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Seasonal and spatial variability in the abundance of auto- and heterotrophic plankton in Lake Tanganyika

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With 4 figures and 3 tables

Abstract: This study aims to evaluate the seasonal and interannual variability in the importance of the microbial food web in Lake Tanganyika. Phytoplankton, bacteria and protozoa (heterotrophic nanoflagellates and ciliates) were monitored at two contrasting pelagic sites (Kigoma and Mpulungu) during 3 consecutive years. In addition, spatial variation was studied along 3 north-south transects during contrasting seasons. The study period covered a wide range of limnological conditions, with mixing depth ranging from 13 to >100 m and euphotic depth from 14 to 65 m. The consistently high bacterial biomass (up to 62 µg C l^{-1}) and the high contribution of small phytoplankton (< 5 µm) to the total phytoplankton biomass (on average 50 % in Kigoma and 84 % in Mpulungu) point to an important role of the microbial food web in the lake throughout the year. Total phytoplankton biomass increased during periods of low water column stability, with an increased biomass of small eukaryotic phytoplankton (2 to 5 µm) at both stations, together with autotrophic prokaryotic picoplankton at the southern station Mpulungu and diatoms at the northern station Kigoma. Heterotrophic bacteria, heterotrophic nanoflagellates (0.06 to 11.01 µg C l^{-1}) and ciliates (up to 8.16 µg C l^{-1}) did not show this seasonality. The main seasonal and spatial variability in the importance of the microbial food web seems therefore primarily linked to the contribution of small phytoplankton, which may be better adapted to lower average light intensities and higher N:P ratios during periods of deep mixing.

Key words: Lake Tanganyika, microbial food web, picoplankton, heterotrophic nanoflagellates, ciliates.

Introduction

Since the early 1980's, heterotrophic bacteria, autotrophic picoplankton (< 2 µm), heterotrophic nanoflagellates (2 to 20 µm) and ciliates, together forming the microbial food web, are recognised as important components of aquatic ecosystems, especially in oligotrophic environments. The microbial food web is considered to play an important role in nutrient limited conditions for two main reasons. First, under nutrient limitation, a large part of the primary production is exuded by phytoplankton in the form of dissolved organic matter and is processed by heterotrophic bacteria (Dubinsky & Berman-Frank 2001). Secondly, autotrophic picoplankton tends to have a higher contribution to phytoplankton biomass in oligotrophic ecosystems (Weisse 1991, Bergeron & Vincent 1997, Schallenberg & Burns 2001, Jasser 2002, Samuelsson et al. 2002) and forms an important food source for heterotrophic flagellates and ciliates. Increased nutrient inputs into an ecosystem generally result in a reduced importance of the microbial food web (Weisse 1991, Lacroix et al. 1999).

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Lake Tanganyika is a large oligotrophic, meromictic lake situated in the East African rift valley. Until recently however, little was known about the role of the microbial food web in the lake. Internal mixing during the annually recurring limnological cycle (Plisnier et al. 1999) is considered to be the main source of inorganic nutrients to the epilimnion of the lake. During the dry season, south-eastern monsoon winds move warm surface water to the north of the lake, resulting in upwelling of deeper nutrient richer water in the south of the lake. These monsoon winds initiate an oscillation of the thermocline, which results in its erosion throughout the lake (Coulter & Spigel 1991, Naithani et al. 2003). Water column stability is maximal and nutrient inputs to the epilimnion are expected to be minimal at the end of the rainy season (Plisnier et al. 1999).

Due to this variability in mixing regime and nutrient input, changes in the contribution of the microbial food web can be expected. At present, only a limited amount of data is available to test this hypothesis. Hecky & Kling (1981) presented the first detailed study on spatial-temporal dynamics (Feb. to Nov. 1975) of nano- and microphytoplankton (2 to 20 µm and 20 to 200 µm, respectively), ciliates and heterotrophic bacteria in the northern basin of the lake. These authors reported the occurrence of diatoms during periods of intense mixing and of filamentous cyanobacteria during periods of rapid surface warming after the dry season mixing. They also reported a ciliate community dominated by taxa belonging to the order Oligotrichida, which were prominently present during the stratified rainy season, and heterotrophic bacterial densities between 1.5×10^5 to 1.5×10^6 cells ml^{-1} during the whole study period. In a recent phytoplankton study, Cocquyt & Vyverman (2005) detected peaks in the biomass of diatoms during the dry-mixing season and observed a shift from a cyanobacteria-chrysophyte-chlorophyte community in 1975 (Hecky & Kling 1981) to a cyanobacteria-chlorophyte-diatom community in 2002 near Kigoma in the northern basin. The almost complete absence of cryptophytes and chrysophytes in the phytoplankton in the northern basin had already been observed by Verburg et al. (2003) based upon a number of sampling events during the dry-mixing season of 2000 and 2001.

These studies did, however, not include the smallest fraction of the phytoplankton, viz. the picophytoplankton (< 2 µm). Vuorio et al. (2003) reported high densities of autotrophic picoplankton (10^4 to 6×10^5 cells ml^{-1}) during research cruises in March 1998, but attributed only a low biomass to this phytoplankton group. Descy et al. (2005) studied the phytoplankton community using HPLC pigment analysis and found an overall important contribution of *Synechococcus*-type cyanobacteria (which likely corresponds to the picoplankton size fraction) to total chlorophyll-*a* (Chl-*a*) of around 31 % at the northern station Kigoma and 56 % at the southern station Mpulungu. They further observed a dominance of chlorophytes at the northern station and of the *Synechococcus*-type cyanobacteria in the south of the lake. Pirlot et al. (2005, 2006) reported the first data on heterotrophic nanoflagellates (HNF) from two sampling events during the rainy-stratified and dry-mixing season of 2002 at the same study sites. Their study indicated relatively high densities of HNF (0.3 to 1.83×10^6 cells l^{-1}), bacteria (2.28 to 5.30×10^6 cells ml^{-1}) and ciliates (up to 3.25×10^3 cells l^{-1}). In a more recent study, Pirlot (2006) confirmed the high overall heterotrophic biomass (heterotrophic bacteria, HNF and ciliates) during 6 sampling campaigns between 2002 and 2004.

The aim of the present study is to provide detailed information on the seasonal and spatial dynamics of the microbial communities in Lake Tanganyika and their importance in the pelagic food web. As Lake Tanganyika is an oligotrophic lake, we expected that the microbial food web contributes significantly to the particulate carbon pools. We specifically wanted to test whether the importance of the microbial food web decreases during periods of more intense mixing. Increased nutrient supply during these periods could favor the growth of larger phytoplankton organisms, which can directly be consumed by copepod grazers.

Material and methods

Study site

Lake Tanganyika is situated in East Africa and is bordered by Burundi, Tanzania, Zambia and the Democratic Republic of Congo. The lake measures roughly 650 by 50 km and has a maximum depth of 1470 m (Coulter 1991). Two pelagic sampling stations, Kigoma (04º51.26'S, 29º35.54'E, maximum depth: 250 m; Tanzania) and Mpulungu (08º43.98'S, 31º02.43'E, maximum depth: 120 m; Zambia), respectively, in the northern and the southern basin of the lake were simultaneously sampled fortnightly from February 2002 up to August 2004 (Fig. 1). These stations are accessible from the respective research centres of TAFIRI (Tanzanian Fisheries Research Institute) and DOF (Department of Fisheries) and are identical to the stations sampled during the FAO/FINNIDA LTR (Lake Tanganyika Research) project from 1992 to 1997 (Mölsä et al. 1999a). Additional samplings along a north-south transect (station TK1-11) were performed during the dry-mixing season of 2002 (July 10 to 16) and 2003 (July 7 to 13) and the rainy-stratified season of 2004 (January 30 to February 5).

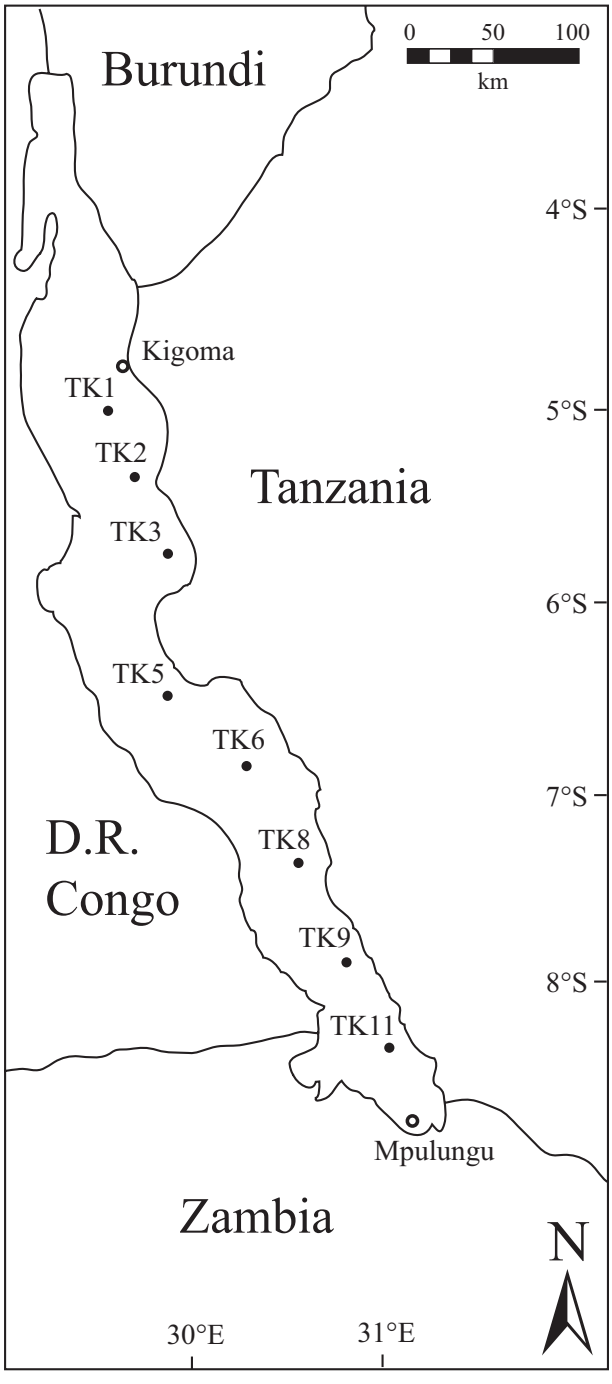

Fig. 1. Map of Lake Tanganyika with indication of the sampling sites. Open circles indicate the sampling sites (Kigoma and Mpulungu) during the seasonal monitoring (Feb. 2002 to Aug. 2004). Filled circles indicate the sites sampled during three north-south transects (Jul. 2002, Jul. 2003, Feb. 2004).

Sampling

On each sampling occasion, conductivity, temperature, pH and oxygen depth profiles were recorded using a CTD (Seabird SBE-19 in Kigoma and Hydrolab Datasonde 4A in Mpulungu) to a depth of about 100 m. Water transparency was determined routinely using Secchi disc depth measurements. The light extinction coefficient (k expressed in m^{-1}) was determined by measuring the irradiance using LICOR quantum sensors. Fortnightly sampling started at 9 am at both stations. Water samples were collected using Hydrobios (5 l) or Go-Flo (up to 12 l) sampling bottles from a depth of 20 m. This depth was mainly chosen to reduce the number of samples and is always situated in the epilimnion. It generally corresponds to the depth where primary production is maximal (Sarvala et al. 1999) and photoinhibition is not experienced (Lindqvist et al. 1999). Subsamples for nutrient analysis, the preparation of epifluoresence slides and the enumeration of larger phytoplankton (≥ 5 µm) were collected in separate containers. The samples for the enumeration of planktonic organisms were immediately fixed using the lugol-formaldehyde-thiosulphate method, which ensures both a good preservation of autofluorescence and keeps flagellates and ciliates more intact than aldehyde fixation alone (Sherr & Sherr 1993).

Laboratory procedures

Water for analysis of dissolved nutrients was pre-filtered over a Macherey-Nägel GF-5 filter (nominal pore size 0.7 µm) on the sampling day. Nutrient analysis was performed within 24 h after sampling. Nitrate (NO_3-N), nitrite (NO_2-N) and silicon (Si) concentrations were determined spectrophotometrically using commercially available standard test reagent kits (Macherey-Nägel) with detection limits of respectively 0.1, 0.005 and 0.01 mg l^{-1}. Soluble reactive phosphorus (SRP; PO_4-P) and ammonium (NH_4-N) were measured according to standard methods (Greenberg et al. 1992).

Slides for epifluorescence microscopy were prepared on the day of sampling. A 10 ml subsample was stained with DAPI (4',6'-diamidino-2-phenylindole; Porter & Feig 1980) and filtered onto a 0.2-µm pore size membrane filter (Nucleopore) for the enumeration of bacteria. A 100 ml subsample was filtered onto a 0.8-µm pore size membrane filter (Nucleopore) and stained with DAPI for the enumeration of phytoplankton < 5 µm (autotrophic picoplankton and phytoplankton 2–5 µm) and heterotrophic nanoflagellates (HNF). Slides were stored in a freezer at –20 ºC and kept in a cool box during transport to Belgium. Samples for enumeration of phytoplankton ≥ 5 µm and ciliates (1 l) were concentrated by sedimentation (48 h) and kept in the dark during storage and transport.

All phytoplankton enumerations were performed in the lab in Belgium. Phytoplankton < 5 µm was enumerated on a 0.8-µm filter (due to the use of this filter size the smallest autotrophic picoplankton representatives may have been overlooked) using violet-blue illumination (395–440 nm excitation filter and 470 nm emission filter) in a Zeiss Axioplan microscope. At least 400 autotrophic picoplankton cells and 100 small (2 to 5 µm) phytoplankton cells were counted. As the autotrophic picoplankton was exclusively composed of prokaryotic cyanobacteria, they could be distinguished from the predominantly eukaryotic 2 to 5 µm phytoplankton by switching to green light (510–560 nm excitation filter and 590 nm emission filter for excitation of picocyanins and type II phycoerythrin; MacIsaac & Stockner 1993). Colonial cells were not counted in order to avoid overlap with the inverse microscopy counts.

Phytoplankton cells and colonies ≥ 5 µm were counted according to the Uthermöhl method (Uthermöhl 1931) and identified up to the highest feasible taxonomic level using a Zeiss Axiovert 135 inverted microscope. More details can be found

in Cocquyt & Vyverman (2005). For Mpulungu, the samples from 2004 were not included in the study due to loss during transport. Phytoplankton biomass was estimated from cell biovolume calculations (from mean linear cell dimensions) and published biovolume to carbon conversions (Menden-Deuer & Lessard 2000). For the phytoplankton < 5 µm, we used a fixed conversion factor based on an average cell diameter of 1 µm for the autotrophic picoplankton cells and 2 µm for the phytoplankton 2–5 µm (corresponding to respectively 0.12 and 0.83 $\times 10^{-12}$ g C cell^{-1}).

On the 0.2-µm filter slides, at least 400 bacterial cells were counted in a minimum of 10 randomly chosen fields at 1000× magnification with UV illumination (365-nm excitation filter and 397-nm emission filter). Although we did not perform systematic cell measurements, the diameter of the bacterial cells was always well below 1 µm. Bacterial densities were converted to biomass using a fixed conversion factor of 10×10^{-15} g C per cell. This conversion factor was taken from the average cell carbon content calculated by Pirlot et al. (2005) based on cell measurements using image analysis on bacterial samples from 2002 in Lake Tanganyika.

At least 100 heterotrophic nanoflagellates (HNF) were counted on 0.8-µm filter slides using UV-illumination (365-nm excitation filter and 397-nm emission filter). HNF was distinguished from autotrophic phytoplankton by checking for autofluorescence using green and blue light illumination. As the HNF cells were always in the size range between 2 to 5 µm a single average biovolume of 14 µm^3 cell^{-1} was used for the conversion to carbon biomass according to Putt & Stoecker (1989).

The dominant ciliate species were identified using the quantitative protargol staining technique (Montagnes & Lynn 1993) on selected samples from 2002, following the taxonomy according to Foissner et al. (1999). Ciliates were enumerated using inverted microscopy in the sedimentation samples used for phytoplankton ≥ 5 µm counts. The biovolume of ciliates, calculated from mean linear cell dimensions, was converted to biomass according to Putt & Stoecker (1989).

Data analysis

The depth of the euphotic zone (Zeu) was calculated from the Secchi depth measurements using an experimentally established relationship between light extinction (k) and Secchi depth (k = 1.57/Secchi depth). The depth of the mixed layer (Zm) was visually estimated from temperature profiles. The average light value for the mixed layer (in % of surface light) was obtained by dividing the integrated light % by the depth of the layer. To obtain a quantitative measure of water column stability at each site, the Potential Energy Anomaly (PEA) for the upper 100 m of the water column was calculated according to Simpson et al. (1982):

$$PEA = -\frac{1}{h}\int_{-h}^{0}(\overline{\rho} - \rho)gzdz$$

with h the lake depth (we used a depth of 100 m as data were only available up to this depth), average water density (between 0 and h depth), ρ water density at depth, g the gravitational acceleration and z the depth. Based on changes in rainfall and wind patterns, the dry-mixing season was defined from the

Table 1. Abiotic and biotic data showing averages of all samples during rainy-stratified (RS) and dry-mixing seasons (DS) respectively at the northern (Kigoma) and southern (Mpulungu) sampling station in Lake Tanganyika (Feb. 2002 to Aug. 2004). All data, except PEA, Zm, Zeu, average light concentration in Zm and Zm:Zeu, were obtained from a depth of 20 m only. Standard deviation is given between brackets. Differences between seasons and stations were tested with a 2-Way ANOVA and LSD post-hoc test; <: $p < 0.05$, <<: $p < 0.01$ and <<<: $p < 0.001$. Comparison between stations was done for both seasons individually. * missing data for Kigoma up to May 2003.

	Kigoma			Between	**Mpulungu**		
	RS		DS	stations (RS/DS)	RS		DS
Temperature (°C)	26.83 (0.39)	>	26.51 (0.55)	</>>>	27.16 (0.61)	>>>	25.12 (0.86)
PEA (J m^{-3})	15.82 (3.04)	>>	13.19 (4.02)	–/>>>	17.59 (3.55)	>>>	6.01 (4.87)
Zm	35 (9)	–	43 (14)	>/–	29 (11)	<<<	53 l(30)
Zeu	38 (6)	–	39 (7)	–/>>>	41 (12)	>>>	29 (8)
Average light concentration in Zm (%)	25 (8)	–	21 (7)	–/>>	31 (12)	>>>	17 (11)
Zm:Zeu	1.00 (0.34)	–	1.21 (0.36)	–/<<<	0.76 (0.34)	<<<	1.98 (1.41)
SRP (µg l^{-1})	5.0 (9.4)	–	9.2 (10.3)	–/–	3.7 (3.4)	<<<	13.3 (13.2)
NO_3-N (µg l^{-1})	18.3 (20.9)	–	21.8 (30.8)	–/<	16.8 (12.7)	<<	34.3 (20.4)
NO_2-N (µg l^{-1})	2.0 (2.2)	–	1.6 (1.9)	<</–	8.3 (16.0)	>>	2.2 (2.6)
NH_4^+-N (µg l^{-1}) *	3.3 (4.7)	–	11.7 (31.7)	–/–	12.4 (6.9)	–	11.6 (6.9)
Si (µg l^{-1})	742.9 (143.1)	–	860.1 (204.1)	</–	857.4 (257.8)	–	962.1 (275.2)
Picocyanobacteria (µg C l^{-1})	2.40 (1.20)	–	2.91 (1.68)	</<<<	3.47 (2.34)	<<<	5.67 (1.96)
Eukaryotic phytoplankton < 5 µm (µg C l^{-1})	1.01 (0.48)	–	1.37 (0.88)	<</<<<	2.99 (3.60)	<<<	11.61 (12.58)
Phytoplankton ≥ 5 µm (µg C l^{-1})	4.10 (2.77)	–	4.65 (3.35)	>>/>>	2.32 (2.48)	–	1.62 (1.84)
Total phytoplankton (µg C l^{-1})	7.09 (3.28)	–	8.63 (4.03)	</<<<	10.95 (6.34)	<<<	19.69 (14.28)
Bacteria (µg C l^{-1})	25.68 (8.60)	–	26.89 (8.35)	<</<<	34.50 (10.63)	–	35.73 (13.69)
HNF (µg C l^{-1})	1.66 (1.07)	–	1.93 (0.99)	–/<<	1.90 (0.81)	<<	3.14 (2.58)
Ciliates (µg C l^{-1})	0.71 (1.04)	–	1.02 (1.06)	–/–	1.62 (2.16)	–	1.87 (1.85)

end of April up to the end of October. Differences between the dry-mixing and the rainy-stratified season and between the two sampling stations were tested using 2-way ANOVA followed by LSD post-hoc tests. In case of deviances from homogeneity as indicated by Levene's < 0.01, data were log transformed prior to the ANOVA-analysis. As the seasons are not delineated based on changes in water column stability, we also calculated the Pearson's correlation coefficient for abiotic and biotic variables with the PEA in Statistica 6 (Statsoft).

Results

Averages of abiotic and biotic variables at the two sites for different seasons are shown in Table 1. Water column temperature (Table 1) and PEA (Figs 2 and 3) were significantly lower during the dry-mixing compared to the rainy-stratified season. The lowest PEA was observed during the dry-mixing season at the southern station Mpulungu, indicating upwelling of deep water. As can be appreciated on Fig. 3, there is a good match between the dry seasons and the period of minimal stability at the southern station Mpulungu. At the northern station Kigoma (Fig. 2), however, lower PEA is observed later during the dry season and tends to continue for a few months during the rainy season. During the dry-mixing season transects, sampled in 2002 and 2003, the PEA decreased towards the southern stations. During the 2004 rainy-stratified season transect, PEA was high at all stations (Fig. 4).

Mixing depth ranged from 18 to 78 m in Kigoma and from 13 to the whole 100 m water column during the dry-mixing season in Mpulungu. The euphotic depth ranged from 25 to 56 m in Kigoma and from 14 to 65 m in Mpulungu, where it was significantly lower during the dry-mixing season. The light intensity in the mixed layer was on average 23 % of the surface light and was significantly reduced during the dry season at the southern station (17 vs. 31 % during the rainy season). At the southern station Mpulungu, there was a significant change in Zm, Zeu and average light intensity in Zm with PEA. The ratio of the mixing zone depth on the euphotic depth (Zm:Zeu) (Figs 2 and 3) was significantly higher during the dry-mixing season at the southern station (Table 1) and was negatively correlated with the PEA at that site (Table 2). While SRP and NO_3-N concentrations were significantly higher during the dry-mixing season at the southern station, no clear seasonal differences were observed for the northern station. However, as can be observed in Fig. 2 and 3 peaks of increased nutrient concentra-

Table 2. Correlation of abiotic and biotic variables at the northern (Kigoma) and southern (Mpulungu) sampling station in Lake Tanganyika with the potential energy anomaly (PEA). The *p* value of the correlation is given in parentheses.

	Kigoma PEA	**Mpulungu** PEA
Abiotic variables		
Temperature	0.981 (p = 0.000)	0.976 (p = 0.000)
Zm	0.063 (p = 0.605)	–0.594 (p = 0.000)
Zeu	0.198 (p = 0.101)	0.454 (p = 0.000)
Average light concentration in Zm (%)	0.048 (p = 0.688)	0.528 (p = 0.000)
Zm:Zeu	–0.030 (p = 0.000)	–0.600 (p = 0.000)
SRP	–0.450 (p = 0.000)	–0.633 (p = 0.000)
NO_3-N	–0.075 (p = 0.548)	–0.432 (p = 0.000)
Si	–0.114 (p = 0.423)	–0.339 (p = 0.004)
Biotic variables		
Picocyanobacteria	–0.177 (p = 0.174)	–0.440 (p = 0.000)
Eukaryotic phytoplankton < 5µm	–0.264 (p = 0.040)	–0.411 (p = 0.001)
Phytoplankton (≥ 5µm)	–0.357 (p = 0.009)	0.290 (p = 0.066)
Total phytoplankton	–0.364 (p = 0.013)	–0.312 (p = 0.050)
Cyanobacteria (≥ 5µm)	–0.118 (p = 0.404)	0.259 (p = 0.102)
Chlorophytes (≥ 5µm)	–0.224 (p = 0.111)	0.450 (p = 0.003)
Diatoms (≥ 5µm)	–0.309 (p = 0.026)	0.071 (p = 0.659)
Bacteria	–0.085 (p = 0.519)	0.144 (p = 0.260)
HNF	0.229 (p = 0.082)	–0.367 (p = 0.002)
Ciliates	–0.215 (p = 0.134)	0.077 (p = 0.628)

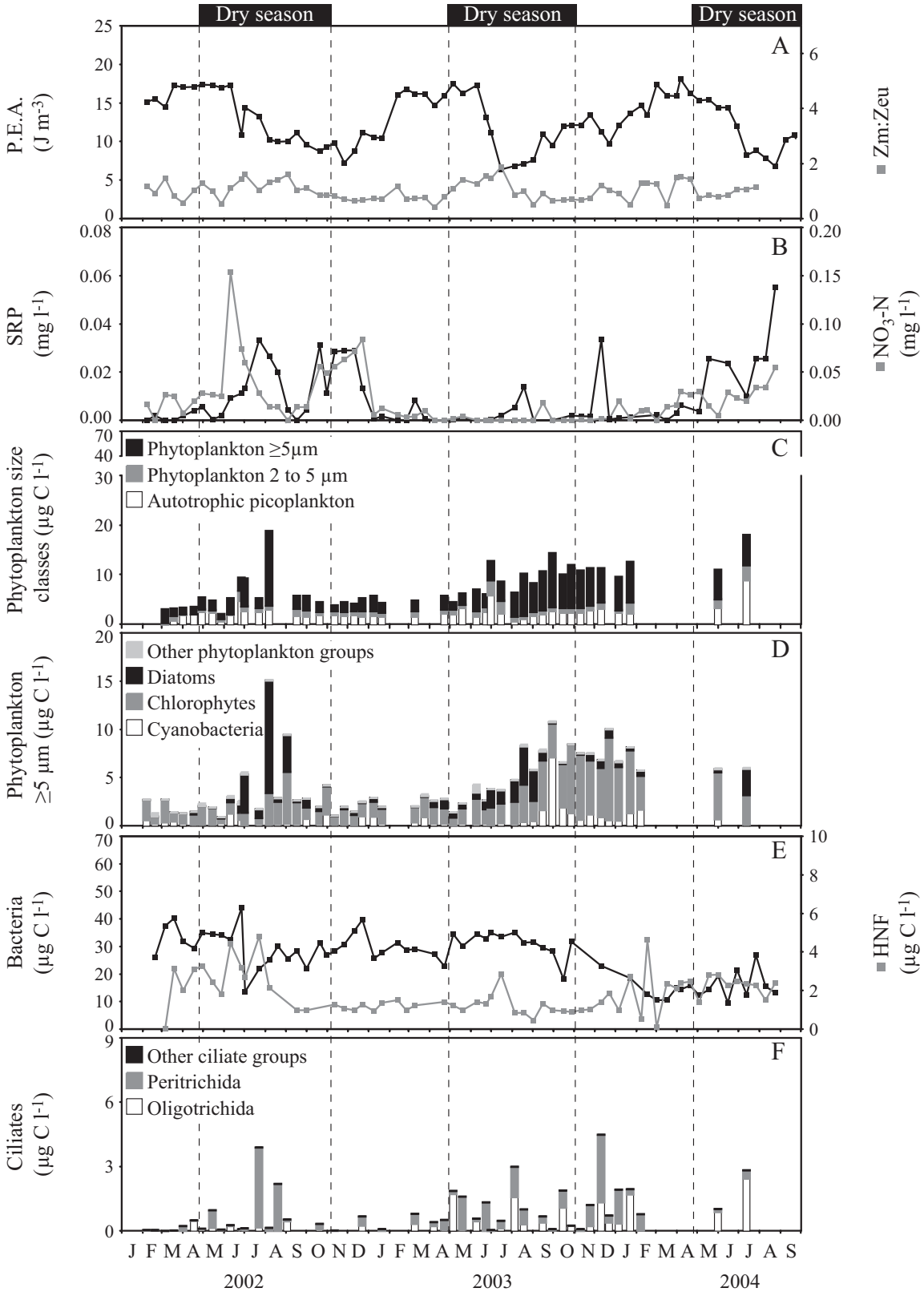

Fig. 2. Monitoring data for the northern station Kigoma in Lake Tanganyika. **(A)** Potential energy anomaly (PEA) calculated for the upper 100 m and the mixing depth over euphothic depth ratio Zm:Zeu. **(B)** Soluble reactive phosphorus (SRP) and nitrate (NO_3-N) concentrations at a depth of 20 m (C to F) temporal changes in biomass at a depth of 20 m for: **(C)** phytoplankton size classes, **(D)** biomass of phytoplankton groups obtained from inverted microscope (≥ 5 µm), **(E)** bacterial and HNF biomass, **(F)** biomass of different ciliate groups.

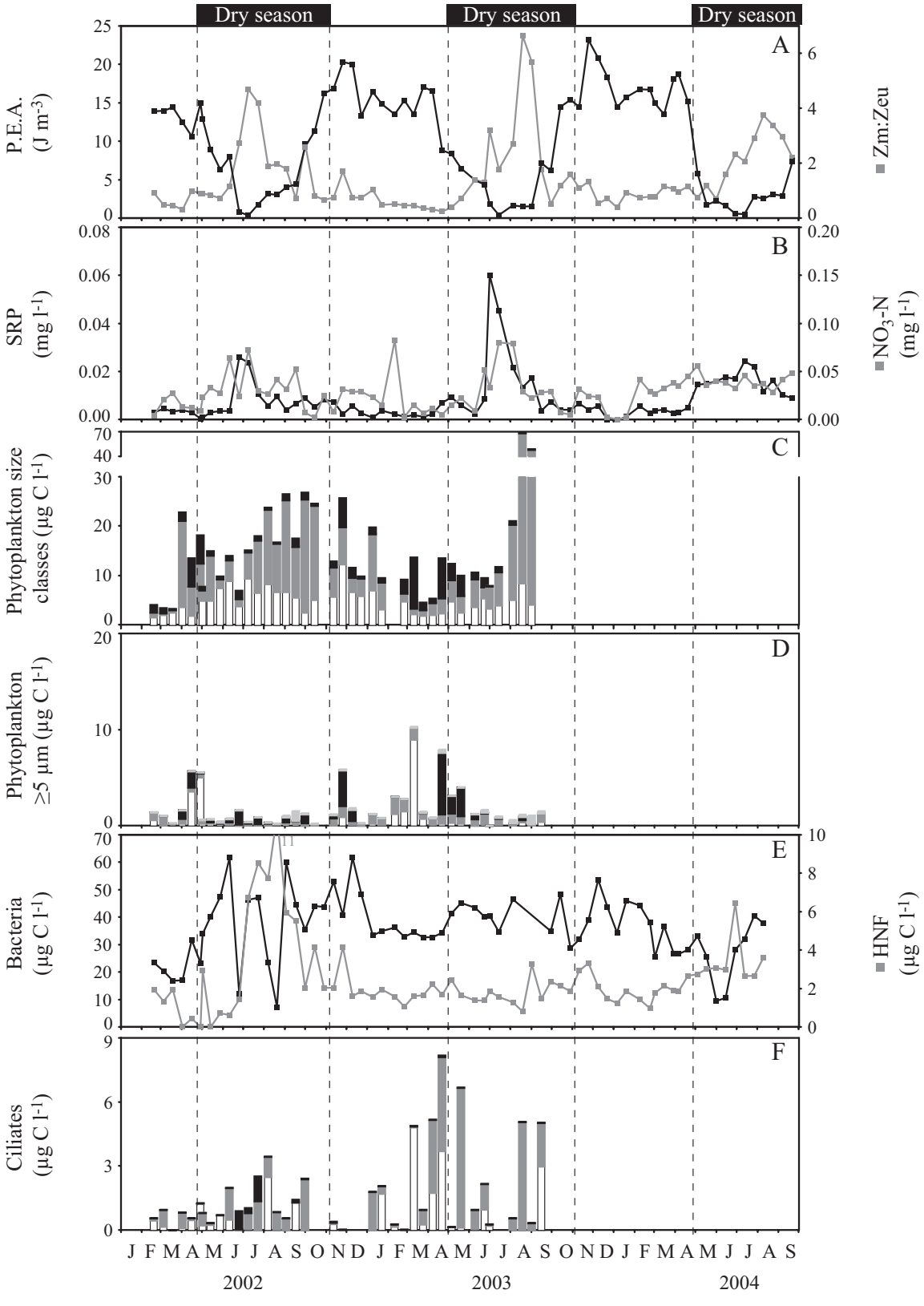

Fig. 3. Monitoring data for the southern station Mpulungu in Lake Tanganyika. Panels as in Fig. 2.

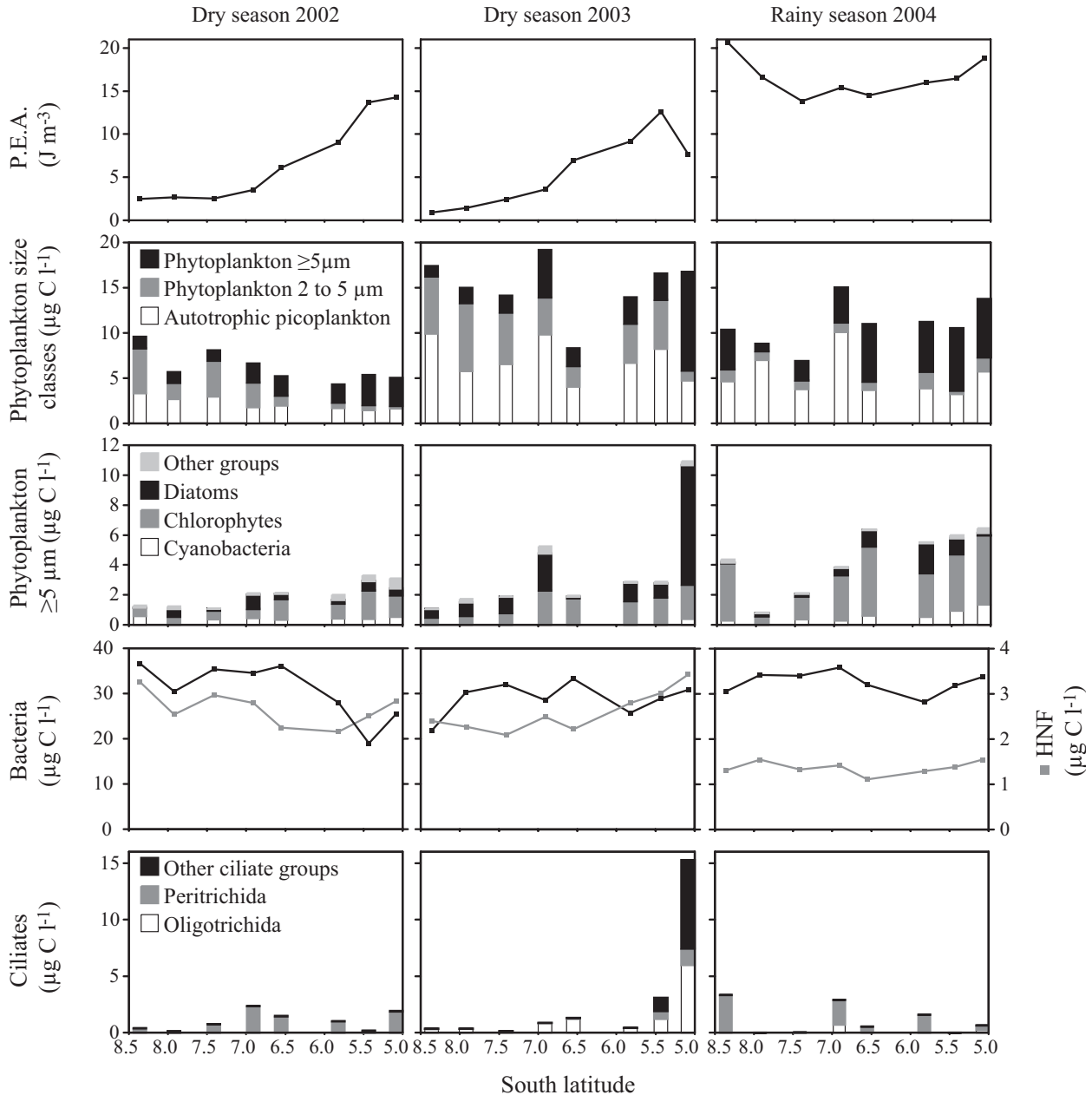

Fig. 4. Horizontal profiles (from south to north) of measured biotic variables and the PEA as recorded during the dry-mixing season transects of 2002 and 2003 and the rainy-stratified season transect of 2004 in Lake Tanganyika. Panels from top to bottom as C to F in Fig. 2.

tion can especially be observed during periods of more intense mixing. Correlation analysis supports this notion showing significant increases in SRP concentrations with decreasing PEA at both sites, while a significant negative correlation of PEA with NO_3-N and Si was only observed at the southern station (Table 2). At the northern station Kigoma, no clear nutrient increases were observed during the dry-mixing season of 2003 in contrast to 2002 and 2004. At the southern station Mpulungu, the highest increases were observed during the dry-mixing season of 2003 when the lowest PEA was observed. NO_2-N and NH_4^+-N concentrations were generally very low and did not show a clear seasonality or relation to PEA.

The variation in the biotic variables is shown in Figs 2, 3 and 4 and Tables 1 and 2. Total phytoplankton biomass was significantly higher in Mpulungu (ranging from 3.31 to 68.69 µg C l^{-1}) compared to Kigoma

(ranging from 2.74 to 18.53 µg C l^{-1}). On average, 50 % of total phytoplankton biomass in Kigoma and 84 % of the phytoplankton biomass in Mpulungu was composed of cells < 5 µm. Autotrophic (prokaryotic) picoplankton (< 2 µm) accounted for on average 34 % and 39 % of the total phytoplankton biomass respectively in Kigoma and Mpulungu. At both stations total phytoplankton biomass increased when PEA decreased (Table 2). In Kigoma, this increase in phytoplankton biomass was mainly due to an increase in (eukaryotic) phytoplankton 2 to 5 µm and phytoplankton ≥ 5 µm, while in Mpulungu it was only due to an increase in phytoplankton < 5 µm (autotrophic picoplankton and phytoplankton 2 to 5 µm). At the northern station Kigoma, a short peak in phytoplankton biomass was observed during the dry-mixing season of 2002 (due to increase of diatoms). The biomass increase during the dry-mixing season of 2003 was maintained throughout the following rainy-stratified season (succession of diatoms, cyanobacteria and chlorophytes). At the southern station the highest biomass increase was observed during the dry–mixing season of 2003 (mainly due to the increase of phytoplankton 2–5 µm).

The autotrophic (prokaryotic) picoplankton biomass was higher in Mpulungu and increased significantly during the dry-mixing season, while no seasonal pattern was observed in Kigoma. During the 2002 transect, autotrophic picoplankton biomass increased from the north towards the south of the lake (Fig. 4). No particular latitudinal gradient was observed during the transects in the dry-mixing season of 2003 and the rainy-stratified season of 2004.

The biomass of (eukaryotic) phytoplankton 2 to 5 µm ranged from 0.00 to 3.39 µg C l^{-1} in Kigoma and 0.25 to 59.56 µg C l^{-1} in Mpulungu with a higher average in Mpulungu (8.39 vs. 1.21 µg C l^{-1} in Kigoma). It showed a significant increase during the dry-mixing season at the southern station Mpulungu and increased towards the south during the dry-mixing season transects of 2002 and 2003, while densities were generally low (0.95 µg C l^{-1} on average) during the rainy-stratified season transect of 2004.

Larger phytoplankton (≥ 5 µm) biomass varied between 0.97 and 15.12 µg C l^{-1} in Kigoma and between < 0.01 and 10.28 µg C l^{-1} in Mpulungu. Their average biomass was significantly greater at Kigoma (on average 4.36 vs. 1.93 µg C l^{-1}). A significant negative correlation with PEA was observed at the northern station (Table 2). During the north-south transects a higher biomass was generally observed in the north of the lake (although less clear in 2003).

The phytoplankton (≥ 5 µm) community was dominated by cyanobacteria, chlorophytes and diatoms. Cryptophytes, chrysophytes, dinophytes and euglenophytes contributed hardly to the total phytoplankton biomass (generally less than 5 %) and most of their taxa were only sporadically observed, for example euglenophytes were observed in may 2002 and June 2003 in Kigoma, chrysophytes had a higher contribution in September 2002 in Mpulungu and higher contributions of dinophytes and cryptophytes were observed in Augustus and September of 2003 in Mpulungu. A detailed description of the species composition of the phytoplankton ≥ 5 µm in Kigoma for the year 2002 can be found in Cocquyt & Vyverman (2005). At Kigoma, chlorophytes were permanently high in abundance (on average 64 % of the phytoplankton biomass recorded during inverted microscopy counts) and dominated the phytoplankton community during the rainy-stratified season. Diatom peaks were observed during the dry-mixing season months June to August in both 2002 and 2003. An increase in filamentous cyanobacteria was observed at the end of the dry-mixing season in 2003 (50% of the total phytoplankton biomass; Fig 2C) but not in 2002. At Mpulungu the succession of phytoplankton groups was dominated by small phytoplankton species, while phytoplankton species ≥ 5 µm had only a minor contribution to the total phytoplankton biomass. Increases in the contribution of cyanobacteria (≥ 5 µm), due to the occurrence of small coccoid taxa, were observed near the end of the rainy-stratified season in both 2002 and 2003. The same dominant phytoplankton groups were observed during the latitudinal transects. During the dry-mixing season transect of 2002 and the rainy-stratified season transect of 2004, chlorophytes were the dominant group, with the highest biomass observed at the northern stations, while diatoms dominated the dry-mixing season transect of 2003, with the highest biomass at the northernmost station.

Bacterial biomass ranged from 9 to 44 µg C l^{-1} in Kigoma and 7 to 62 µg C l^{-1} in Mpulungu and was significantly higher at the southern station (Figs. 2 and 3E). No clear seasonal pattern in the bacterial biomass was observed during the monitoring period. The bacterial biomass during the 2002 transect was higher at the southern stations (from 30 to 37 µg C l^{-1}) compared to the three northernmost stations (from 19 to 28 µg C l^{-1}). During the 2003 and 2004 transects, no clear latitudinal patterns were observed.

The heterotrophic nanoflagellate (HNF) biomass ranged from 0.09 to 4.80 µg C l^{-1} in Kigoma and 0.06 to 11.01 µg C l^{-1} in Mpulungu with a significantly higher average in Mpulungu. HNF biomass was negatively correlated with the water column stability and higher during the dry season in Mpulungu. At Kigoma, no

clear seasonal patterns were apparent. No latitudinal variation was observed during the transects of 2002, 2003 and 2004. During the rainy season transect of 2004, the HNF densities were however considerably lower than during both dry season transects (on average 1.37 compared to 2.66 and 2.59 µg C l^{-1}).

Ciliate biomass ranged from 0.01 to 4.49 µg C l^{-1} in Kigoma and from 0.01 to 8.16 µg C l^{-1} in Mpulungu. No clear seasonal and latitudinal patterns in the ciliate biomass were observed. The main ciliate orders were the Peritrichida (*Vorticella* cf. *aquadulcis,* cf. *Pseudohaplocaulus infravacuolatus*) and the Oligotrichida (*Pelagostrombidium* sp.).

Discussion

The data obtained during this 3-year monitoring study in Lake Tanganyika allow comparison with previous studies (Table 3) and the evaluation of the seasonal and spatial variability of both auto- and heterotrophic components of the microbial food web. Biomass of phytoplankton > 2 µm estimated from epifluorescence and inverted microscopy counts are comparable to previous studies in which phytoplankton biomass was estimated using microscopy (Hecky & Kling 1981, Verburg et al. 2003). Densities of autotrophic picoplankton observed using epifluorescence microscopy were much lower than those observed by Vuorio et al. (2003) in the lake. This is probably a consequence of the 0.8-µm filter we used to count autotrophic picoplankton, due to which we have missed the smallest cells during enumeration. However, biomass estimates of autotrophic picoplankton were higher than those of Vuorio et al. (2003) because of the higher average cell size (1 µm diameter) used for biomass calculation.

The chlorophyll-*a* data obtained during the same study period display the same major patterns in the phytoplankton community composition (with cyanobacteria of the *Synechococcus* pigment type dominant at the southern station, chlorophytes dominant at the northern station and diatoms developing during the dry season). While wet biomass data are generally in the same range as the other studies, we did not detect a high increase in the wet biomass due to a bloom of cyanobacteria (> 600 µg l^{-1}) as observed by Hecky &

Table 3. Comparison of data on the microbial food web components with data obtained during previous studies on Lake Tanganyika. Mean values are shown, ranges are included in parenthesis. Data sources: (1) Hecky & Kling 1981, (2) Sarvala et al. 1999, (2b) Mölsä et al. 1999b, (2c) Langenberg 1996 & Langenberg et al. 2003, (3) Vuorio et al. 2003, (4) Verburg et al. 2003, (5) Descy et al. 2005, (6) Pirlot et al. 2005 and 2006, (7) Cocquyt & Vyverman 2005. * Inverse microscopy counts (this study ≥ 5 µm).

		This study		Previous studies
		Kigoma	Mpulungu	
Autotrophic picoplankton (<2 µm)	Densities (× 10^3 cells ml^{-1})	22 (5–76)	39 (11–105)	Up to 600 (3)
	Wet biomass (µg l^{-1})	11.5 (2.6–39.5)	20.5 (6.0–55.1)	1.8–8.8 (3)
	C-biomass (µg C l^{-1})	2.6 (0.6–8.9)	4.6 (1.3–12.4)	<2.5 (3)
	% (of total C-biomass / of Chl-*a*)	34 (10–59)	39 (9–81)	31% Kigoma and 56% Mpulungu (5)
Large phytoplankton*	Wet biomass (µg l^{-1})	33 (6–159)	13 (1.5–69.6)	160 (37–685) (1), 31 / 17 (4), 12 / 61
	incl. 2–5 µm fraction	39 (9–163)	60 (3–314)	/ 21 / 64
	C-biomass (µg C l^{-1})	4.3 (0.9–15.1)	1.9 (0.0–10.3)	(7; this study)
	incl. 2–5 µm fraction	5.4 (1.5–15.9)	11.0 (0.6–60.7)	
Phytoplankton total	Wet biomass (µg l^{-1})	49 (10–175)	82 (15–352)	13–88 (3)
	C-biomass (µg C l^{-1})	7.7 (2.1–18.9)	16.0 (3.3–69.2)	2.4 g C m^{-2} (2)
	Chl-*a* (µg l^{-1})	(5): 0.72 (0.35–1.96)	(5): 0.81 (0.07–3.40)	0.1–4.5 (1), ±1 (2), 0.91–1.76 (max: 17.3) (2c)
Bacteria	Densities (× 10^6 cells ml^{-1})	2.6 (1.0–4.4)	3.6 (0.7–6.2)	0.4 (0.3–0.5) (1), 1–4 (2b), 2.3–5.3 (6)
	C-biomass (µg C l^{-1})	26 (10–44)	36 (7–62)	27 (18–49) (6)
HNF	Densities (× 10^3 cells ml^{-1})	0.64 (0.01–1.70)	0.88 (0.00–3.90)	0.30–1.83 (6)
	C-biomass (µg C l^{-1})	1.8 (0.0–4.8)	2.5 (0.0–11.0)	5.1–10.8
Ciliates	Densities (× 10^3 cells l^{-1})	0.80 (0.03–6.63)	0.74 (0.00–5.45)	<3.25 (6)
	Wet biomass (µg l^{-1})	6 (0–32)	12 (0–58)	90 (18–415) (1)
	C-biomass (µg C l^{-1})	0.9 (0.0–4.5)	1.7 (0.0–8.2)	0.7–3.0 (6)

Kling (1981). Both Verburg et al. (2003) and Cocquyt & Vyverman (2005) observed a chlorophyte-bacillariophyte-cyanobacteria phytoplankton community in contrast to the cyanobacteria-chrysophyte-chlorophyte community found in 1975. According to Verburg et al. (2003), this shift in phytoplankton community composition as well as the lower wet biomass they observed, could be related to the reduced production of the lake as had been inferred from carbon isotope records in sediment cores (O'Reilly et al. 2003). However, as discussed in Cocquyt & Vyverman (2005), caution is needed when data from a limited number of sampling occasions are considered, as they are likely to represent an incomplete picture of the long term changes because of the interannual variability in phytoplankton biomass and community composition.

Microscopical analyses suggest a consistently high contribution of autotrophic picoplankton to the total phytoplankton biomass (on average 34 % in Kigoma and 39 % in Mpulungu) in Lake Tanganyika. This is also supported by HPLC-pigment data, which show a high contribution of phytoplankton with the *Synechococcus* pigment type (on average 31 % in Kigoma and 56 % in Mpulungu; Descy et al. 2005). Such a high contribution is not exceptional for oligotrophic systems (e.g. comparable to summer values (18–58 %) in the St. Lawrence Great Lakes; Fahnenstiel et al. 1998).

Our estimates of total phytoplankton biomass from epifluorescence and inverted microscopy counts were very low when compared to those estimated from chlorophyll-*a* data measured during this study (Descy et al. 2005) or during previous studies (Hecky & Kling 1981, Langenberg 1996, Mölsä et al. 1999b, Sarvala et al. 1999, Langenberg et al. 2003). The carbon to chlorophyll-*a* ratio estimated from these counts was on average only 15. This is unrealistically low as oligotrophic systems generally display high carbon to chlorophyll-*a* ratios (e.g., Buck et al. 1996). It is unlikely that this was due to sample conservation problems specific to our study as a low phytoplankton (wet) biomass was also observed in previous studies where biomass was estimated using microscopical methods. Possibly, this may point to the fact that the biovolume to C-biomass conversion factor used may not be optimal for oligotrophic phytoplankton communities dominated by small phytoplankton species. Indeed, Menden-Deuer & Lessard (2000) indicate that further work is necessary in order to improve this conversion factor, especially for chlorophytes. We therefore restrict comparisons of heterotrophic to autotrophic biomass to estimates based on Chl-*a* data.

Using a C:Chl-*a* ratio of 100 (average value estimated from the C:Chl-*a* relation as outlined in Buck et al. 1996), the average H:A-ratios were 0.5 and 0.6 (for Kigoma and Mpulungu, respectively). Such values are not exceptional and agree with those observed in both lacustrine and oceanic environments receiving limited external carbon input (Simon et al. 1992, Del Giorgio & Gasol 1995, Buck et al. 1996, Gasol et al. 1997).

The epilimnetic bacterial densities observed during this study (0.7 to 6.2 × 10^6 cells ml^{-1}) are in the high range observed in oligotrophic systems in temperate lakes (e.g., Wetzel 2001), but match the ranges mentioned by Mölsä et al. (1999b) and Pirlot et al. (2005) for Lake Tanganyika. It is unclear whether the low densities (< 1.5 × 10^6 cells ml^{-1}) observed by Hecky & Kling (1981) may be due to differences in the methods used (acridine orange staining) or reflect changes in the abundance or community composition of heterotrophic predators.

The HNF and ciliate densities were comparable to those observed by Pirlot et al. (2005). The observed ciliate densities and biomass also agree well with those found in Lake Malawi (1.5 cells ml^{-1} and 0.03 to 7.82 µg C l^{-1}; Yasindi & Taylor 2003). While the ciliate densities observed during this study may in some cases have been too low (< 30 cells l^{-1}) for accurate enumeration, and ciliates may disappear when stored in liquid samples (Sherr & Sherr 1993), these factors are unlikely to explain the high variability in the densities (< 30 up to > 5000 cells l^{-1}) completely. Hecky & Kling (1981) observed a higher wet biomass for ciliates and a dominance of oligotrichous ciliate taxa, while the ciliate community observed during this study was dominated by peritrich ciliates. As peritrich ciliates depend on the presence of large phytoplankton species due to their attached lifestyle, the change in the ciliate community composition may be related to the shift in phytoplankton community composition observed during the past decades.

Whereas both the high biomass of heterotrophic bacteria and the high contribution of autotrophic picoplankton to the total phytoplankton biomass suggest that the microbial food web is a major pool of particulate carbon at both sites in the lake, the importance of the microbial food web components changed considerably in relation to water column stability.

Water column stability (expressed as the potential energy anomaly; PEA) displayed a clear seasonal variation at both stations, with a lower stability during the dry-mixing season. The lowest PEA values were observed at the southern station (this was also

observed during the dry season transects), most likely reflecting the upwelling of deep water resulting from the south-eastern monsoon winds. These observations on the changes in thermal stratification agree with the seasonal limnological cycle as described by Plisnier et al. (1999) and as supported by the changes in isotherm depth (Langenberg et al. 2003).

Lower water column stability is expected to result in higher dissolved nutrient concentrations (Langenberg et al. 2003). Such an inverse relation between PEA and dissolved nutrients was indeed observed for the southern station (Table 2), but was only detected for SRP at the northern station. Possibly, small increases in the nutrient supply may go unnoticed because of rapid consumption of nutrients by phytoplankton (Zimmerman et al. 1987). The changes in PEA and associated shifts in nutrient concentration and supply are expected to affect both primary production and food web structure.

The autotrophic organisms showed marked seasonal variation in biomass and composition. At both sampling stations, the total phytoplankton biomass was inversely related to the water column stability. This may point to a higher primary production during periods with more intense mixing as suggested by Langenberg et al. (2003) and Plisnier & Coenen (2001). Due to the annual upwelling, the southern part of Lake Tanganyika (Mpulungu) was expected to be more productive than the north (Kigoma). This was supported by the observed higher total phytoplankton biomass at Mpulungu.

One of the most remarkable seasonal changes in phytoplankton biomass is the increase of picocyanobacteria during upwelling at the southern station. This response of phytoplankton to presumed nutrient increases during upwelling in the south of Lake Tanganyika may be due to a combination of factors. First, Descy et al. (2005) noted that upwelling of deep water in Mpulungu is associated with a high mixing depth to photic depth ratio. This would favour small phytoplankton like the autotrophic picoplankton and phytoplankton 2 to 5 µm as they are more efficient in capturing light than large phytoplankton (Glover et al. 1987, Moore et al. 1995). Second, nutrient addition assays have indicated that, in Lake Tanganyika, autotrophic picoplankton is stimulated by iron additions (De Wever et al., unpubl.). Although iron is present in relatively high amounts, much of the iron may be unavailable to phytoplankton due the high pH of Lake Tanganyika's surface waters. Differences in phytoplankton community composition between the north and south of the lake may also be related to differences in the N:P supply ratio between the north and the south of the lake (Bulgakov & Levich 1999). While data on the actual nutrient supply rates are lacking, nitrate concentrations during the dry season upwelling in the south of the lake were significantly higher than at the northern station and the ratio of the dissolved inorganic nitrogen vs. phosphorus was on average higher in the south of the lake (4.8 in Mpulungu vs. 2.6 in Kigoma). This contrast in both nitrogen concentration and N:P ratio probably reflects differences in nutrient requirements of the dominant phytoplankton groups. The picocyanobacterium *Synechococcus* sp., which is more abundant at the southern station, is characterised by relatively high N:P ratios (> 24 mol/mol; Bertilsson et al. 2003), while the diatom genus *Nitzschia*, which is more abundant at the northern station, has an optimal growth rate at N:P ratios between 5 and 20 (Bulgakov & Levich 1999). This difference in stoechiometry was confirmed in culture experiments by Suttle & Harrison (1988), who observed a dominance of coccoid cyanobacteria at high N:P supply and diatoms at low N:P supply. In contrast to the autotrophic plankton, the heterotrophic components of the microbial food web displayed only limited seasonal variation. The bacterial biomass was generally quite high and did not show any clear variation in relation to either environmental variables or phytoplankton biomass. This limited variation may be related to either a sustained high production of dissolved organic carbon (DOC) or to a low predation pressure. The DOC exudation by phytoplankton organisms is not necessarily linearly related to phytoplankton biomass, as DOC is especially exuded in nutrient limited conditions, when carbon fluxes exceed the intake of other essential nutrients (Dubinsky & Berman-Frank 2001). A low predation pressure on bacteria in Lake Tanganyika is supported by unpublished size fractionation experiment results (De Wever 2006), which suggest higher predation pressure on the autotrophic compartments compared to bacteria. This may be related to the composition of bacterial communities in lake Tanganyika as some of the bacterial groups that occur in the lake, like Actinobacteria and Betaproteobacteria (De Wever et al. 2005), have representatives that escape predation due to their small size (Pernthaler et al. 2001, Hahn 2003).

The HNF biomass, which was highly variable at both sampling stations, was negatively correlated with PEA and significantly higher during the dry season at the southern station. In 2002, this increase in HNF biomass occurred during a period with higher biomass of small phytoplankton (< 5 µm). Such an increase in HNF biomass was however not observed during peri-

ods with a high biomass of small phytoplankton during other years. The ciliate community, dominated by peritrichous species with a predominantly bacterial diet (Foissner et al. 1999) showed a high degree of variation in biomass. As the bacterial densities remained relatively stable, top-down control by copepod grazers might have contributed to this variation. Although no data on copepods are available for our study period, historical data suggest that the copepod biomass can be relatively high (1 g C m^{-3}; Sarvala et al. 1999) and highly variable in time (Kurki et al. 1999).

In addition to the seasonal changes in water column stability, we also observed interannual differences during this study period. The PEA was reduced for a shorter period of time during the dry season in 2002 compared to the dry season of 2003 and 2004 (averages over the dry season 6.9 vs. 4.9 and 3.9 J m^{-3}; but differences are not significant). Interannual changes in hydrodynamics are assumed to drive variation in production of the lake (Plisnier & Coenen 2001). While we did not observe significant interannual differences based on seasonal averages, higher peaks in SRP, NO_3-N and the phytoplankton biomass can be observed during the dry season of 2003 at the southern station Mpulungu.

Conclusions

During this 3-year study, we monitored the biomass and composition of the microbial food web components in order to study changes in the microbial food web in relation to changes in water column stratification. Both the high bacterial biomass and the high contribution of picocyanobacteria suggest an important contribution of the microbial food web throughout the year, with only minor seasonal changes. The lack of spatial and temporal variability in the bacterial biomass may be due to low grazing pressure or to a sustained high dissolved organic carbon production. Heterotrophic nanoflagellates increased significantly during the dry season upwelling in Mpulungu, when higher densities of phytoplankton < 5 µm were observed. The ciliate community dominated by presumably bacterivorous peritrich taxa did not show any clear seasonal or spatial variation. Clear seasonal and spatial differences were observed for the autotrophic biomass, especially in the contribution of phytoplankton < 5 µm. Contrary to our expectations, we did not observe an increase in large phytoplankton during the dry season upwelling in the south of the lake. Instead, autotrophic picoplankton (< 2 µm) and small eukaryotic phytoplankton (2 to 5 µm) densities increased during this season. At the northern station, on the other hand, diatoms increased during periods of stronger thermocline oscillations during the dry-mixing season. We propose that this difference in response may be caused by a combination of factors including the higher mixing depth to photic depth ratio, changes in bioavailability of iron and differences in N:P-ratio during the upwelling. As no clear relation between the variation in the autotrophic components and the heterotrophic components could be established, it is however unclear to what extend the contribution of small phytoplankton influences the importance of the microbial food web in different parts of the lake.

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