Abundance and biomass of heterotrophic microorganisms in Lake Tanganyika

SAMUEL PIRLOT,* JULIE VANDERHEYDEN,* JEAN-PIERRE DESCY* AND PIERRE SERVAIS†
*Laboratory of Freshwater Ecology, URBO, Department of Biology, University of Namur, Namur, Belgium
†Ecology of Aquatic Systems (ESA), Free University of Brussels, Brussels, Belgium

SUMMARY

1. This study focused on heterotrophic microorganisms in the two main basins (north and south) of Lake Tanganyika during dry and wet seasons in 2002. Bacteria (81% cocci) were abundant (2.28–5.30 × 10^6 cells mL^-1). During the dry season, in the south basin, bacterial biomass reached a maximum of 2.27 g C m^-2 and phytoplankton biomass was 3.75 g C m^-2 (integrated over a water column of 100 m).
2. Protozoan abundance was constituted of 99% of heterotrophic nanoflagellates (HNF). Communities of flagellates and bacteria consisted of very small but numerous cells. Flagellates were often the main planktonic compartment, with a biomass of 3.42–4.43 g C m^-2. Flagellate biomass was in the same range and often higher than the total autotrophic biomass (1.60–4.72 g C m^-2).
3. Total autotrophic carbon was partly sustained by the endosymbiotic zoochlorellae Strombidium. These ciliates were present only in the euphotic zone and usually contributed most of the biomass of ciliates.
4. Total heterotrophic ciliate biomass ranged between 0.35 and 0.44 g C m^-2. In 2002, heterotrophic microorganisms consisting of bacteria, flagellates and ciliates represented a large fraction of plankton. These results support the hypothesis that the microbial food web contributes to the high productivity of Lake Tanganyika.
5. As the sole source of carbon in the pelagic zone of this large lake is phytoplankton production, planktonic heterotrophs ultimately depend on autochthonous organic carbon, most probably dissolved organic carbon (DOC) from algal excretion.

Keywords: bacteria, ciliates, flagellates, microbial loop, Tanganyika

Introduction

East African Rift Lakes are among the most fascinating ecosystems in the world, well-known for their astonishing biodiversity and endemic fauna (Lowe-McConnell, 2003). Among them, Lake Tanganyika has attracted scientists for decades (Coulter, 1991), and has been recently a focus of paleoclimatic and limnological studies, often centered on the unusually high yield of its pelagic fisheries (Hecky et al., 1981) and on the ecological changes that may have resulted from global warming (Plisnier et al., 1999; Livingstone, 2003; O’Reilly et al., 2003; Verburg, Hecky & Kling, 2003; Verschuren, 2003). Despite recent studies (Sarvala et al., 1999), the debate about the high productivity of Lake Tanganyika is not fully closed yet, in particular because the role of the microbial food web has not been comprehensively assessed.

Lake Tanganyika is a large meromictic lake in the East African Rift Valley, with two deep basins, one in the north (maximum depth of 1310 m) and one in the south (maximum depth of 1470 m), separated by a sill of 600 m depth. The surface area of the lake is 32 600 km^2; its volume is 18 940 km^3 and its mean depth 572 m (Hutchinson, 1957). The mixolimnion of
the lake is permanently stratified, and the depth of the mixed layer varies with time and location. Particularly, when the south-east trade winds blow during the dry season (May to September), deeper vertical mixing occurs and, at the southern end, an upwelling takes place (Coulter, 1991; Plisnier et al., 1999). In October, with the return of the rainy season, the tilting of the thermocline and water movements generate internal waves (Plisnier & Coenen, 2001), which have been shown to depend primarily on the periodicity of wind forcing (Naithani, Deleersnijder & Plisnier, 2002, 2003). All these water movements favour the input of nutrients from water below the thermocline, and direct entrainment of deep waters occurs from the upwelling (Coulter, 1991). Also, a deep mixed layer favours efficient nutrient recycling in large tropical lakes (Hecky & Kling, 1987; Kilham & Kilham, 1990). The lake being meromictic, it never mixes vertically beyond the oxycline, which is located around 100–150 m, depending on the location. Therefore, all the lake auto- and heterotrophic production takes place in a relatively ‘shallow’ mixolimnion, on top of a monimolimnion reaching some 1400 m depth.

Hecky (1978), Hecky & Kling (1981) and Hecky (1991) were the first to estimate bacterial and protozoan abundance and bacterial production in Lake Tanganyika. The context of their study was an assessment of the lake food web and its trophic efficiency, with the apparent paradox of high consumer biomass and production, particularly of planktivorous fish, in an otherwise oligotrophic lake, with low phytoplankton biomass and low net primary production (290 g C m\(^{-2}\) year\(^{-1}\)). Therefore, Hecky & Kling (1981) highlighted the remarkably high efficiency of carbon transfer from primary production to fish with a fishery yield approaching that of the most productive marine systems.

A possible explanation for this high productivity is that selection operated as the Miocene and ‘sufficient time has been available to allow for selection of trophically efficient populations’ (Hecky & Kling, 1981). Another hypothesis is a possible underestimation of the average primary production, because of important spatial and temporal fluctuations in algal abundance (Dubois, 1958; Coulter, 1963, 1991). Coulter (1963) emphasised the high algal density found in some bays on the lake, although he described the pelagic area as oligotrophic. Subsequently, Coulter (1991) stressed that the primary production estimates of Hecky & Fee (1981) could be readily criticised because of their poor temporal coverage: for instance, discrete upwelling events had not been sampled. Actually an upwelling usually occurs annually in the south basin of Lake Tanganyika during the dry season, and allows increased primary production (Coulter, 1991; Plisnier et al., 1999) that could be transferred through the food web to sustain consumer production in the southern part of the lake, and possibly in the whole lake. A third hypothesis, proposed by Hecky & Kling (1981) for solving the paradox of high fishery yield with low phytoplankton production, was that bacterial (160 g C m\(^{-2}\) year\(^{-1}\)) and protozoan production, taking place over the whole mixolimnion, could supplement autotrophic production in the transfer of carbon and nutrients to higher consumers.

Bacterial biomass, not confined to the euphotic layer but extending throughout the oxic zone, could enlarge the basis of the trophic pyramid (Fig. 1). Van Meel (1954) had already mentioned abundant bacteria and ciliates in his plankton samples and envisaged that a high heterotrophic microorganisms production might be channelled to the pelagic fishes via copepod grazing. Recent studies (Sarvala et al., 1999) paid little attention to the microbial food web, except for some measurements of bacterial production. Rather, Sarvala et al. (1999) promoted a view of a more eutrophic Lake Tanganyika with gross primary production sufficiently high (426–662 g C m\(^{-2}\) year\(^{-1}\)) to support high fish yields. However, subsequent studies based on stable isotope analyses in various food web components suggested a microbial contribution to the diet of

![Fig. 1](image-url)
large zooplankton (Sarvala et al., 2003). This called for a re-assessment of the heterotrophic plankton in Lake Tanganyika, as previous studies used techniques with a poor resolution and may have missed some organisms or underestimated abundance and biomass of small bacteria and protozooplankton.

Another incentive for undertaking a more detailed study of bacteria and protozooplankton of Lake Tanganyika is that there are few data on the microbial loop and its importance in large tropical lakes. However, there are obvious indications that heterotrophic processes exploiting autochthonous dissolved organic carbon released by phytoplankton should be significant in these systems (Johannes & Webb, 1970; Cole, Likens & Strayer, 1982; Olsen, Varum & Jensen, 1986; Baines & Pace, 1991). So far, the different authors addressing the productivity of large tropical lakes measured particulate production using the $^{14}$C technique (Steemann Nielsen, 1952), and did not account for production of dissolved organic carbon (DOC) and its re-assimilation by heterotrophic bacteria. As the advent of the concept of microbial loop (Pomeroy, 1974; Azam et al., 1983), there is increasing evidence that heterotrophic protists are ubiquitous and comprise a substantial fraction of the plankton biomass in aquatic systems (Pace & Orcutt, 1981). Consequently, interactions within aquatic food webs are now recognised as being highly dynamic and much more complex than previously thought (Arndt, 1993).

The Belgian CLIMLAKE project (Descy & Gosselain, 2004), carried out in collaboration with the Tanzanian and Zambian fishery departments, provided a framework for a study of the planktonic heterotrophic microorganisms in Lake Tanganyika, in parallel with a detailed limnological and planktological survey. Here, we report and discuss the results of a study undertaken in two contrasting seasons and at two distant sites in Lake Tanganyika, in 2002. Data obtained during a dry season cruise between these two sites are also presented. This paper focuses on abundance and biomass of bacteria, heterotrophic nanoflagellates (HNF) and ciliates.

**Methods**

In 2002, two sampling campaigns were carried out: one in January to February during the rainy season, and another in July during the dry season. Samples were collected at different depths in the north (off Kigoma, Tanzania; 04°51.26’S, 29°35.54’E) and in the south (off Mpulungu, Zambia; 08°43.98’S, 31°02.43’E). Discrete water samples were collected with 5-L Plastic Water Sampler (PWS NISKIN type, Hydro-Bios Apparatebau GmbH, Kiel-Holtenau, Germany) and 12-L GO-FLO Water Sampler (General Oceanics, Inc., Miami, FL, U.S.A.) at 20 m intervals from the surface to 100 m. In addition, during the dry season, a cruise from Kigoma to Mpulungu was organised on board the Congolese boat ‘Maman Benita’, with sampling at several locations along this north-south transect (Fig. 2).

Vertical profiles of water temperature, conductivity, oxygen and pH were obtained using a SBE-19 CTD probe (Sea-Bird Electronics, Inc., Bellevue, WA, U.S.A.) and a Hydrolab Datasonde 4A (Hach Company, Loveland, CO, U.S.A.) in Mpulungu. The depth of the mixed layer (Zm) was estimated from those

![Fig. 2 Map of Lake Tanganyika, with location of the sampling sites of the regular survey (1 and 2) and of the research cruise (TKn).](image-url)
vertical profiles. Euphotic depth (depth at which light is 1% of subsurface light) was derived from Secchi depth (SD) by calculating the vertical light attenuation coefficient ($k = 1.57/SD$). The conversion coefficient was obtained by calibration with measurement of photosynthetically alive radiation (PAR) downward attenuation with a surface LICO (Lincoln, NE, U.S.A.) flat plate quantum sensor and underwater spherical quantum sensor. Conversion of Secchi depth to the light attenuation coefficient was determined from these data using a linear regression.

Nutrient analyses were carried out using standard spectrophotometric techniques (APHA, 1992) or Macherey-Nagel® analytical kits (Macherey-Nagel GmbH & Co., Düren, Germany). For dissolved inorganic N (DIN) and P forms, absorbance of coloured samples was measured in 40 or 50 mm cells, with an estimated detection limit of 0.16 μmol L$^{-1}$ for SRP (soluble reactive phosphate), 0.36 μmol L$^{-1}$ for ammonium, 0.71 μmol L$^{-1}$ for nitrate and 0.07 μmol L$^{-1}$ for nitrite. In addition to the measurements carried out during our sampling, a monitoring program was conducted throughout the year 2002 off Kigoma and Mpuungu (Descy & Gosselain, 2004).

Total phytoplankton biomass was estimated from chlorophyll $a$ (Chl $a$) concentration. Three litres of each sampling depth were filtered under moderate vacuum on GF/5 Macherey-Nagel filters (porosity 0.7 μm). Extraction and analysis of pigments was carried out as described in Descy et al. (2005). All chromatograms were checked for the presence of Chl $a$ derivatives that can result from post-sampling degradation of the extracts. No degradation products other than those expected from in situ transformation processes were observed.

Samples for bacteria counting were preserved by the addition of filtered (0.22 μm Millex (Millipore, Billerica, MA, U.S.A.)) formaldehyde (2% final concentration) and stored at 4°C until analysis. Bacterial abundance was determined using epifluorescence microscopy at 1000× magnification, following the procedure proposed by Porter & Feig (1980). After staining the cells with DAPI (4,6-diamidino-2-phenylindole; 10 μg mL$^{-1}$, final concentration), 600–1200 cells were counted after filtration of 1 mL of water on a 0.2 μm pore-size black filter (Nucleopore, Whatman International Ltd, Maidstone, U.K.). Bacterial cells were classified into 24 size classes using a graduated eyepiece to measure cell dimensions, and then biovolume determined using formulae for the closest geometric shape. Image analysis was also used to carry out automatic counting and measurement of bacterial cell size. After image acquisition using a digital camera (Nikon DMX 1200; Nikon Instruments Europe B.V., Badhoevedorp, The Netherlands), the LUCIA G program (Laboratory Imaging Ltd, Prague, Czech Republic) was used for counting around 2000 cells per slide; cell dimensions were measured and biovolume was calculated. We verified that bacterial abundance and biovolume estimated by image analysis were similar to those obtained by direct observation (data not shown).

Biomass was estimated from the abundance and biovolume distribution using the relationship $C_{\text{bact}} = 92 \times V^{0.598}$, relating carbon content per cell (C$_{\text{bact}}$, μg C cell$^{-1}$) to biovolume ($V$, μm$^3$) determined from the data of Simon & Azam (1989).

Samples for protozoan counts were preserved with glutaraldehyde (2% final concentration) and stored at 4°C until analysis. Abundance was determined by epifluorescence microscopy using the same staining procedure as for bacteria (see above). Flagellates and ciliates were collected after filtration of 10 and 30 mL of water on 0.8 and 10 μm pore-size black filters (Nuclepore, respectively). Protozoans were counted and classified into several size and shape classes. We did not identify taxonomic categories, with the exception of the ciliates Strombidium and Vorticella which were distinguished because of their specific characteristics.

### Table 1 Size and taxonomic classes of flagellates and ciliates in Lake Tanganyika in 2002, with average per cell biovolume and biomass in each class

<table>
<thead>
<tr>
<th>Size Class</th>
<th>Average length (μm)</th>
<th>Average width (μm)</th>
<th>Biovolume (μm$^3$ per cell)</th>
<th>Biomass (μg C per cell)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Flagellates (μm)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>8–12</td>
<td>10</td>
<td>5</td>
<td>1309</td>
<td>2.88 × 10$^{3}$</td>
</tr>
<tr>
<td>4–6</td>
<td>7</td>
<td>6</td>
<td>924</td>
<td>2.03 × 10$^{3}$</td>
</tr>
<tr>
<td>2–5</td>
<td>4</td>
<td>3</td>
<td>75.4</td>
<td>1.66 × 10$^{3}$</td>
</tr>
<tr>
<td>&lt;2</td>
<td>1</td>
<td>1</td>
<td>0.52</td>
<td>1.15 × 10$^{3}$</td>
</tr>
<tr>
<td>Ciliates</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Strombidium (μm)</td>
<td>20–100</td>
<td>30</td>
<td>188 496</td>
<td>3.58 × 10$^{8}$</td>
</tr>
<tr>
<td>Vorticella (μm)</td>
<td>10–18</td>
<td>18</td>
<td>54 965</td>
<td>1.04 × 10$^{8}$</td>
</tr>
</tbody>
</table>

Four size classes of flagellates and six of ciliates were considered (Table 1). Average biovolume per cell in each size class ($\mu m^3$ cell$^{-1}$) was calculated by considering flagellates and ciliates cells as spheroids using the average length and width in each size class. Biomass was estimated from abundance and the distribution of biovolume using the following carbon content per biovolume unit: $190 \times 10^{-15}$ g C $\mu m^{-3}$ for ciliates (Putt & Stoecker, 1989) and $220 \times 10^{-15}$ g C $\mu m^{-3}$ for flagellates (Børsheim & Bratbak, 1987).

For the estimation of metazooplankton biomass, sampling was carried out by a vertical tow from 100 m depth to the surface in daytime using 100 $\mu m$ mesh size plankton net with a 24 cm aperture. The hauling speed was around 0.5 m s$^{-1}$. The methods used were similar to those described in Kurki (1993); Vuorinen (1993) and Vuorinen & Kurki (1995). The samples were preserved in 4% formalin. Copepods were identified to species with an inverted microscope LEICA DMIL at 400× magnification. Dry weight conversion values were derived from Bottrell et al. (1976).

### Results

**Limnological profiles and the depth of the mixed layer**

In the North Basin (Kigoma), similar limnological conditions were observed at both seasons (12 Febru-
ary 2002 and 23 July 2002; Fig. 3a,b). The thermocline was located between 40 and 60 m, but the temperature gradient was weaker during the dry season.

During the rainy season (Fig. 3c), a vertical stratification of the water column was observed at both sites, but at Mpolungu, the thermocline was a little higher (around 30–40 m) and the dissolved oxygen (DO) in the hypolimnion was >4 mg L\(^{-1}\) down to 100 m depth. In the dry season, deeper mixing (down to 50–65 m) usually occurred at Kigoma (Descy et al., 2005); at Mpolungu, the temperature gradient was much weaker, because of lower surface temperature (24.8–25.2 °C), indicating deep mixing conditions. Accordingly, DO was above 6 mg L\(^{-1}\) down to 90 m, and surface nutrient concentrations reached levels typical of deeper waters in stratified conditions. Fortnightly monitoring of temperature showed that upwelling of deep water and complete destratification of the mixolimnion occurred at this southern station in the first part of June (Descy & Gosselain, 2004). The depth of the euphotic zone was comprised between 35 and 40 m at both stations.

Data from the limnological monitoring (Descy & Gosselain, 2004) reveals better the seasonal changes in nutrient availability to the euphotic zone than measurements of our sampling. These data show that SRP averaged 0.19 µmol L\(^{-1}\) in the rainy season and 0.43 µmol L\(^{-1}\) in the dry season at Kigoma, versus 0.17 and 0.36 µmol L\(^{-1}\), respectively, at Mpolungu. Average DIN concentrations showed similar contrast between the two main seasons at both stations, with at Kigoma 0.48 (rainy season) and 0.69 µmol L\(^{-1}\) (dry season) and 0.17 (rainy season) and 1.19 µmol L\(^{-1}\) (dry season) at Mpolungu. All nutrients increased below the thermocline, reaching 1.30 µmol L\(^{-1}\) at 100 m depth.

**Chlorophyll a and phytoplankton biomass**

Similar vertical profiles were observed at both stations (Fig. 4). In the rainy season, Chl a concentration was greatest in the 0–40 m layer and decreased below. The dry season profiles showed higher maxima in the upper water column, up to 1 mg Chl a m\(^{-3}\), and a slower decrease with depth, as a result of deeper mixing. The average Chl a concentration in the mixed layer for both seasons was 0.66 ± 0.21 mg m\(^{-3}\) in the north, and 0.73 ± 0.27 mg m\(^{-3}\) in the south. When integrated over the 100 m water column, the Chl a average of the rainy season was 30.3 mg m\(^{-2}\) in Kigoma and 38.0 mg m\(^{-2}\) in Mpolungu. No significant difference between seasons was found at Mpolungu in 2002, whereas at Kigoma the dry season average Chl a reached 44.2 mg m\(^{-2}\) and was significantly different from that in the rainy season (Student’s t-test; \(P = 0.01\)). Phytoplankton carbon biomass was estimated using a C : Chl a ratio of 100 (Descy & Gosselain, 2004), obtained from a regression analysis of Chl a versus particulate organic carbon, using data from the 0–40 m layer. Multiplying mean seasonal Chl a concentration in the 100 m water column by this factor gave phytoplankton biomass estimates in the
range of 3.0–4.4 g C m$^{-2}$, which were used for comparison with heterotrophic biomass (Fig. 8).

**Bacteria**

In the mixed layer, bacterial abundance was between 2.28 and 3.36 $\times 10^6$ cells mL$^{-1}$, except at Mpulungu during the dry season when abundance reached $5.30 \pm 0.31 \times 10^6$ cells mL$^{-1}$. In the thermocline, bacterial numbers decreased progressively and reached minimal values in the hypolimnion (Fig. 5). Bacterial numbers in the thermocline and in the hypolimnion were not significantly different between seasons at both sites. In contrast, maximal bacterial abundance was observed in the mixed layer, where most of the phytoplankton biomass occurred.

In the epilimnion and in the thermocline, the dominant bacteria were cocci, with more than 81% of bacterial numbers; the remaining cells were vibrio (11%), ellipsoids (6%) and rods (3%). Only total bacterial abundance was obtained in the hypolimnion, without recording detailed morphology. In spite of

---


---

**Fig. 5** Vertical abundance profiles for bacteria ($10^9$ L$^{-1}$) and protozoa ($10^6$ L$^{-1}$) measured in Lake Tanganyika off Kigoma and Mpulungu during the rainy season. (a) 07 February 2002 at Kigoma, (b) 02 July 2002 at Kigoma, (c) 29 January 2002 at Mpulungu, (d) 23 July 2002 at Mpulungu.
morphological differences, the community located between 0 and 100 m depth comprised very small heterotrophic bacteria, with an average cell diameter rarely exceeding 0.7 μm. The smallest cells were found when bacterial abundance was highest.

In each season, no significant difference was found in terms of bacterial biomass between the north and the south (Student’s t-test; \( P = 0.01 \)). Average biomass in the mixed layer was \( 23.9 \pm 3.3 \text{ mg C m}^{-3} \) in the rainy season and \( 39.6 \pm 2.1 \text{ mg C m}^{-3} \) in the dry season. The biomass at Kigoma in the dry season corresponded to a quite low bacterial abundance, but resulted from the presence of large bacteria in the surface layers (0–30 m), with a mean carbon content of 14.1 fg per cell. This carbon content was the highest observed during this study. Bacterial carbon content ranged between 4.3 and 15.6 fg C, with an annual mean of 9.0 fg C per cell.

Bacterial biomass, estimated over the entire water column to 100 m depth, during the rainy season, was 1.77 and 0.84 g C m\(^{-2}\) at Kigoma and Mpulungu, respectively. During the dry season, the integrated bacterial biomass was 1.65 and 2.27 g C m\(^{-2}\), respectively.

Protozoa

In terms of abundance, flagellates represented the bulk of protozoa (99%). Flagellate numbers in the mixed layer varied between 0.30 and \( 1.83 \times 10^6 \text{ L}^{-1} \) (Fig. 5). Ciliate numbers never exceeded \( 3.25 \times 10^3 \text{ L}^{-1} \). The distribution of protozoa in the size classes and taxonomic classes varied with season and site. The flagellates were usually the most abundant (54–76%) in the size class 2–5 μm, except off Kigoma in February 2002. For this latter sampling period, total flagellate abundance was low and the most abundant flagellates (39%) were in the 8–12 μm size class.

Among ciliates, Strombidium (presumably \( S. \) viride Stein, as mentioned by Hecky & Kling, 1981) was the most abundant taxon: considering all observations, they represented 28–73% of total ciliate abundance overall. In the dry season off Kigoma, however, the occurrence of Vorticella increased, and their numbers exceeded those of Strombidium in July (64% against 28%). All Strombidium contained endosymbiotic zoochlorellae, and were essentially located in the euphotic zone. Below the euphotic layer, the most abundant ciliates had a diameter of <10 μm or were in the 10–20 μm range.

 Protozoa biomass, estimated over the entire water column to 100 m depth, during the rainy season, was 1.77 and 0.84 g C m\(^{-2}\) at Kigoma and Mpulungu, respectively. During the dry season, the integrated ciliate biomass was 1.65 and 2.27 g C m\(^{-2}\), respectively.

Protozoan biomass was large, and was sometimes the major plankton compartment. Total protozoan biomass ranged from 76.4 mg C m\(^{-3}\) (off Kigoma, rainy season) to 130.1 mg C m\(^{-3}\) (off Mpulungu, dry season), then equalling or exceeding that of the phytoplankton (Fig. 6). Strombidium was, on all but one occasion, the main contributor to total ciliate biomass. The symbiotic algae present in every Strombidium represented an important fraction of its
biomass. From their studies in Lake Tanganyika, Hecky & Kling (1981) estimated that only 25% of Strombidium biomass is constituted by animal protoplasm. Thus, 75% of the Strombidium biomass must be considered as part of the autotrophic compartment. During the rainy season, Strombidium represented 81.3 and 95.5% of the ciliate biomass, respectively, off Kigoma and Mpulungu, while during the dry season, they represented 55.5 and 90.5%, respectively. For the rainy season, based on the estimate of autotrophic biomass in S. viride, these percentages corresponded to a biomass of zoochlorellae of 19.3 mg C m$^{-3}$ in Kigoma and 42.4 mg C m$^{-3}$ in Mpulungu. For the dry season, the figures were even higher, with 8.0 and 56.2 mg C m$^{-3}$ of autotrophic carbon in Strombidium. Therefore, this autotrophic biomass within S. viride could have represented a significant part of total autotrophic carbon (Fig. 6).

North-south transect

During the north-south transect between Kigoma and Mpulungu carried out in July 2002, large changes in bacterial and protozoan biomass were observed from the north basin off Kigoma to the extreme south off Mpulungu (Fig. 7). In the south basin a progressive increase in biomass was recorded approaching Mpulungu. In terms of carbon, bacterial biomass doubled from the north to the south and protozoan biomass increased by a factor of four in the south relative to the north. A similar trend (i.e. towards higher Chl a in sampling sites of the south basin during the dry season) was observed for phytoplankton biomass (Descy et al., 2005).

Discussion

In this study, we focused on the heterotrophic microorganisms of the planktonic food web in the pelagic waters of Lake Tanganyika. In both basins of the lake, samples were collected from the surface to 100 m, with the objective of evaluating the biomass of heterotrophic plankton, as compared with phytoplankton biomass. Like Hecky & Kling (1981), we found a high abundance and biomass of heterotrophic bacteria and ciliates, but also of HNF, which were not recorded in previous studies on Lake Tanganyika. Data about bacteria and protozoa are scarce for large tropical lakes, and comparisons have to be extended to other great lakes at any latitude, such as Lake Baikal, Lake Michigan and Lake Constance.

Limnological measurements confirmed the seasonal variation previously observed in Lake Tanganyika (Plisnier et al., 1999). While conditions were similar at the north and south stations in the rainy season (shallow thermocline, low nutrients), they were different in the dry season. In the north, stratification was maintained while in the south an upwelling occurred. Although the entrainment of nutrient-rich deep water toward the euphotic zone typically results in increased primary production (Coulter, 1991), large differences in phytoplankton biomass between seasons at both sites were not observed in this case. Only the longitudinal profile from the cruise conducted in the dry season showed a significant increase of Chl a in the southern basin. Actually, phytoplankton biomass peaks in 2002 were not recorded in the dry season in Mpulungu (Descy et al., 2005), and this explains why we did not observe a significant difference between the two seasons at this site. Although we do not report phytoplankton composition here, it is worth mentioning that the phytoplankton was comprised of large cyanobacteria, chlorophytes and diatoms, but also that a significant fraction of the autotrophic plankton was in the picoplankton size range (Vuorio et al., 2003; Descy et al., 2005). Comparison with the Chl a range found in other studies (Hecky & Kling, 1981; Salonen et al., 1999; Sarvala et al., 1999; Langenberg et al., 2002; Langenberg, Sarvala & Roijackers, 2003) showed a good correspondence as far as the minimal concentrations are concerned, but our maximal concentrations were lower (3.40 mg Chl a m$^{-3}$ at Mpulungu; 1.96 at Kigoma) and were observed in the dry season.
However, Descy et al. (2005) pointed out differences in analytical techniques, in sampling conditions and in temporal and spatial coverage, and stressed that no conclusion should be drawn about changes in phytoplankton biomass in Lake Tanganyika between 1975 and the present (Verburg et al., 2003).

In Lake Tanganyika, Hecky & Kling (1981) found $0.14–1.4 \times 10^6$ bacteria mL$^{-1}$ in October to November 1975 (on average 190 mg m$^{-3}$ in terms of wet weight). Our bacterial numbers in 2002 were always at least twice as high as these maxima, but very small cells constituted the bacterial community. In terms of bacterial abundance, our figures are high for a lake usually classified as oligotrophic. Such values, however, can be found in large lakes, e.g. in Lake Baikal (Saunders, 1980 in Servais et al., 1995), in Lake Constance before the spring bloom (Weisse, 1990), in Lake Michigan (Scavia, Laird & Fahrenstiel, 1986) but also in eutrophic lakes and in estuaries (Servais et al., 1995).

In Lake Tanganyika, the highest bacterial abundances were always found in the mixed layer, whatever the location and the season, with maxima off Mpulungu in the dry season, i.e. in deep mixing conditions. In these conditions, abundances were very high and comparable with those of some eutrophic systems (Servais et al., 1995), although the bacterial community was composed of very small cells (100% of bacterial cells were under 1 μm diameter). Small bacteria are usually found in oligotrophic waters. In Lake Constance, this size class included 77% of free-living bacterioplanktonic cells (Simon, 1987).

Cellular bacterial carbon content from Lake Tanganyika was variable (4.3–15.6 fg C per cell) but remained in the lower part of the range of values recorded in aquatic environments (Troussellier et al., 1997). According to the literature, the standard bacterial carbon content per cell in inland and marine waters is 20 fg C per cell (Lee & Fuhrman, 1987). It is known, however, that bacterial cell size and thus bacterial carbon content are lower in oligotrophic systems than in nutrient-rich systems (Billen, Servais & Becquevort, 1990). Accordingly, in the open ocean, the carbon content is typically lower (13.2 fg C per bacteria; Simon & Azam, 1989; Wylie & Currie, 1991). Garrison et al. (2000) reported bacterial carbon content of 12 fg C per cell in the Arabian Sea. In Lake Tanganyika, low carbon content was often associated with high abundance. This may be related to the usually low concentration of nutrients and available organic carbon of the mixed layer, where small spherical cells, with high surface to volume ratio, are better adapted to take up resources at low concentra-

---

Fig. 8 Estimates of the biomass of different plankton compartments integrated in the water column (0–100 m) of Lake Tanganyika. (a) Kigoma in February and July 2002, (b) Mpulungu in January and July 2002.

© 2005 Blackwell Publishing Ltd, *Freshwater Biology, 50*, 1219–1232
tion. In bacteria, this morphology allows a quicker utilisation of organic matter which is available principally through exudation and lysis of phytoplankton (Sundh & Bell, 1992).

Even with their small carbon content per cell, bacteria were well represented in terms of total biomass in Lake Tanganyika: bacterial biomass in the euphotic layer approached primary producer biomass. Moreover, as bacteria were present throughout the mixolimnion, from the surface to the oxic-anoxic boundary, while phytoplankton was mostly restricted to the (35–40 m) euphotic zone, integrated bacterial biomass over the (100 m) water column gives values close to the phytoplankton biomass, whatever the basin and the season. Bacteria presence from the surface to the oxic-anoxic boundary suggests their central role in nutrient recycling, in biogeochemical processes and in organic matter production (Bidlanda, Ogdahl & Cotner, 2001), as in the ocean (Ducklow, 1999). These conclusions about the relatively high bacterial biomass in Lake Tanganyika, compared with phytoplankton and protozoan biomass were already drawn by Hecky & Kling (1981). In Fig. 8, estimates of standing crop for all the plankton compartments are given for our 2002 samples (e.g. for the rainy season sampling off Kigoma: average bacterial biomass was 1.77 g C m⁻² while phytoplankton was 2.22 g C m⁻²). These results, however, may not include the maxima of plankton biomass recorded in 2002 (Descy et al., 2005). Our results for integrated bacterial biomass, in contrast to abundances, are in the same range as those estimated by Hecky & Kling (1981), who used higher cell carbon content than in our study: they calculated bacterial biomass using a mean cell biovolume of 0.25 μm³, converted to wet weight assuming a specific gravity of 1 and then to carbon using a factor of 0.05 mg C (g wet wt)⁻¹.

Hecky & Kling (1981) reported a relatively low protozoan biomass (dry weight on average 32–54 mg m⁻³, depending on the season) compared with bacterial biomass. However, probably because they used only counting under the inverted microscope with relatively poor resolution, they mentioned only ciliates of different classes, among which were the presumably symbiotic Strombidium cf. viride (Hecky & Kling, 1981). In our study, flagellates were the major component of the protozooplankton assemblages in Lake Tanganyika in terms of cell numbers. Dominance of heterotrophic flagellates among planktonic protists has been reported for the pelagic zone of various great lakes, often oligotrophic and thermally well stratified, such as Lake Constance and Lake Erie (Bloem & Bar-Gilissen, 1989; Weisse, 1990; Hwang & Heath, 1997). Flagellate abundance often differed from the north to the south of Lake Tanganyika, depending on the season: like bacteria and phytoplankton biomass, HNF and total protozoan biomass were higher in the southern basin during the dry season. These small heterotrophic protists occupy a key position in the microbial food web, because they are the main predators of bacteria (Sanders, Caron & Berninger, 1992) and can be grazed by a large range of planktonic consumers (Jürgens et al., 1996). In Lake Tanganyika in 2002, flagellates were abundant, most of them were small (80% of the total flagellates were <5 μm) and they presumably fed on bacteria, so that their grazing was probably the main loss process for bacteria.

The symbiotic Strombidium and the heterotrophic Vorticella were the most abundant ciliates in Lake Tanganyika, as reported previously by Hecky & Kling (1981). Compared with flagellates, ciliate numbers were quite low, in the range of 1–10 cells mL⁻¹, as in offshore samples of other great oligotrophic lakes such as Lakes Huron, Michigan and Ontario (Taylor & Heynen, 1987; Carrick & Fahrenstiel, 1990). They represented a significant biomass, however, owing to their high individual biovolume: Strombidium specimens with a length of up to 100 μm were observed. As a large part of the Strombidium biomass is constituted of small endosymbiotic green algae, they occupy an intermediate position between autotrophic and heterotrophs. This autotrophic biomass is included in the estimate of ‘phytoplankton biomass’, (Fig. 6), as we calculated it from Chl a concentration. However, results of zoochlorellae biomass remain to be confirmed because of a possible overestimation of Strombidium biovolume induced by the preservation technique. Also, we based our calculations on the estimates by Hecky & Kling (1981) and assumed 75% of autotrophic carbon in the total Strombidium biomass, although this was not verified in the present study. It is worth mentioning that mixotrophic protists have not been found so far in Lake Tanganyika.

The role of ciliates in bacteria predation in Lake Tanganyika remains unknown. Nevertheless, preliminary observations indicate that Strombidium and
**Vorticella** ingested small particles in the size range of bacteria (0.5 μm in diameter). Ciliates can prey upon algae, bacteria and protozoans; they can be an important trophic link in the microbial food web, as they are in a size edible by adult copepods (Jack & Gilbert, 1993).

*Total protozoan biomass was high in comparison with that of autotrophic plankton and of heterotrophic bacteria, as shown by the estimates of Fig. 8.* At our two sampling sites, and along the north–south transect (Fig. 7), *total protozoan biomass was always about three times greater than bacterial biomass*. Bacteria, flagellates and ciliates were well represented in terms of biomass, indicating the strong trophic links among these microorganisms. Accordingly, the role of heterotrophic plankton in the Lake Tanganyika food web, already hypothesised by Hecky & Kling (1981), has recently received some support from stable isotope studies (Sarvala et al., 2003). Indeed, they concluded that picocyano-bacteria and possibly larger nitrogen-fixing cyanobacteria were consumed by small cyclopoids and shrimps, but they did not provide direct evidence of copepod grazing on heterotrophic protists. This paper, by emphasising the importance of microzooplankton in Lake Tanganyika, suggests that protozoans must have a key trophic role that may contribute to the high productivity of the lake food web.

Finally the key issue is to determine the origin of the organic carbon which can sustain a heterotrophic biomass greater than autotrophic biomass. As mentioned above, the question was already addressed by Hecky & Fee (1981) and Hecky (1991). A first source other than photosynthetic fixation could be dissolved organic carbon from the deep waters, while inputs from incoming rivers and from the littoral zone seem negligible in this large lake. However, the adequacy of the dissolved carbon pool as a substrate for heterotrophic bacteria is not known. Alternatively, it may well be, as suggested by Hecky (1991), that the bacterial carbon demand is fuelled by an autochthonous labile DOC pool coming from pelagic photosynthesis, via phytoplankton excretion of organic compounds, which has never been accounted for in photosynthesis measurements carried out in the lake, but which has to be large enough to sustain bacterial activity. Moreover, direct grazing of nanoflagellates and ciliates on picoautotrophs, making a direct link between the most important primary producers (Descy et al., 2005) and microzooplankton, might be a key reason why abundance and biomass of heterotrophic protists are so high in this lake.

**Acknowledgments**

This study was supported by the FRIA (Fonds Nationaux pour la Recherche Scientifique) through the PhD scholarship to S. Pirlot. Thanks to the Belgian SSTC project CLIMLAKE, Dr H. Phiri from the Department of Fisheries (DOF) of Mpuilungu, Zambia and Dr Chitamwebwa from TAFIRI, Kigoma, Tanzania. The authors are indebted to Bruno Leporcq for his helpful support on the field as in the lab.

**References**


(Manuscript accepted 2 May 2005)