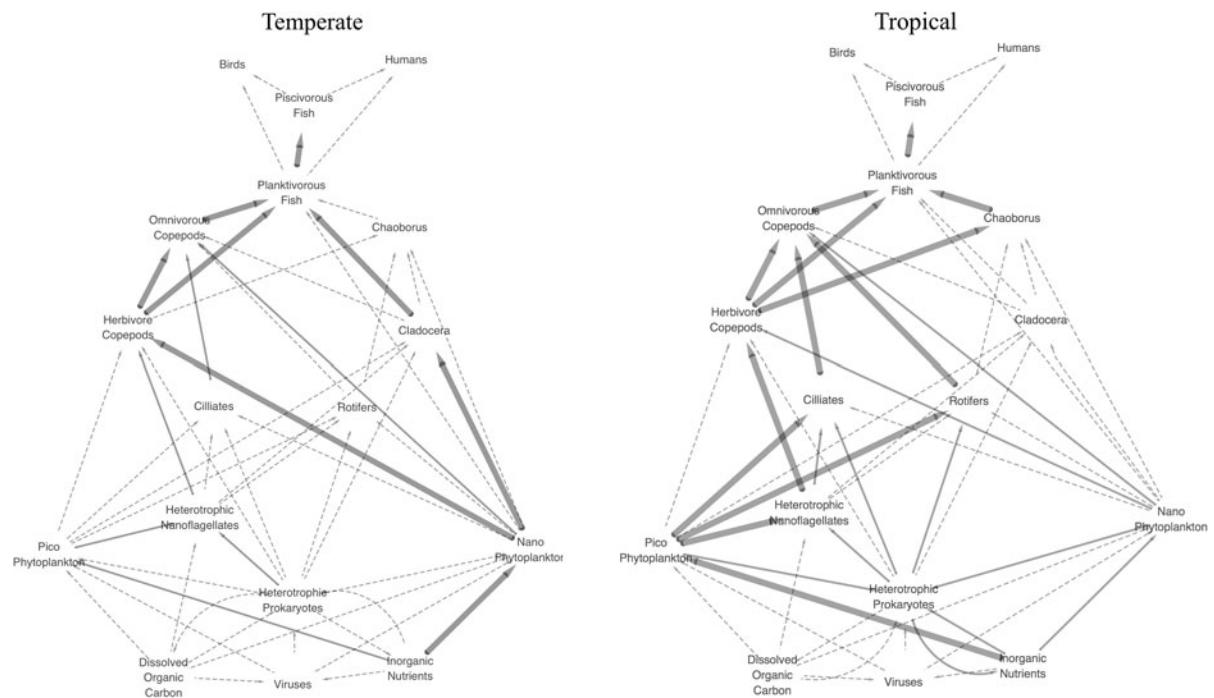


Fig. 7 Carbon flows in generic temperate (left) and tropical (right) food webs. Line width is a schematic representation of the interaction strength (carbon flow) roughly divided in three

categories: strong (thick line), medium (thin line) and weak (dashed line). This information was taken from bibliographic references cited on the main text

planktonic community structure (Pace et al., 1990), which in temperate lakes is marked by successional changes. Estimates for Lake Biwa (Japan), indicated that only 2% of the phototrophic picoplankton carbon passed to mesozooplankton through heterotrophic nanoflagellates (Nagata et al., 1996). Other studies reported an efficient carbon flux from picoplankton (including bacteria) to zooplankton in Lake Michigan (Carrick et al., 1991), with higher rates (comparable to those observed in Lake Tanganyika) only in summer. In any case, it seems clear that additional steps in the food web may not improve its efficiency.

The few observations available for tropical lakes provide strong indications that an additional trophic level (formed by microzooplankton, mainly HNF) exists and persists between primary producers (with a large fraction of phototrophic picoplankton) and metazooplankton and carries a large proportion of the carbon flow. This explains the high phytoplankton:zooplankton biomass ratio (e.g. Burgis, 1971; Mengestou & Fernando, 1991) and the low energy transfer efficiency (e.g. Irvine & Waya, 1999; Sarvala et al., 1999) reported in the tropics. However, the

major role played by *Chaoborus* controlling secondary production should not be neglected in the regions where this genera is present (e.g. Saunders & Lewis, 1988). These processes may also occur in temperate lakes, but the data available support the hypothesis that in tropical lakes an important part of the carbon passes through these microbial compartments of the food web in larger periods of time.

Integrating microbes in the food web

The analysis of latitudinal variations on size spectrum, energy fluxes and food web organization suggests a coherent conceptual framework (Fig. 8). In accordance to the predictions from the metabolic theory of ecology (Brown et al., 2004), the prevalence of small-bodied organisms in warmer systems (Yvon-Durocher et al., 2011) seem to be typical of tropical lakes (Figs. 5, 6). Organism size determines food selection and thus the food web configuration (reviewed by Woodward et al., 2010). A dominance of small and very efficient primary

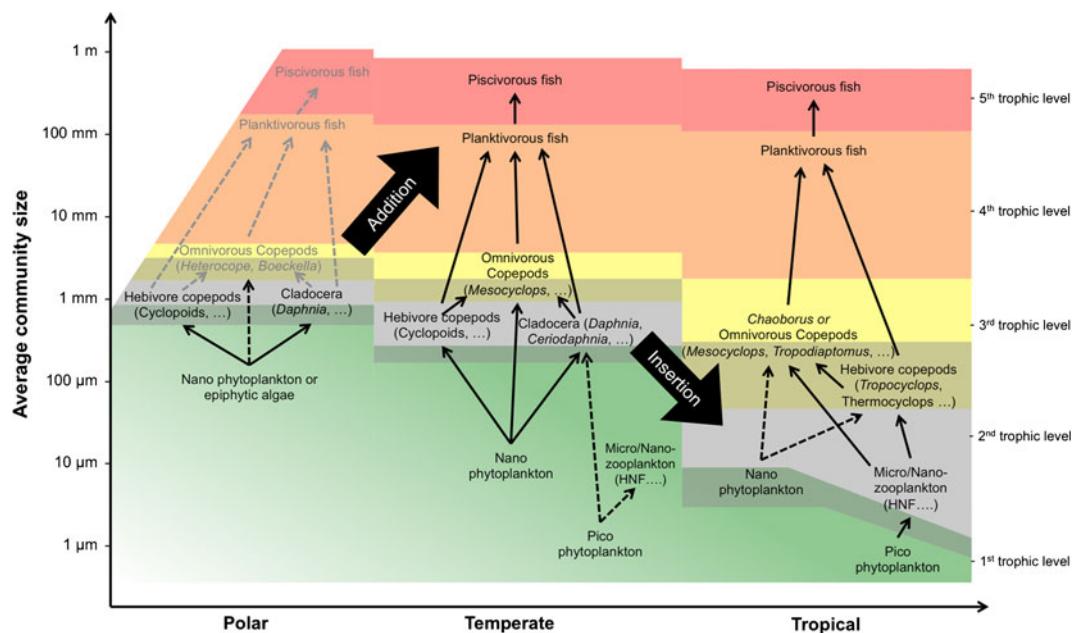


Fig. 8 Integrating some principles of theoretical ecology and empirical observations: hypothetical model of the distribution of organism size at the different trophic levels along the latitudinal gradient and its implications on the length of the food web. The main hypothetical carbon flows are represented according to their relative contributions to the total carbon flow within the food web (thick arrows major flow; dashed arrows

minor flow). Addition processes dominate in the transition from polar to temperate (some polar lakes do not have more than two trophic levels, show in pale grey), whilst insertion would be more common in the transition from temperate to tropical. Colours on the background correspond to trophic levels that are typically obtained by stable isotope signatures in the different categories of organisms. (Color figure online)

producers opens the way for the insertion of intermediate trophic levels (Fig. 8), which suggests an increase in the food-chain length. However, this is not as simple as it appears. Food-chain length has been under debate for decades (reviewed by Post, 2002). The length of the food-chain (mostly determined by stable isotope composition analysis) may be primarily determined by ecosystem size (Post et al., 2000) but other factors such as dynamic stability (Sterner et al., 1997) and resource availability may be important as well under certain circumstances (Jake Vander Zanden & Fetzer, 2007). Post & Takimoto (2007) proposed two processes that affect food-chain length along a resource gradient: (1) processes by which new trophic levels are added to the food-chain, as would be most common in the low resource range of the spectrum; (2) insertion processes where the inclusion of an intraguild predator on the food-chain (which adds trophic complexity but does not necessarily make the food chain larger), could be most common in productive systems.

According to the conceptual framework shown in Fig. 8, in the transition from polar to temperate lakes, additive processes would dominate because the growing season becomes long enough to support sufficient resources that are able to carry an additional trophic level. In the transition from temperate to tropical lakes, however, insertion processes at intermediate trophic levels of the food web could be more relevant and complexity would increase. This does not necessarily imply longer food chains in the tropics, as most of the intraguild predators (nano- and micro-grazers) may be omnivorous (Post & Takimoto, 2007).

Each lake is a lake! Freshwater ecosystems have that amazing capacity of integrating a huge number of biotic and abiotic factors of the surrounding space (geological nature of the bedrock and watershed, regional climate, human impacts, etc.). For that reason, limnology as a science is having a hard time getting apart from the idiosyncratic factors and figuring out the major general patterns, the theoretical

framework defining the common rules amongst different ecosystem distributed around the globe. The study of freshwater food webs along latitudinal gradients is a suitable exercise to generate hypothesis on those major patterns, and eventually useful to improve the forecast of climate change effects on aquatic ecosystems. However, it is nearly impossible to represent a single food web valid in a precise way for all water bodies, in all the regions of the world, at any time of the year. For that reason, the concept presented in Figs. 7 and 8 holds obvious limitations and should be seen with some caution.

Nevertheless, any experimented limnologist would agree that aquatic systems from a certain region or latitude range share some general traits. The exercise of putting together those general traits, even if they do not fit exactly to all the situations there might be, is a decisive step to make limnology a science of broader interest other than local. Moreover, besides identifying possible gaps in certain domains, this holistic approach may give an important contribution in generating new hypothesis and stimulating the debate around important concepts in limnology.

Conclusions

In summary, microbial food web is especially relevant in tropical lakes because it is highly active in larger periods of time, and seemly carries a larger fraction of the carbon flow than in temperate systems. However, the idea that nutrient recycling is higher in tropical lakes still needs to be demonstrated; the data available do not show any notable difference in decomposition (bacterial processes) in epilimnetic waters between temperate and tropical lakes. Most likely, recycling rates are higher in warmer hypolimnion of tropical lakes, and nutrient supply by epilimnetic thickening associated with temporary reduction in the stability of layering is highly probable.

Another notable difference is the autotrophic and consumer community composition and body size, which constrain the rest of the food web in a deterministic way. Small phytoplankton (phototrophic picoplankton), especially picocyanobacteria, seems to be more abundant and persists for longer periods of time in the tropics. The few observations available provide strong indications that an additional trophic level exists and persists between primary producers

(with a large fraction of phototrophic picoplankton) and metazooplankton, explaining the high phytoplankton:zooplankton biomass ratio and the low energy transfer reported in the tropics.

Finally, this study highlights the scarcity of limnological data, especially long-term series, in a vast region of the world comprising some of the most unique freshwater ecosystems. Research programs in the tropic should be reinforced and put more emphasis on microbial processes.

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