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Abundance and production of bacteria, and relationship to phytoplankton production, in a large tropical lake (Lake Tanganyika)

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SUMMARY

1. Abundance and bacterial production (BP) of heterotrophic bacteria (HBact) were measured in the north and south basins of Lake Tanganyika, East Africa, during seasonal sampling series between 2002 and 2007. The major objective of the study was to assess whether BP can supplement phytoplankton particulate primary production (particulate PP) in the pelagic waters, and whether BP and particulate PP are related in this large lake. HBact were enumerated in the 0–100 m surface layer by epifluorescence microscopy and flow cytometry; BP was quantified using ^{3}H-thymidine incorporation, usually in three mixolimnion layers (0–40, 40–60 and 60–100 m).

2. Flow cytometry allowed three subpopulations to be distinguished: low nucleic acid content bacteria (LNA), high nucleic acid content bacteria (HNA) and *Synechococcus*-like picocyanobacteria (PCya). The proportion of HNA was on average 67% of total bacterial abundance, and tended to increase with depth. HBact abundance was between 1.2×10^5 and 4.8×10^6 cells mL^{-1}, and was maximal in the 0–40 m layer (i.e. roughly, the euphotic layer). Using a single conversion factor of 15 fg C cell^{-1}, estimated from biovolume measurements, average HBact biomass (integrated over a 100-m water column depth) was 1.89 ± 1.05 g C m^{-2}.

3. Significant differences in BP appeared between seasons, especially in the south basin. The range of BP integrated over the 0–100 m layer was 93–735 mg C m^{-2} day^{-1}, and overlapped with the range of particulate PP (150–1687 mg C m^{-2} day^{-1}) measured in the same period of time at the same sites.

4. Depth-integrated BP was significantly correlated to particulate PP and chlorophyll-*a*, and BP in the euphotic layer was on average 25% of PP.

5. These results suggest that HBact contribute substantially to the particulate organic carbon available to consumers in Lake Tanganyika, and that BP may be sustained by phytoplankton-derived organic carbon in the pelagic waters.

Keywords: bacterial biomass, bacterial production, microbial food web, large tropical lake, Lake Tanganyika

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Introduction

Organic carbon flows in Lake Tanganyika, the largest lake of the African Great Rift Valley, have been a matter of debate since the first assessments in the 1970s. Indeed, some fish yield estimates, notably by Coulter (1977), seemed remarkably high when compared with particulate primary production (PP) (Hecky *et al.*, 1981), which situates the lake at the oligotrophic end of the trophic spectrum. From food web studies in Lake Tanganyika, two contrasting views of the functioning of the pelagic ecosystem have emerged.

The first view, formulated by Hecky *et al.* (1981), describes the lake's pelagic food web as having a high trophic efficiency, supported by a marine-like structure. Phytoplankton biomass is low (*c.* 1 μg Chl-*a* L^{-1}) and net PP is 290 g C m^{-2} $year^{-1}$. As this low phytoplankton particulate production seemed too low to sustain consumer production, Hecky *et al.* (1978, 1981) proposed that heterotrophic bacteria (HBact), which develop all over the oxic layer (roughly 120 m deep), contribute organic carbon to consumers, while net PP is limited to the upper 30 m depth (Hecky *et al.*, 1981). More recently, particulate PP in Lake Tanganyika has been re-assessed in order to detect a possible effect of climate change (Stenuite *et al.*, 2007) and low estimates of annual rates were reported (123–205 g C m^{-2} $year^{-1}$), comparable with those reported earlier by Hecky *et al.* (1981).

However, temporal and spatial heterogeneity in phytoplankton production of the pelagic ecosystem (Dubois, 1958; Coulter, 1963, 1991; Langenberg *et al.*, 2003a; Langenberg, Sarvala & Roijackers, 2003b) can also be an important factor. Major hydrodynamic events, such as the seasonal upwelling that occurs in the south of the lake, increase nutrient availability and allow pulses of high particulate PP to take place (Coulter, 1991; Plisnier *et al.*, 1999). Internal waves may also enhance diffusion of nutrients through the thermocline (Plisnier & Coenen, 2001) all over the lake, and some particular regions of the lake as the northern end near Bujumbura exhibit higher phytoplankton biomass and production at all times (Sarvala *et al.*, 1999). Thus Sarvala *et al.* (1999), based on the data collected during the FAO-FINNIDA LTR project (1993–95), presented the alternative view of Tanganyika as a relatively productive lake, with particulate PP ranging from 426 to 662 g C m^{-2} $year^{-1}$, a lower consumer production than estimated in previous studies and hence of lower trophic efficiency, similar to that of other great lakes. In other words, the view proposed by Hecky *et al.* (1981) of an inverted pyramid, where both autotrophic and heterotrophic microorganisms should have high turnover rates in order to sustain consumer production, was replaced by a classic, broad-based trophic pyramid.

In fact, recent studies may have brought some support to the first view of an important role for microorganisms and heterotrophic production in the pelagic ecosystem of Lake Tanganyika (reviewed by Descy & Sarmento, 2008). Our view of the ecology of Lake Tanganyika has changed completely since enumeration of the real abundance of picocyanobacteria (PCya) was achieved in recent years (Vuorio *et al.*, 2003; Descy *et al.*, 2005; Sarmento *et al.*, 2008). Descy *et al.* (2005) detailed autotrophic communities and showed that 50% of the total chlorophyll-*a* (Chl-*a*) was comprised in the <2-μm size fraction, and was made of cyanobacteria with the *Synechococcus* pigment type. This was confirmed when flow cytometry and epifluorescence microscopy enumerations revealed that the abundance of PCya in Lake Tanganyika was among the highest ever recorded (Sarmento *et al.*, 2008). Moreover, Sarvala *et al.* (2003) reported stable isotope analyses of various food web components which suggested a microbial contribution to the diet of large zooplankton.

Pirlot *et al.* (2005) and Pirlot, Servais & Descy (2006) presented high estimates of bacterial biomass in the oxic zone (up to 3.3 g C m^{-2}) and protozoan biomass (composed especially by flagellates that represented up to 1.1 g C m^{-2}) in two distant sites at different seasons. The biomass of heterotrophic microorganisms was sometimes in the same range as autotroph biomass, when integrated through a 100-m depth layer. Grazing studies confirmed consumption of HBact by flagellates and ciliates as a major mortality process for bacteria (Pirlot *et al.*, 2007). From these recent reports, clues have accumulated to suggest an important microbial food web in Lake Tanganyika, whose role would be to supplement the low phytoplankton particulate production.

However, data about production of particulate organic carbon by bacteria in Lake Tanganyika are still scarce. Bacterial production (BP) was first estimated from measurements of heterotrophic respiration in 1975 (Hecky *et al.*, 1978). From these rates of oxygen consumption in the dark performed on euphotic zone

water samples, Hecky *et al.* (1981) calculated that average BP would be 14.7 mg C m^{-3} day^{-1}. In 1995, BP was assessed by the radioactive leucine incorporation method (Kirchman, K'Nees & Hodson, 1985) during two sampling cruises in April–May and October–November (Sarvala *et al.*, 1999). During the first cruise, BP ranged between 0.1 to 4.9 mg C m^{-3} day^{-1} but during the second cruise, three sites on five presented higher production up to *c.* 35 mg C m^{-3} day^{-1} in the epilimnion (Sarvala *et al.*, 1999). The highest values usually occurred in the upper water layers, although at one site the maximum values were recorded below the thermocline. BP represented on average 21% of phytoplankton particulate production estimated from Chl-*a* and the average phytoplankton assimilation parameters (Sarvala *et al.*, 1999). However, leucine uptake by *Synechococcus*, abundant in the lake, has been reported (Paoli *et al.*, 2008), which may cast some doubt on those results.

The objectives of this work were (i) to collect seasonal and inter-annual data of bacterial abundance and production in the two main basins of L. Tanganyika; (ii) to examine whether BP can supplement particulate PP in the pelagic waters and (iii) to assess the relationship between bacterial and phytoplankton particulate production.

Methods

Study sites and samples collection

The sampling strategy involved seasonal surveys over several years (2002–07) at two stations of Lake Tanganyika, Kigoma (north basin, Tanzania) and Mpulungu (south basin, Zambia). Each year between 2002 and 2005, sampling was carried out in both basins in January–February during the wet season and in July–August during the dry season. Additional series were carried out in 2006–07, but only at Mpulungu. Occasionally, sampling and measurements were also done at other stations located in the north basin and in the south basin of the lake, during north–south cruises organised from 2002 to 2004 (see Stenuite *et al.*, 2007, for the location of the cruises sampling sites). At all sites, limnological profiles performed using a Seabird CTD (Sea-Bird Electronics Inc., Belluvue, WA, U.S.A.) or a Hydrolab DS4 (Hach, Loveland, CO, U.S.A.) datasonde allowed determination of the structure of the water column, based on measurements of temperature, pH, conductivity and dissolved oxygen.

Phytoplankton biomass and particulate production

The methods used for determining phytoplankton biomass and particulate production were described in Stenuite *et al.* (2007). Briefly, for biomass measurements, 3–4 L of water were filtered on Whatman GF/F (Whatman International Ltd., Maidstone, U.K.) or Macherey-Nägel GF5 filters (0.7-μm nominal pore-size (Macherey-Nägel, Düren, Germany)). Chlorophylls and carotenoids extracted in 90% acetone were analysed by high performance liquid chromatography (HPLC), following Descy *et al.* (2005). Phytoplankton particulate production was measured using the ^{14}C method (Steeman Nielsen, 1952), as described in Stenuite *et al.* (2007), in order to obtain estimates of daily integrated photosynthesis. Due to cell size overlap between photosynthetic picoplankton and HBact, it was not possible to measure dissolved organic carbon (DOC) exudation and DOC uptake by HBact by selective size filtration.

Bacterial biomass and production

Water samples for the determination of bacterial abundance were collected in the pelagic zone from surface to a depth of 100 m (0, 10, 20, 30, 40, 50, 60, 80 and 100 m), using a Niskin 5 L sampling bottle. Bacterial abundances were determined by epifluorescence microscopy (2002–04), and by flow cytometry for samples since dry season 2004.

For epifluorescence microscopy, fixed cells (glutaraldehyde 1% final concentration) were stained with DAPI (4, 6 diamidino-2-phenyl-indole; 10 μg mL^{-1} final concentration) and filtered onto a 0.2-μm pore-size black membrane filter (Millipore, Billerica, MA, U.S.A.). 500–2000 cells from 10 randomly chosen fields were enumerated using a Zeiss Axioplan microscope (Carl Zeiss MicroImaging GmbH, Göttingen, Germany) at ×1000 magnification.

The flow cytometry enumeration of HBact was carried in the same way as described in Sarmento *et al.* (2008). Four millilitres of water were collected and fixed immediately with cold glutaraldehyde 10% (final concentration 1%), left in the dark for 10 min at room temperature, and stored at −20 °C for a maximum of 2 weeks, before transfer to Belgium and

storage at −80 °C until analysis. Four hundred microlitre of sample were stained with a diluted SYTO-13 (Molecular Probes Inc., Eugene, OR, U.S.A.) stock (10 : 1) at 2.5 μmol L^{-1} final concentration, left for about 10 min in the dark to complete the staining, and run in a FacsCalibur (Becton Dickinson, Franklin Lakes, NJ, U.S.A.) flow cytometer equipped with a 15 mW Argon-ion laser (488 nm emission). At least 30 000 events were acquired for each sample. Fluorescent beads (1 μm, Fluoresbrite carboxylate yellow–green microspheres; Polysciences Inc., Warrington, PA, U.S.A.) were added at a known density as internal standards. The bead standard concentration was determined by epifluorescence microscopy. HBact were detected by their signature in a plot of side scatter (SSC) versus FL1 (green fluorescence) and were separated into two sub-populations: high nucleic acid content (HNA) and low nucleic acid (LNA) content bacteria in the SSC versus FL1 plot (Gasol & del Giorgio, 2000; Bouvier, del Giorgio & Gasol, 2007). PCya were also visible in the cytograms (Fig. 1).

A comparison of the epifluorescence microscopy and flow cytometry enumeration methods was performed with samples from the wet season 2006. A significant correlation passing through the origin was found between both abundance estimates (Pearson's $r = 0.7$; $P < 0.05$; $n = 18$; data not shown) with a slope very close to 1 (0.99) indicating the equivalence of both estimates of bacterial abundance.

In order to calculate bacterial biomass, 500–2000 cells were sized using digital image analysis (Zeiss KS300; Carl Zeiss MicroImaging GmbH) and a Zeiss Axioplan microscope at ×1000 magnification and average biovolume was calculated. The relationship $C_{bact} = 92 \times V^{0.598}$, determined from the data of Simon & Azam (1989), was used to calculate the carbon content per cell (C_{bact}: fg C $cell^{-1}$) from the biovolume (V: μm^3). An average cell carbon content of 15.0 ± 3.8 fg C $cell^{-1}$ (data not shown) was found and used to calculate bacterial biomass from bacterial abundance data.

Bacterial production was estimated from tritiated thymidine (^{3}H-Thy) incorporation rates in the dark (Fuhrman & Azam, 1982). Although the structure of the mixolimnion changes seasonally and may vary within seasons [see, for instance, Descy *et al.* (2005)], we applied a constant sampling strategy (excepted for the dry season 2006, see below): water samples were taken from three different layers: 0–40, 40–60 and 60–100 m. The 0–40 m layer corresponds to the euphotic zone, where samples for PP measurements were collected; the 40–60 and 60–100 m layers roughly correspond to the metalimnion and hypolimnion when the mixolimnion is stratified. Several samples were collected in the 0–40 m layer at fixed depths (0, 10, 20, 30 and 40 m) and an average sample was made by mixing equal water volumes. A unique sample was taken from the two other layers, at a depth depending on the water column structure determined from the limnological profile. The same protocol was followed during all the study, excepted for the dry season 2006 (see below). Twenty millilitre of sample from the three layers were incubated with ^{3}H-Thy (*c.* 80 Ci $mmole^{-1}$) for 2 hours in the dark at lake water temperature, at different concentrations of ^{3}H-Thy (6, 12, 24, 48 nM) to determine saturating concentration. The three highest concentrations always induced similar results and allowed saturation to be reached (data not shown); they were thus considered as triplicates at saturating concentration. Only for the dry season of 2006 was the protocol slightly modified. Samples collected every 10 m along a vertical profile were incubated at a unique concentration of ^{3}H-Thy

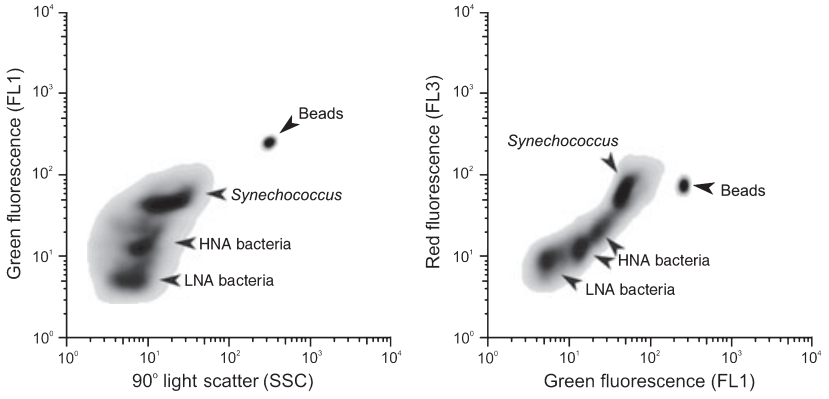

Fig. 1 Examples of Syto-13 stained picoplankton cytograms of Lake Tanganyika water samples obtained by flow cytometry; green fluorescence (FL1) versus side scatter (SSC) (left panel) and red fluorescence (FL3) versus green fluorescence (FL1) (right panel). Identification of the three populations (HNA, LNA, *Synechococcus* spp.) and the Polysciences 1 μm beads.

(30 nM), assuming from our previous experiments that this concentration was saturating. After incubation, cold trichloroacetic acid (TCA) was added (final concentration 5%) and the samples were filtered after 15 min through a 0.2-μm pore-size cellulose nitrate membrane. Filters were stored in the dark at −20 °C. Radioactivity associated with the filters was estimated by liquid scintillation, using a Beckman Coulter LS 6000 (Beckman Coulter Inc., Fullerton, CA, U.S.A.). Cell production was calculated from the ^{3}H-Thy incorporation rate using the conversion factor 1.2×10^{18} cells produced per mole of ^{3}H-Thy incorporated into the cold TCA fraction. This conversion factor was experimentally determined in batch experiments where the increase of bacterial abundance and ^{3}H-Thy incorporation were simultaneously followed (data not shown). Cellular production was multiplied by the average cell carbon content of 15.0 fg C cell^{-1} (see above) to obtain BP data. Daily BP was estimated from the experimental values considering constant activity over 24 h, and expressed per unit volume of water (mg C m^{-3} day^{-1}) or integrated per unit area (mg C m^{-2} day^{-1}) over the 0–40 m layer, the 40–60 m layer, the 60–100 m layer or over the 0–100 m layer.

Two-way ANOVA was applied to test for differences in HBact biomass and BP between seasons and basins. For this comparison, only biomass and production data from 2002 to 2005 study period were used when sampling campaigns were performed in both basins at the same period.

Results

During the study periods, the depth of the mixed layer (Zm) oscillated between 10 m and 100 m, with the lower values during the wet seasons. Mixing depth increased during the dry seasons, especially in the south basin. Depths of the euphotic zone were significantly different between seasons, with average values of 36 and 45 m during the wet season, and 41 and 28 m during the dry season, for the north and south basins respectively.

Average Chl-*a* concentrations in the 0–40 m layer in the wet season were 0.74 ± 0.43 μg L^{-1} in the north basin and 0.77 ± 0.96 μg L^{-1} in the south basin. In the dry season, they were 0.64 ± 0.25 μg L^{-1} (north) and 1.06 ± 0.49 μg L^{-1} (south). Values integrated over a 100-m water column depth were similar for both basins during the rainy season (*c.* 40 mg Chl-*a* m^{-2}), while, during the dry season, they were higher in the south basin (*c.* 67 mg Chl-*a* m^{-2}) than in the north basin (45 mg Chl-*a* m^{-2}). HPLC pigment analysis showed that chlorophytes and cyanobacteria belonging to pigment type 1 (T1) (*Synechococcus* type; Jeffrey, Mantoura & Wright, 1997) were the main contributors to Chl-*a* concentration in the north basin, whatever the season, while cyanobacteria T1 were always dominant in the south basin, especially during the dry season.

Syto-13 stained cytograms allowed identification of one population of PCya, and two populations of HBact with different nucleic acid content, the HNA content and LNA content bacteria (Fig. 1). Abundance of HBact estimated by epifluorescence microscopy or flow cytometry varied between 1.2×10^5 and 4.8×10^6 cells mL^{-1}, in the 0–100 m water column. No significant differences were found between seasons or stations. Highest abundances were observed in the upper layers, and cell number then decreased with depth (Fig. 2). In the 0–100 m water column, HNA bacteria represented an average 67% of the total HBact abundance. This percentage was generally higher in the hypolimnion than in the upper layers (Fig. 3).

Integrated over the different layers, HBact biomass was always higher in the 0–40 m layer, while values found in the 40–60 and 60–100 m layers were lower and not significantly different (Fig. 4). When integrated over a 100-m water column depth, HBact biomass was on average 2.2 and 1.9 g C m^{-2}, for north and south basins, during the wet season, and 1.5 and 1.9 g C m^{-2} during the dry season. No statistically significant differences in integrated HBact biomass were found between the seasons or the stations.

On average, HBact production (BP) did not vary among layers in the dry season but, in the wet season, BP in the 0–40 m layer was significantly greater than that in the hypolimnion at both main study sites (Fig. 5). Significant differences were found in BP in the euphotic zone between seasons ($P = 0.021$), but not between basins. When integrated over a 100-m water column depth, average BP was 183 ± 89 and 185 ± 59 mg C m^{-2} day^{-1} for the north basin, in the wet and dry seasons respectively. Values were higher for the south basin, with 309 ± 130 and 415 ± 215 mg C m^{-2} day^{-1}, during wet and dry seasons. However, due to the high variability of measured BP, no significant difference in depth-integrated BP was found between basins or between seasons.

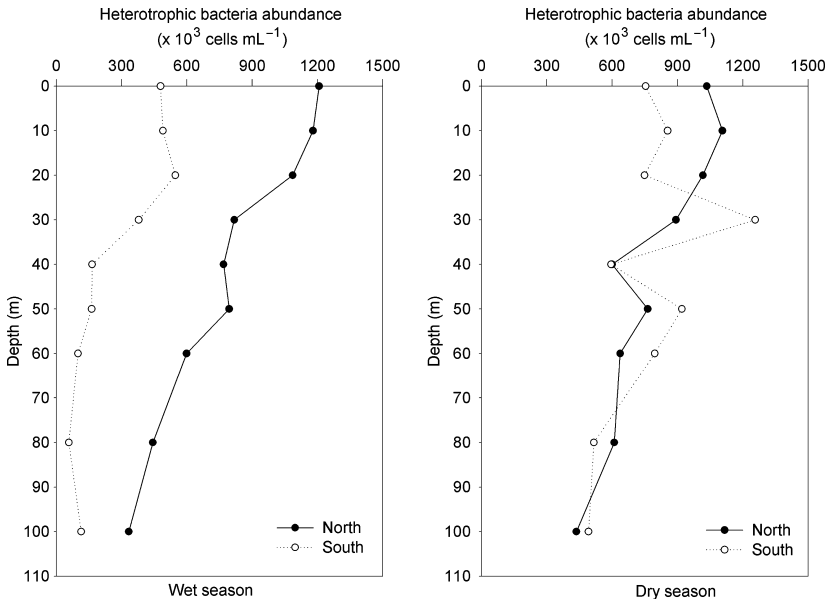

Fig. 2 Examples of vertical profiles of heterotrophic bacteria abundances, in the north and south basins of Lake Tanganyika, during wet and dry seasons (dates of sampling: wet-north: 30 January 2006; wet-south: 24 February 2007; dry-north: 26 August 2004; dry-south: 19 September 2007).

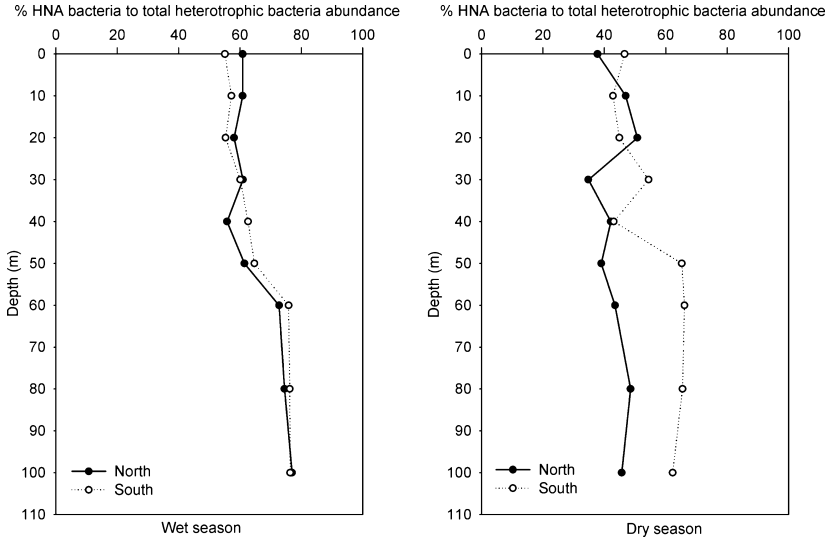

Fig. 3 Examples of vertical profiles of % HNA bacteria with respect to total heterotrophic bacteria abundance, in the north and south basins of Lake Tanganyika, during wet and dry seasons (dates of sampling: wet-north: 30 January 2006; wet-south: 24 February 2007; dry-north: 26 August 2004; dry-south: 19 September 2007).

A significant positive correlation was found between integrated BP and % contribution of HNA to total HBact abundance (Fig. 6a). Similarly, during the study periods, BP was significantly correlated to total phytoplankton biomass (Fig. 6b). Phytoplankton particulate production varied between 150 and 1687 mg C m^{-2} day^{-1}, and showed a clear seasonal pattern. The average value for both basins during the wet season was 448 ± 239 mg C m^{-2} day^{-1} and 859 ± 410 mg C m^{-2} day^{-1} during the dry season. When integrated over a 100-m water column depth, BP showed a significant positive correlation with phytoplankton particulate production (Fig. 6c).

Discussion

Values of BP obtained in this study were low compared to earlier estimates reported by Hecky *et al.* (1981), but were in the same range as values found by Sarvala *et al.* (1999). Between 2002 and 2007, average BP in the 0–100 m layer ranged from 0.13 to 16.97 mg C m^{-3} day^{-1}, with an average value of 3.54 ± 2.79 mg C m^{-3} day^{-1} (136 sample incubations); these can be compared with the values obtained by Hecky *et al.* (1981) of 14.7 mg C m^{-3} day^{-1} and by Sarvala *et al.* (1999) of 2.8 mg C m^{-3} day^{-1}. BP in the pelagic zone of Lake Tanganyika was actually of the

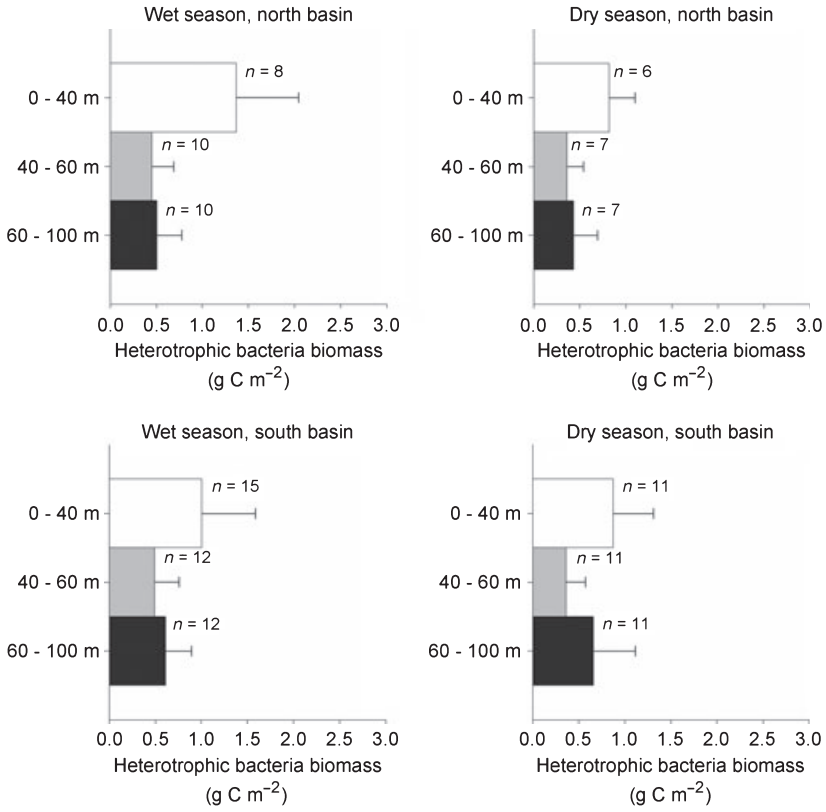

Fig. 4 Average heterotrophic bacteria biomass, in the north and south basins of Lake Tanganyika, during wet and dry seasons from three layers (0–40, 40–60 and 60–100 m) (2002–07 values).

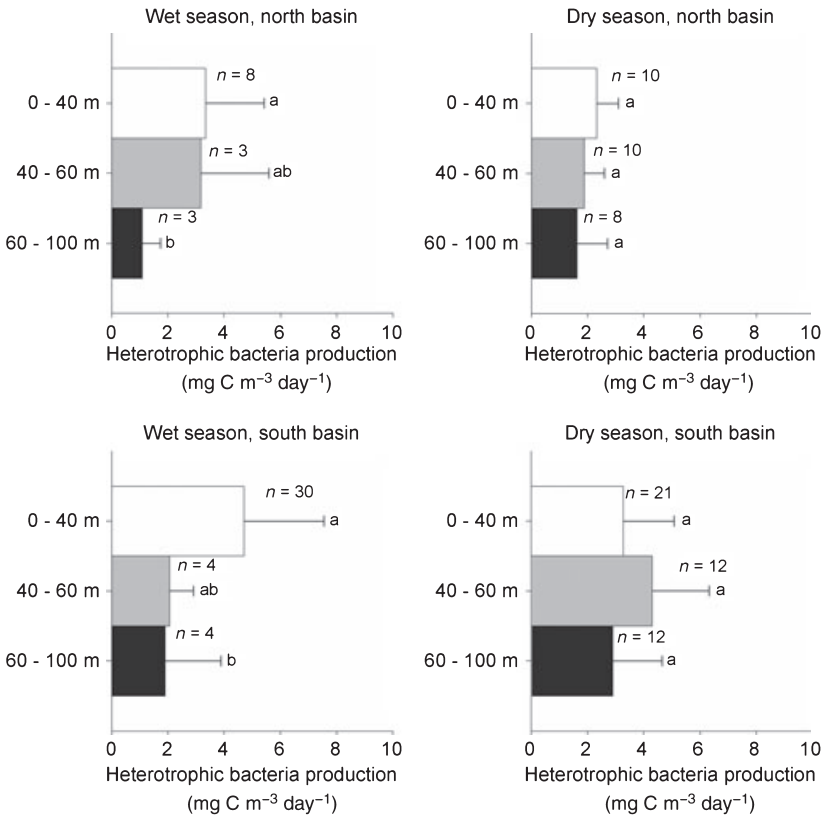

Fig. 5 Average heterotrophic bacteria production, in the north and south basins of Lake Tanganyika, during wet and dry seasons (0–40, 40–60 and 60–100 m), with significant differences (two-way ANOVA, $P < 0.05$) (2002–07 values).

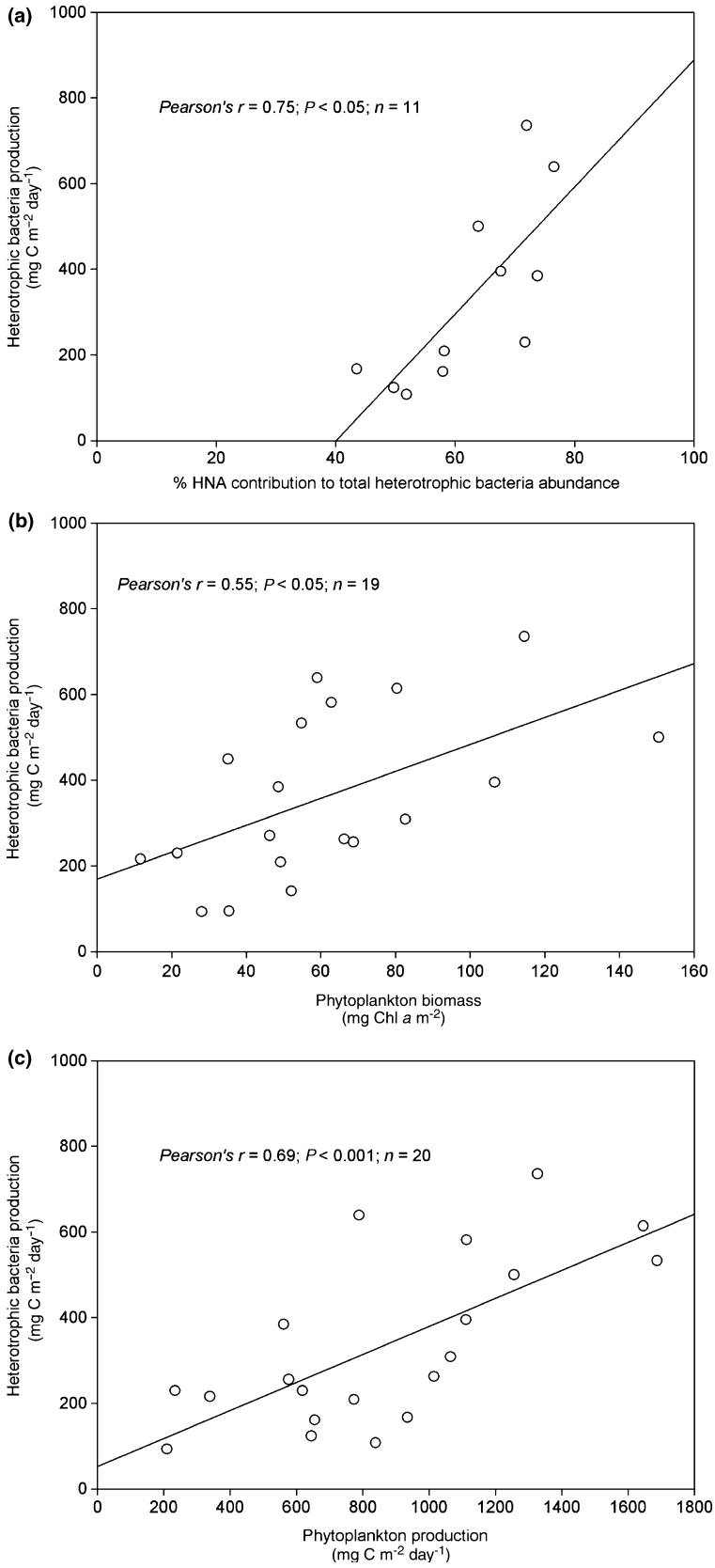

Fig. 6 Relationships between integrated (0–100 m) heterotrophic bacterial production and (a) % of HNA bacteria with respect to total heterotrophic bacteria abundance, (b) phytoplankton biomass and (c) phytoplankton particulate production in Lake Tanganyika (2004–07 values).

same order of magnitude as BP estimated with thymidine incorporation in oligotrophic marine systems (Iriberri *et al.*, 1990; Ducklow, Kirchman & Anderson, 2002; Torreton, Pages & Talbot, 2002). However, comparison of our values with those obtained previously in Lake Tanganyika should be made with caution. Hecky *et al.* (1981) used heterotrophic respiration of samples from the euphotic zone, and estimated average BP for this layer. Sarvala *et al.* (1999) used the radioactive leucine incorporation method, with samples mainly originating from the upper layers. In our study, BP was assessed with the ^{3}H-thymidine method, on samples originating from the entire 0–100 m water column.

The only significant differences observed in BP appeared between seasons, and were highly significant in the south basin. No significant difference in BP was observed between the basins, but the power of this comparison may be weakened by the high variability of measured BP. Bacterial biomass did not show any significant differences between seasons or basins, which probably reflects balanced bacterial growth and mortality in Lake Tanganyika, as proposed by Pirlot *et al.* (2007).

High nucleic acid bacteria constituted the main fraction of the bacterial community, and increased slightly towards the hypolimnion. The usual observation that HNA bacteria dominate in phytoplankton-rich waters, while LNA bacteria do so in phytoplankton-poor waters (Li, Jellett & Dickie, 1995) seems to be applicable here, since abundance of HNA bacteria was correlated to Chl-*a* biomass (Pearson's $r = 0.45$; $P < 0.001$; $n = 76$), in accordance to the results of Sarmento *et al.* (2008), who reported a significant correlation between phytoplankton biomass and HNA biomass. Using a different method (cell-staining with 5-cyano-2,3-ditolyl tetrazolium chloride, a cellular activity probe) Gasol & Aristegui (2007) showed that there were no labelling amongst the LNA bacteria, and that the most active cells belonged to the HNA subpopulation. Although still under debate, it is now widely accepted that HNA bacteria represent the most active fraction of the bacterial communities, whereas the LNA bacteria correspond to inactive or dead cells (Gasol *et al.*, 1999; Lebaron *et al.*, 2001; Bouvier & del Giorgio, 2002; Bouvier *et al.*, 2007). In our study, the significant correlation found between BP and % of HNA cells in HBact abundance tends to support this view, and suggests that HNA bacteria would be the major contributor to BP in Lake Tanganyika.

Considering all data, BP was on average 310 mg C m^{-2} day^{-1} in the 0–100 m layer, and average particulate PP was *c.* 654 mg C m^{-2} day^{-1}. Hence, BP in the 0–100 m layer was on average 47% of the phytoplankton particulate production. In the 0–40 m layer, roughly the euphotic layer, BP was on average *c.* 166 mg C m^{-2} day^{-1}, which corresponded to *c.* 25% of particulate PP. A rough estimate of the bacterial carbon demand (BCD) can be made by considering a bacterial growth efficiency (BGE) of 20%; this value is in the middle of the range given in large literature reviews on BGE values in aquatic systems (del Giorgio, Cole & Cimbleris, 1997; del Giorgio & Cole, 1998) and was previously used by Pirlot *et al.* (2007) to calculate BCD from BP data of lake Tanganyika. Using this BGE value, the BCD estimated from our data would range between 97 and 2872 mg C m^{-2} day^{-1} in the 0–40 m layer. Hence, the maximal BCD could not entirely be met by phytoplankton particulate production. In a large lake such as Lake Tanganyika, the huge volume of the lake relative to the hydrological loading from the drainage area allows the presumption that allochthonous DOC inputs are very low (Langenberg *et al.*, 2003a), and BP should be sustained by DOC from phytoplankton excretion and by lysis of all planktonic organisms (Sundh & Bell, 1992). Such production of DOC was not measured in our study, but can be as high as 80% of total C fixation by phytoplankton in oligotrophic systems (Baines & Pace, 1991; Bertilsson *et al.*, 2005). Based on a likely high DOC exudation by phytoplankton in the well-lit, nutrient-poor surface waters of Lake Tanganyika, we can reasonably speculate that dissolved production could have provided highly labile organic carbon (Davis & Benner, 2007) to fuel the highest BP rates we measured. This leads to the view that typical rainy season situations (the greatest part of the year) can correspond to periods of heterotrophy, when BP may exceed particulate PP, and that dry season situations, providing more nutrients for algal growth, are net autotrophy periods, with particulate PP exceeding BCD. To support this view, average particulate PP : BCD ratios calculated from our data would be 0.6 during the wet season, and 1.6 during the dry season. In order to test this hypothesis, the respiration rate of HBact should be measured and compared to total phytoplankton production. The latter, however,

cannot be easily measured, as data on DOC exudation are missing. We suggest that ^{13}C enrichment experiments (Van den Meersche *et al.*, 2004) could be used in the future to trace organic carbon production and assimilation by different planktonic compartments.

In our data, collected on a relatively large temporal and spatial scale, a significant correlation was found between particulate PP and BP. This suggests coupling between particulate PP and BP, as reported by Cole, Findlay & Pace (1988) who gathered phytoplankton and BP data from a wide range of aquatic systems. The significant relationship observed in our study suggests that phytoplankton production is a major carbon source for HBact in the pelagic waters of Lake Tanganyika. A significant correlation was also found between BP and phytoplankton biomass. This suggests that BP is likely to be higher when phytoplankton biomass and particulate production are increasing, conditions that typically occur in the south basin during the dry season (Descy *et al.*, 2005; Stenuite *et al.*, 2007). A possible explanation for this positive response of HBact would be a greater release of organic matter during the dry season, due to the higher lysis of increased phytoplankton biomass. However, the higher BP could also result from the response of bacteria to increased nutrient availability during the dry season, and therefore would not be directly related to increased phytoplankton biomass. It is well known that bacteria and phytoplankton compete for nutrients, in particular inorganic phosphorus, which typically increases in the dry season, especially in the south of Lake Tanganyika, where deep mixing events occur.

In Lake Tanganyika, conditions favouring DOC release are typically found during the rainy season: due to thermal stratification, phytoplankton is then facing low nutrient concentrations and high light climate in the water column (Descy *et al.*, 2005; Stenuite *et al.*, 2007). Since particulate PP to BCD ratio is usually <1 during this period, DOC release by phytoplankton is likely to supplement the PP we measured. Sarvala *et al.* (1999) found that DOC levels (2.2–2.9 mg C L^{-1}) were relatively low in Lake Tanganyika. Low levels of DOC in waters often mean that it is rapidly consumed by HBact (Sell & Overbeck, 1992). This view would also be consistent with the idea of nutrient-limited microbial growth (bottom–up control) in oligotrophic systems, and bacterivore or viral control (top–down control) in more productive systems (Cotner & Biddanda, 2002).

In conclusion, this study confirms that BP contributes substantially to the particulate organic carbon available to consumers in Lake Tanganyika, and that BP may be sustained by phytoplankton-derived organic carbon in the pelagic waters. Moreover, the fact that BP is well correlated to particulate PP suggests that autotrophic and heterotrophic production are coupled, at least in the pelagic waters where our observations were made. By contrast, BP does not seem to respond to the differences in hydrodynamics between the north and the south basins of the lake, related in particular to the upwelling that occurs in dry season at the southern end of the lake. In fact, our analysis shows clear seasonal differences in BP and suggests contrasting ecosystem functioning between seasons, with heterotrophic activity dominating in the wet season, and autotrophic production dominating in the dry season, the latter being supported by increased nutrient availability.

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