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Phytoplankton production and growth rate in Lake Tanganyika: evidence of a decline in primary productivity in recent decades

STEPHANE STENUITE, SAMUEL PIRLOT, MARIE-ASTRID HARDY, HUGO SARMENTO, ANNE-LAURE TARBE, BRUNO LEPORCQ AND JEAN-PIERRE DESCY
Laboratory of Freshwater Ecology, Department of Biology, FUNDP – University of Namur, Namur, Belgium

SUMMARY

1. This study focused on phytoplankton production in Lake Tanganyika. We provide new estimates of daily and annual primary production, as well as growth rates of phytoplankton, and we compare them with values published in former studies.
2. Chlorophyll-*a* (chl-*a*) in the mixed layer ranged from 5 to 120 mg chl-*a* m^{-2} and varied significantly between rainy and dry seasons. Particulate organic carbon concentrations were significantly higher in the south basin (with 196 and 166 mg C m^{-3} in the dry and the rainy season, respectively) than in the north basin (112 and 109 mg C m^{-3}, respectively).
3. Carbon : phosphorus (C : P) ratios varied according to season. Phosphorus limitation seemed to occur more frequently than nitrogen limitation, especially during the rainy season. Severe P deficiencies were rare.
4. Measured particulate daily primary production ranged from 110 to 1410 mg C m^{-2} day^{-1}; seasonal contrasts were well marked in the north basin, but less in the south basin, where primary production peaks occurred also in the rainy season. Estimates of annual primary production, based on daily primary production calculated from chl-*a* and water transparency, gave values lower than those reported in previous studies. Picophytoplankton accounted on average for 56% of total particulate production in the south basin during the wet season of 2003.
5. Phytoplankton growth rates, calculated from primary production, ranged from 0.055 to 0.282 day^{-1}; these are lower than previously published values for Lake Tanganyika.

Keywords: growth rate, phytoplankton, production, Tanganyika, tropical lake

Introduction

The fishery yield in Lake Tanganyika is higher than in most great lakes of the world, and the efficiency of carbon transfer from primary producers to fish in this large, ancient lake, seems more like what is expected in marine systems (Hecky & Fee, 1981; Coulter, 1991). The purpose of early studies, conducted in the 1970s, was to reconcile the high fish yield with the oligotrophic status of the lake, indicated by its high transparency and low phytoplankton biomass. Hecky & Fee (1981) supported the hypothesis of high trophic efficiency based on the marine-like structure of the pelagic food web, where phytoplankton biomass is low but has high productivity and growth rate. They estimated a net primary production of 290 g C m^{-2} $year^{-1}$, on the basis of measurements of ^{14}C uptake during cruises from the north to the south of the lake, conducted in two contrasting seasons (April–May and October–November). The results showed high spatial and temporal heterogeneity of biomass and photosynthetic capacity. The relatively high means for chl-*a* (1.7 mg m^{-3}) and primary production (1.4 g C m^{-2} day^{-1}) of the second cruise

Correspondence: Jean-Pierre Descy, Laboratory of Freshwater Ecology, Department of Biology, FUNDP – University of Namur, B-5000 Namur, Belgium. E-mail: jpdescy@fundp.ac.be

accounted for a major part of the whole-lake estimate (0.8 g C m^{-2} day^{-1}). Nevertheless, Hecky & Fee (1981) had to hypothesize that primary production must be supplemented by heterotrophic production by bacteria and protozoans to sustain the high zooplankton production. They showed, for instance, that bacterial production represented about half of net primary production (Hecky & Fee, 1981). Thus, the food web of Lake Tanganyika was described as an inverted trophic pyramid, with high carbon transfer efficiency and high phytoplankton turnover rate, and a significant trophic role was postulated for heterotrophic plankton.

In a more recent study, Sarvala *et al.* (1999) came up with a radically different view (1999), estimating much higher primary production (426–662 g C m^{-2} $year^{-1}$, based on time series at three sites) and 50% lower zooplankton production than previously proposed. Hence, the trophic transfer efficiency was low instead of being high, but still sufficient to support the fishery yield: the trophic pyramid now had a large base, and there was no need to postulate a significant role for planktonic heterotrophs. However, large spatial and temporal heterogeneity was observed, and the systematically high phytoplankton biomass and production near Bujumbura, at the northernmost part of the lake, was averaged with that of the much less productive stations, Kigoma (north basin) and Mpulungu (south basin). Complementary explanations for the high levels of primary production proposed that pulses of primary production occur locally because of hydrodynamic events, such as upwellings in the south which transport nutrients from deep waters to the euphotic zone (Coulter, 1991; Plisnier *et al.*, 1999).

Studies carried out more recently have emphasized the importance of auto- and heterotrophic picoplankton in Lake Tanganyika. After a report by Vuorio *et al.* (2003) on the abundance of picocyanobacteria, Sarvala *et al.* (2003) suggested a microbial contribution to the diet of large zooplankton. Descy *et al.* (2005) focused on the autotrophic communities and showed that 50% of total chlorophyll *a* (chl-*a*) biomass was made up of cyanobacteria in the <2 μm size fraction. Pirlot (2005) estimated large biomass of heterotrophic bacteria (up to 3.3 g C m^{-2}) but also large protozoan biomasses (including, in particular, flagellates that represent up to 1.1 g C m^{-2}). The biomass of heterotrophic plankton, distributed throughout the oxic zone (>100 m depth) can sometimes exceed that of photosynthetic plankton which is limited to the mixed layer. These observations draw attention again to the possible trophic role of heterotrophic plankton, through a microbial loop that would feed ciliates and larger flagellates, which could be preyed upon by the metazooplankton. This view is related to the original hypothesis of Hecky & Fee (1981). However, unless there are exogenous sources of organic matter available to heterotrophic bacteria, bacterial production is essentially dependent on phytoplankton production in the pelagic zone of the lake. Hence, a re-assessment of pelagic primary production in Lake Tanganyika is a pre-requisite to studies on the effects of environmental changes on the lake productivity.

Indeed, recent reports of a negative climate impact on lake productivity over recent decades have been published (in particular by Verburg, Hecky & Kling, 2003 and O'Reilly *et al.*, 2003), which tend to contradict the high primary production figures published by Sarvala *et al.* (1999). Essentially, warming of the surface of the lake would have increased the density gradient, reducing vertical mixing and nutrient availability, thereby reducing phytoplankton biomass and production. Evidence supporting this view includes increased air and water temperatures, diminished P and increased Si concentrations in the surface layer, increased water transparency and decreased phytoplankton biovolume (Verburg *et al.*, 2003). Even though some of this evidence can be challenged, as far as changes in phytoplankton composition and numbers are concerned (Cocquyt & Vyverman, 2005; Descy *et al.*, 2005; Sarvala *et al.*, 2006), a diminishing trend in pelagic primary production is supported by studies of carbon isotopes in several sediment cores (O'Reilly *et al.*, 2002; O'Reilly, Dettman & Cohen, 2005), which indicate a possible 20% decline since the 1950s.

Here, we report a study of particulate primary production in the pelagic zone of Lake Tanganyika during 2002 and 2004. Our aim was to estimate daily and annual production, to examine whether these are lower than in the past, which would confirm the prediction of a decreasing trend. We also estimated the parameters of the photosynthesis-light curve and their variation depending on season and site, and calculated phytoplankton growth rates from primary production. In addition, seston stoichiometry allowed us to examine seasonal differences in nutrient avail-

ability and possible nutrient limitation of phytoplankton growth. Finally, filter fractionation of primary production combined with pigment analysis were used to assess the contribution of picocyanobacteria to phytoplankton biomass.

Methods

Study sites

Measurements were carried out weekly at Kigoma during the rainy season 2002 (February–April), at Mpulungu in the rainy season 2003 (February–May), in the dry season 2004 (August 2004) and during three cruises (July 2002, July 2003 and February 2004), in a variable number of sites. In total, 48 measurements allowing estimates of daily particulate phytoplankton production and evaluation of the photosynthetic parameters are available for the study period. Sampling sites are shown at Fig. 1. Temperature, pH, conductivity and dissolved oxygen were measured using a Seabird CTD (Sea-Bird Electronics Inc., Belluvue, Washington, U.S.A.) or a Hydrolab DS4 sonde (Hach, Loveland, Colarado, U.S.A.). A LICOR

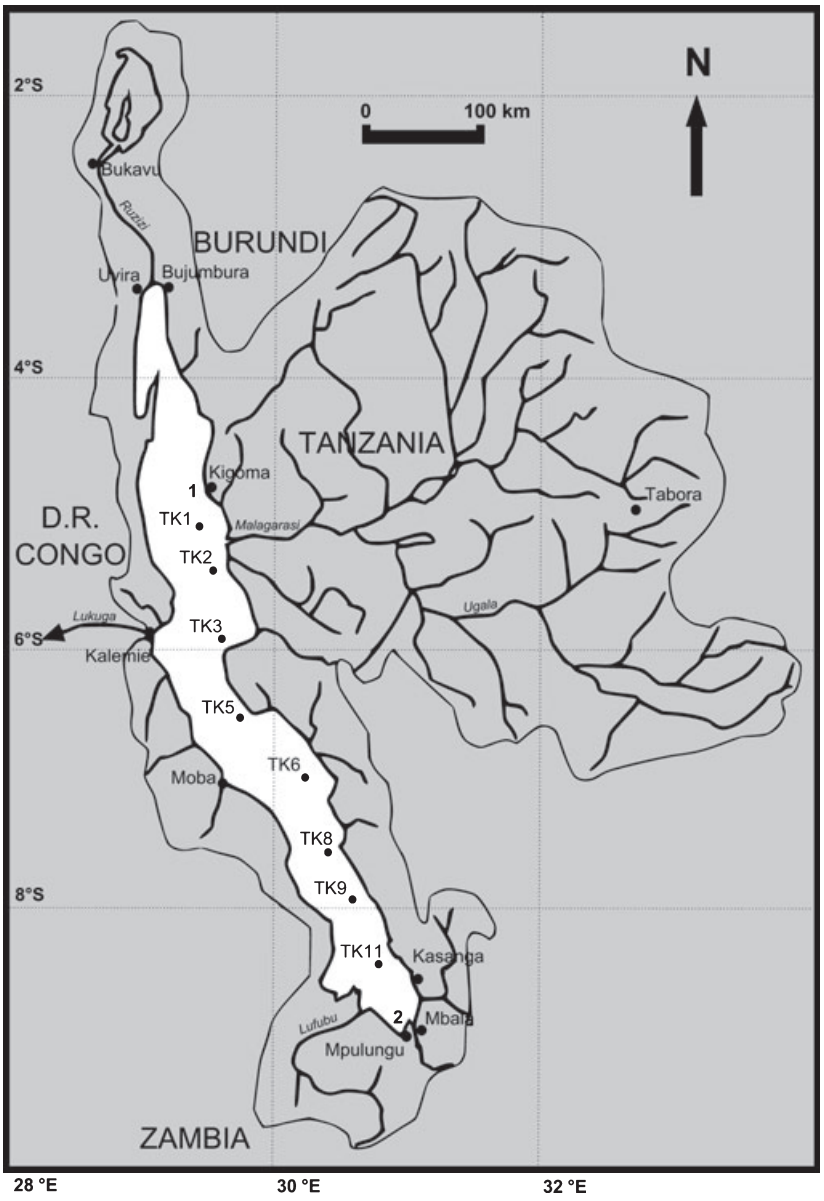


Fig. 1 Map of Lake Tanganyika, showing locations of the sampling sites of the regular survey off Kigoma, North Basin (1) and Mpulungu, South Basin (2) and of the research cruises (TKn).

pyranometer connected to a LICOR LI-1000 (LI-COR Biosciences, Lincoln, Nevada, U.S.A) data logger was used to record air irradiance, while an underwater sensor was used to measure light extinction in the lake. Light extinction coefficients were calculated as the linear slope of transformed underwater irradiances (natural logarithm) as a function of depth, or using Secchi Disk depth ($k = 1.57/SD$). The conversion coefficient was obtained by calibration with measurement of PAR (Photosynthetically Active Radiation) downward attenuation with LICOR quantum sensors. The depth of the euphotic zone was determined as the depth at which light attenuation reaches 1% of subsurface light.

Phytoplankton pigment analysis and primary production measurements

Samples for high performance liquid chromatography (HPLC) analysis of chl-*a* and carotenoid pigment were obtained by collecting water every 10 m down to 60 m and every 20 m below. For each sample, a volume of 3–4 L was sieved on Whatman GF/F (Whatman International Ltd, Maidstone, U.K.) or Macherey-Nägel GF5 filters (Machery-Nagel, Düren, Germany), of 0.7 μm nominal pore size. The subsequent procedure for pigment extraction and analysis followed Pandolfini *et al.* (2000) and Descy *et al.* (2000). Extracts in 90% acetone were then stored in 2 mL amber vials in a freezer (at −25 °C) for several months (under the regular sampling scheme) or for 2–3 weeks at most (for the cruise samples), and transported to Belgium on ice in cooler boxes. A total of more than 800 samples were analysed over the 3 years from the two stations. In the rainy season 2003 (February–April), pooled samples from 0 to 30 m layer were filter-fractionated before collection of the particulate material on the 0.7 μm filters: two subsequent filtrations were carried out on Nytex plankton nets (Sefar AG, Rüschlikon, Switzerland) to retain the particles >28 and >10 μm, followed by a third filtration on a Millipore membrane (Millipore S.A., Brussels, Belgium) of 2 μm pore size. The subsequent treatment was identical to that applied to the non-fractionated samples and allowed estimation of biomass and composition of the following size fractions: >28, 10–28, 2–10 and <2 μm.

The C : chl *a* ratio is usually determined from linear regression of POC (particulate organic carbon) against chl-*a* concentration, and is used for converting chl-*a* biomass into phytoplankton carbon. This ratio is expected to vary as a function of the light climate (Kirk, 1983; Falkowski & Raven, 1997) and can be influenced by nutrients, especially N, availability (Cloern, Grenz & Vidergar-Lucas, 1995). Elemental analysis of the seston was carried out using a Carlo Erba NA1500 elemental analyser (Carlo Erba NA1500, Carlo Erba Strumentazione, Rodano (Milan), Italy) for C (carbon) and N (Nitrogen) determinations, after treatment of the dried filter with hydrochloric acid to remove carbonates possibly present. P (phosphorus) was measured by spectrophotometry of orthophosphate after digestion for 30 min at 120 °C with potassium persulphate. C, N and P content of the seston of the surface waters (0–40 m) was then calculated taking into account the volume of water filtered and expressed in μmoles L^{-1} before calculating the elemental ratios. Limitation of phytoplankton growth by N or P can be appreciated by reference to the elemental ratio in the seston: in optimal growth conditions, the C : N : P proportions (by atoms) are 106 : 16 : 1 (Redfield ratio). A significant P limitation takes place when seston C : P >130 or when N : P exceeds 22. N-limitation is considered to occur when C : N >8.3 or N : P <22 (Healey & Hendzel, 1979; Guildford & Hecky, 2000).

Samples were also preserved for counts by flow cytometry, which allowed enumeration of auto- and heterotrophic picoplankton. Cyanobacteria T1 (pigment type 1, according to Jeffrey, Mantoura & Wright, 1997), corresponded mostly to *Synechococcus* sp., as shown by a correlation analysis with cytometry counts.

Phytoplankton particulate production was measured using the ^{14}C method (Steeman-Nielsen, 1952). An average sample of the euphotic zone obtained by pooling equal volumes of 0, 10, 20, 30 m samples; the 0–30 m layer being most of the time in the mixed layer (Descy *et al.*, 2005), we did not expect differences in phytoplankton photoacclimation in this depth range. This average euphotic zone water was poured into 180–200 mL flasks shaded with neutral screens to obtain a gradient of light (0%, 6.6%, 10.5%, 16.1%, 20.7%, 25.5%, 29.1%, 38.6%, 49.1% and 71.8%). A total of 25–50 μCi ^{14}C-bicarbonate were added in each container, and incubated onboard for 1.5–2 h. Incident solar radiation was recorded during the incubations, using a LICOR LI-1000 data logger. At the end of the incubations, the content of each flask was filtered on

Macherey-Nägel GF 5 filters (porosity 0.7 μm). The radioactivity of the filters was measured by liquid scintillation, and daily production was calculated according to Vollenweider (1974). Chl-*a* of the incubated sample was measured by HPLC. A total of 48 measurements were available for the period 2002–2004. *In situ* measurements of irradiance were used whenever available, whereas irradiance calculated from date and latitude was used when *in situ* light measurements were missing. The method measures only particulate primary production, without accounting for 'dissolved' production (i.e. extracellular release of photosynthetic products). Our analytical methods were essentially similar to those of Hecky & Fee (1981), save for a few details (e.g. extracted chl-*a* was measured with HPLC, which typically yields lower results than the classic spectrophotometric method).

We also re-calculated daily photosynthesis at each routine sampling date of the CLIMLAKE (Climate variability as recorded in Lake Tanganyika) project (Descy *et al*., 2005; Plisnier & Descy, 2005) using chl-*a* in the 0–60 m layer, vertical extinction coefficient and incident light recorded every 5 min (whenever available). We calculated depth-integrated daily photosynthesis with the Vollenweider's (1965) equation, using average photosynthetic parameters. The calculation accounted for a slight photoinhibition by setting to 1 the value of *a* and *n* of the Vollenweider's equation. This calculated photosynthesis was used to infer annual rates.

Phytoplankton growth rate

Whether the radiocarbon method measures gross or net production, or something in between (see e.g. Harris, 1984) is uncertain. In order to allow comparison with the results of Hecky & Fee (1981), and following the reasoning by these authors, we considered that our measurements approximated net production, and calculated phytoplankton growth rate using the Peterson's (1978) formula: $\mu\ (\text{day}^{-1}) = \ln[1 + (\text{C uptake}/\text{C biomass})]$, where C uptake is daily production (g C m^{-2} day^{-1}) and C biomass the phytoplankton biomass as carbon (g C m^{-2}) obtained from chl-*a* using the C : chl-*a* ratio, integrated over the euphotic layer. This production-based growth rate does not account for phytoplankton losses by grazing, sedimentation and mortality.

Results

Limnology and vertical light attenuation

Most limnological data related to this study have already been reported in detail in Descy *et al.* (2005) and Plisnier & Descy (2005). Here, we retain only the variables related to phytoplankton production and growth that are useful for comparison with data from the former studies of Lake Tanganyika primary production. The average euphotic depth was 37.8 m in Kigoma (range: 30.1–56.1 m) compared with 34.6 m in Mpulungu (range: 20.0–45.7 m). Nutrient concentrations (Si, N, P) in the euphotic layer varied seasonally, with higher concentrations in the more windy dry season, when the mixed layer moves deeper and, particularly in the southern end of the lake, when upwelling occurs (Hecky, 1991; Plisnier *et al*., 1999; Langenberg, Sarvala & Roijackers, 2003).

Phytoplankton biomass and particulate organic carbon

As chl-*a* concentration varies with depth (see Descy *et al*., 2005), total phytoplankton biomass in the water column is best evaluated by integrating the vertical chl-*a* profile over the mixed layer. Average chl-*a* in the mixed layer was 23.4 (2002) and 25 (2003) mg m^{-2} at Kigoma, and at Mpulungu 21.7 (2002) and 29.9 (2003) mg m^{-2}. Chl-*a* in the mixed layer (Fig. 2) ranged from 4.8 mg m^{-2} during the rainy season to nearly 120 mg m^{-2} in the dry season. The highest values were usually recorded during the dry season at both stations. A significant difference in chl-*a* content of the water column (Student's t test, $P < 0.05$) was found between the means for the rainy and dry seasons of 2003 at each station. Chl-*a* data for 2004 were lower at both stations, particularly in the dry season. By contrast, POC concentrations (see below) in the dry season in Mpulungu were similar to those of previous years, indicating that chl-*a* measurements at this monitoring site were possibly less reliable in 2004, for technical reasons. Therefore, we did not use the 2004 data for estimating annual primary production (see below). The range of chl-*a* concentrations in the samples used for primary production measurements was 0.23–2.50 mg chl-*a* m^{-3}, and the range for the study period (2002–2004) was 0.3–3.7 mg m^{-3}.

Particulate organic carbon concentration (Fig. 2) can be considered a measure of autochthonous organic

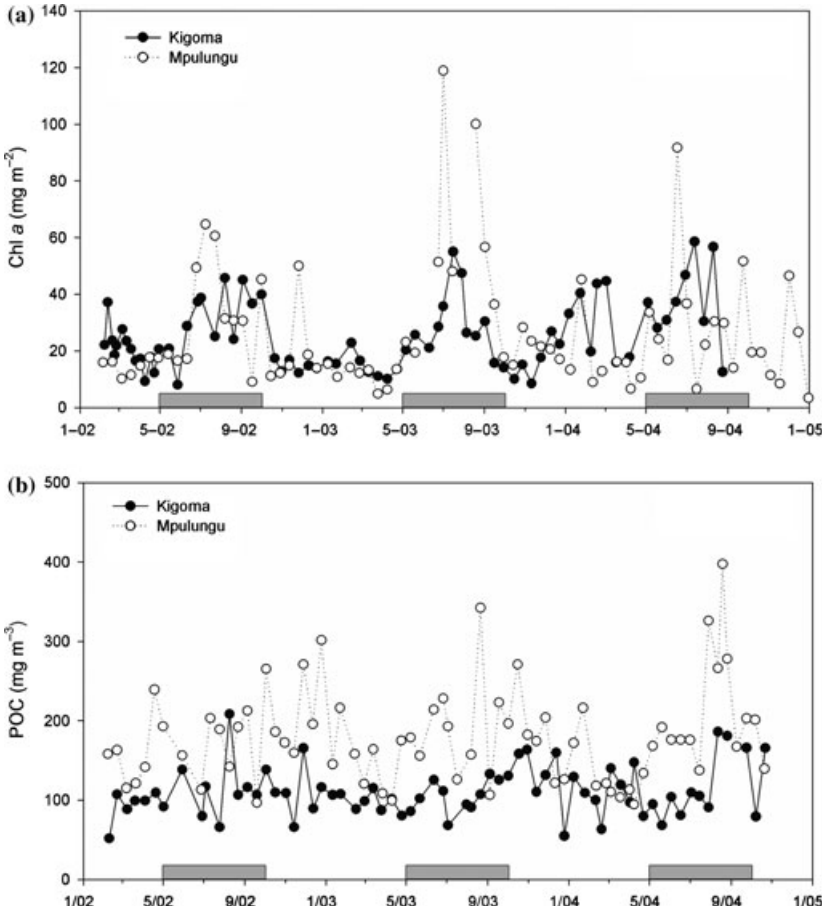


Fig. 2 Chlorophyll-*a* biomass (mg chl-*a* m^{-2}) integrated over the mixed layer in Lake Tanganyika (panel a), and particulate organic carbon (POC) (mg m^{-3}) measured in Lake Tanganyika (panel b), off Kigoma and Mpulungu, for the years 2002, 2003 and 2004. Shaded areas indicate dry season.

matter (in the 0–40 m layer, more or less equivalent to the euphotic zone). Indeed, it can be assumed that, in the pelagic zone of the lake, the amount of detritus is low. If so, POC reflects total plankton biomass, including phytoplankton, bacteria, micro- and mesozooplankton.

As expected from seasonal variations of nutrient availability, maximal plankton biomass tended to occur during the dry seasons, except in 2002 when, as for chl-*a*, maxima were reached after the end of the dry season. POC concentration was higher in Mpulungu than in Kigoma (*t*-test, $P < 0.001$), in agreement with the expected higher production at the southern station. This difference was observed for both seasons: the dry season averages were 112 mg m^{-3} at Kigoma and 196 mg m^{-3} at Mpulungu, and the rainy season averages were 109 and 166 mg m^{-3}, respectively. It is to be noted that POC values at both stations in 2004 were not different from those in 2002–2003, contrary to chl-*a*. A significant linear regression was found for POC against chl-*a* (Fig. 3), and the slope of the regression gave a mean C : chl-*a* ratio of 120 ($R^2 = 0.47$, $n = 139$).

Primary production

All measurements carried out under light saturation exhibited the classic photosynthesis–light curve, with some photoinhibition (Fig. 4). Measured daily phytoplankton production varied between 110 and 1410 mg C m^{-2} day^{-1}. As phytoplankton photosynthetic parameters often varied significantly between seasons and stations (Fig. 5), different values of Pmax and Ik were then used to model daily photosynthesis. For Mpulungu, Pmax was set to the average value of 4.57and 5.91 mg C (mg chl-*a*)$^{-1}$ h^{-1}, for the wet and dry seasons respectively, and for Kigoma we used an average value of 2.77 mg C (mg chl-*a*)$^{-1}$ h^{-1} in the wet season, and 4.66 mg C (mg chl-*a*)$^{-1}$ h^{-1} in the dry season. Values of Ik differed significantly between seasons but not stations, so we used different values

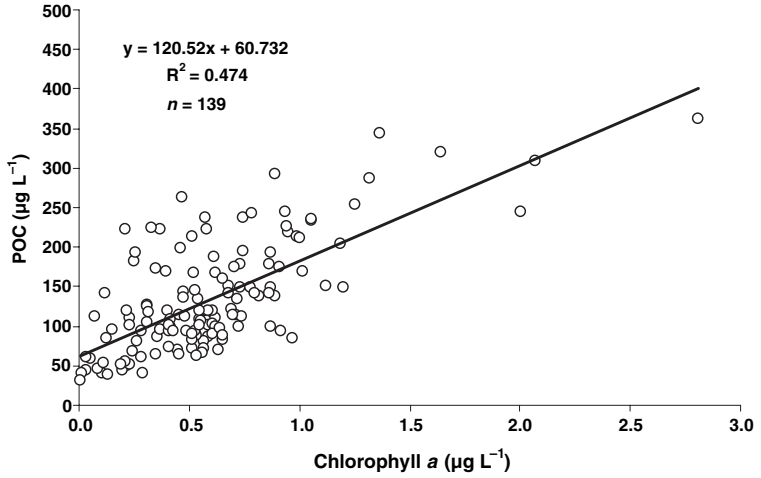


Fig. 3 Relationship between particulate organic carbon (POC) and chlorophyll-*a* in the 0–40 m water column of Lake Tanganyika. Regression line shown.

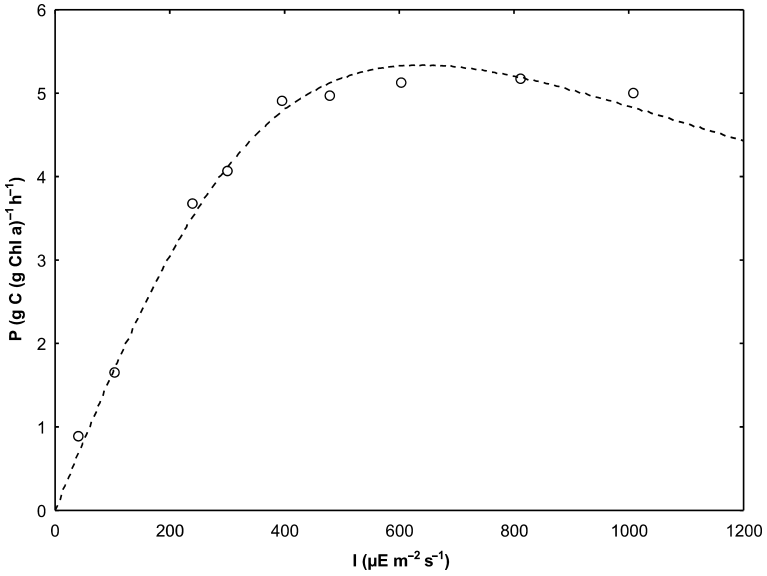


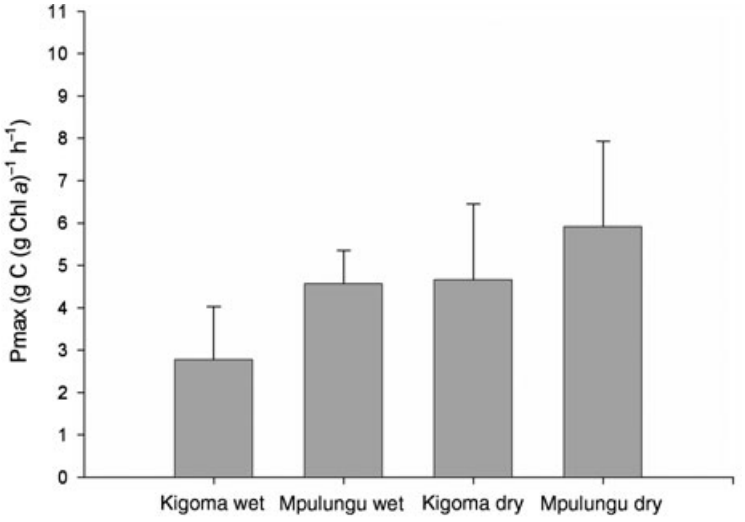
Fig. 4 Example of a photosynthesis–light relationship obtained from an *in situ* radiocarbon incubation under light saturation in Lake Tanganyika.

for the wet season (386 µE m^{-2} s^{-1}) and dry season (315 µE m^{-2} s^{-1}).

Calculated daily primary production for the period 2002–2003 was used to estimate annual production. Off Kigoma, similar values were obtained for the 2 years: 123 (2002) and 130 g C m^{-2} $year^{-1}$ (2003) or 0.34 and 0.36 g C m^{-2} day^{-1}, respectively. Off Mpulungu, primary production amounted to 175 g C m^{-2} $year^{-1}$ in 2002 (0.48 g C m^{-2} day^{-1}) and 205 g C m^{-2} $year^{-1}$ (0.56 g C m^{-2} day^{-1}) in 2003. Daily phytoplankton production in 2002–2003 showed a clear contrast between seasons in Kigoma, with higher production in August–September. This pattern was less obvious in Mpulungu (Fig. 6). Calculated daily photosynthesis generally agreed well with the measured values.

Data obtained for the two dry season cruises tend to confirm a difference of primary production between the north and south of the lake (Fig. 7). Rainy season results were more homogenous over the lake, with the exception of site TK3, which resulted from higher chl-*a* at this site, possibly influenced by the plume of the Malagarazi river that presumably brings nutrients into the lake.

The ^{14}C uptake by different size fractions (Fig. 8) indicated that photosynthesis by phytoplankton <2 µm accounted on average for 56% of total particulate production during the wet season 2003 at Mpulungu.



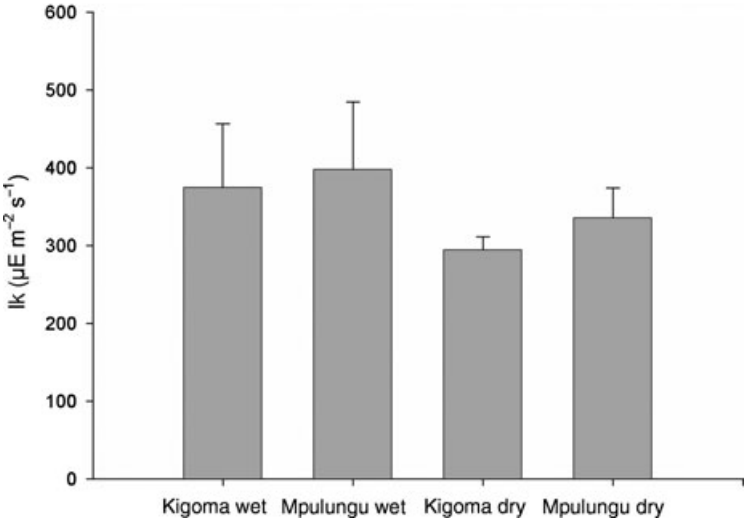


Fig. 5 Mean and standard deviations of photosynthetic parameters Pmax [g C (g chl-*a*)$^{-1}$ h^{-1}] and Ik (µE m^{-2} s^{-1}), obtained from *in situ* measurements in Lake Tanganyika, off Kigoma and Mpulungu, during wet and dry seasons.

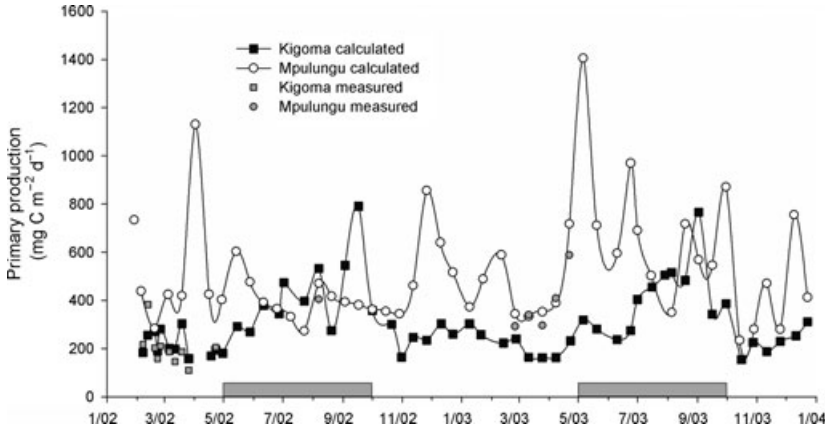


Fig. 6 Daily primary production (mg C m^{-2} day^{-1}) calculated for Lake Tanganyika, off Kigoma and Mpulungu, in 2002 and 2003, and daily primary production obtained from *in situ* measurements. Shaded areas indicate dry season.

Estimates of growth rates

Based on the assumption made above, our calculated phytoplankton growth rates, from fortnightly daily production, were in the range 0.055–0.207 day^{-1} off Kigoma (mean 0.116 day^{-1}) and 0.123–0.282 day^{-1} off Mpulungu (mean 0.172 day^{-1}).

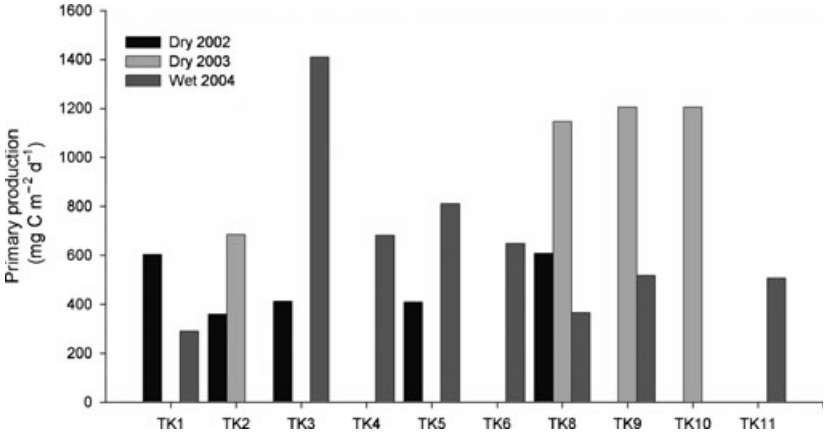


Fig. 7 Daily primary production (mg C m^{-2} day^{-1}) obtained from *in situ* measurements during the cruises in Lake Tanganyika.

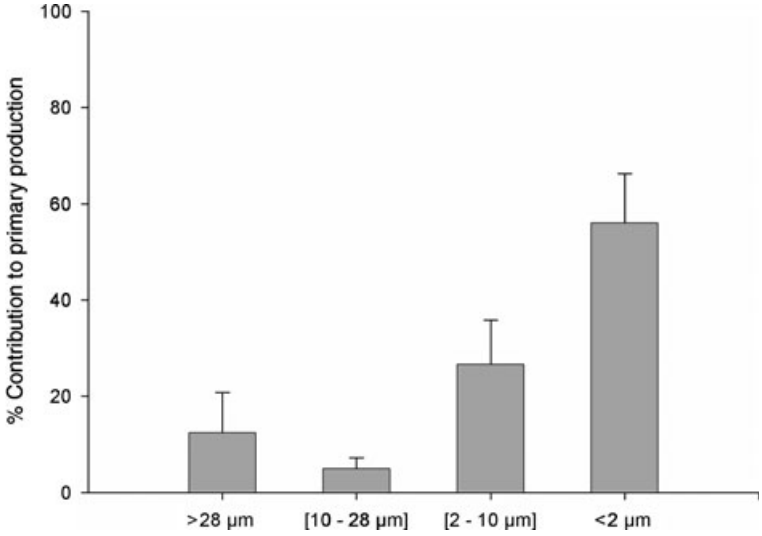


Fig. 8 Contribution of picophytoplankton to primary production in lake Tanganyika, during the wet season 2003 off Mpulungu.

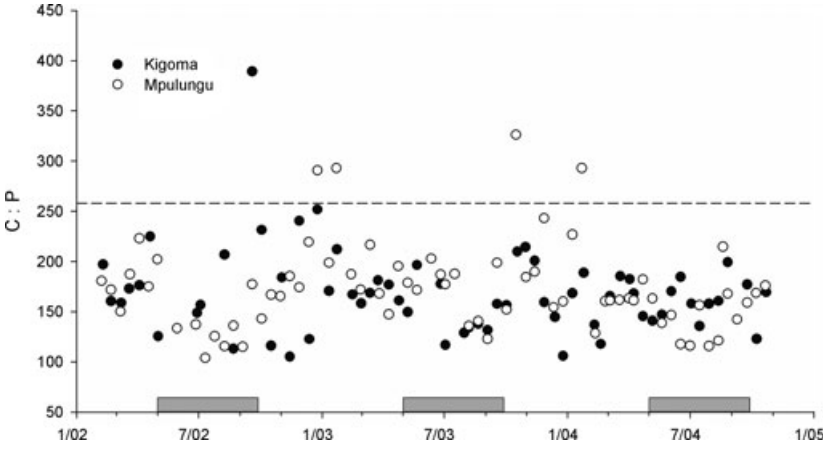


Fig. 9 Carbon :phosphorus (C : P) ratio in the 0–40 m water column of Lake Tanganyika off Kigoma and Mpulungu, for the years 2002, 2003 and 2004. Shaded areas indicate dry season.

Seston stoichiometry and nutrient limitation

Both C : P and C : N ratios suggest that macronutrient limitation of phytoplankton may have occurred in Lake Tanganyika during the study period, but also that P limitation may have been more frequent than N limitation. Indeed, in a total of 134 measurements of seston stoichiometry in the euphotic layer, C : P was

>130 in 114 cases, the proposed threshold for P limitation, while C : N was >8.3 in 51 cases. The N : P ratio exceeded 22, the value indicating a switch to N limitation, in 43 cases. When exceeding the threshold value, both ratios remained in a range where moderate limitation is assumed to occur. Interestingly, the seasonal pattern of the C : P ratio at both stations (Fig. 9) was related to the seasonal mixing pattern of the water column. Neglecting short-term variations, possibly because of internal waves and to variation of phytoplankton nutrient demand, seston C : P tended to be higher in the stratified conditions of the rainy season, and tended to be lower in the dry season, when nutrient availability increased. Overall, the threshold for severe P limitation (258, Guildford & Hecky, 2000) was exceeded only on five occasions, while the threshold for severe N limitation (14.6) was never reached in the study period. However, the degree of N limitation may have been greater in the northern station than in the southern one: a significant difference was found (Student's *t*-test, $P < 0.0001$) between the mean C : N ratio (7.8, $n = 70$) off Mpulungu and the one off Kigoma (8.5, $n = 64$). At this site, the value assumed to indicate moderate N limitation was exceeded in about half of the seston samples. No significant differences between the two sites were found for the C : P and N : P ratios.

Discussion

Daily rates of primary production were usually lowest in the rainy season, as a result of low phytoplankton biomass and, off Kigoma, lower light-saturated rate of photosynthesis. By contrast, the dry season conditions, when deep mixing favours higher nutrient availability (Hecky, 1991; Plisnier & Coenen, 2001), resulted in increased production, but with differences in timing of the maxima at the two sites, and greater variability in the south (Coulter, 1991; Plisnier *et al*., 1999). This is consistent with a recent study of Lake Tanganyika sediment cores (Cohen *et al*., 2006), which detected significant variation in laminae thickness even at subdecadal timescales. The same study points to variability at decadal-multidecadal timescales, which can be related to climate records in the tropics. Such studies are important to interpret differences in productivity between this study and the earlier ones.

Our results can be best compared with those of Hecky & Fee (1981), as the methods for measuring primary production were similar and provided comparable measurements of photosynthetic capacity (or assimilation number) of the phytoplankton and of particulate primary production. Hecky & Fee (1981) reported a substantial variation in assimilation number on the same day in different sites, with a range of 1.7–21 mg C (mg chl-*a*)$^{-1}$ h^{-1}, but used a single value of 6 mg C (mg chl-*a*)$^{-1}$ h^{-1} to determine seasonal and annual rates. Our range of photosynthetic capacity, from incubations mostly run at mid-day and at light saturation, was smaller [1.7–9.8 mg C (mg chl-*a*)$^{-1}$ h^{-1}], but still comparable with those of Hecky & Fee (1981). The daily rates of primary production measured at different points in a lake transect in 1975 ranged between 0.3 and 3.1 g C m^{-2} day^{-1} (Hecky, 1991), while the range in our study was 0.11–1.4 g C m^{-2} day^{-1}. Our minimal primary production results (<0.2 g C m^{-2} day^{-1}) are the lowest ever reported for Lake Tanganyika, and our daily means (0.32 g C m^{-2} day^{-1} in the north and 0.50 g C m^{-2} day^{-1} in the south) are substantially lower than the all-lake estimate (0.8 g C m^{-2} day^{-1}) made from the 1975 study. This implies a reduction in primary production rates >20% decrease proposed by O'Reilly *et al.* (2003).

It could be argued that this difference in present and past primary production estimates may stem from the fact that the mean annual rate of Hecky & Fee (1981) was calculated by averaging data from a typical low-productivity situation (end of the rainy season) and from a relatively high chl-*a* event (up to 4.5 mg m^{-3} in the euphotic zone) encountered after the dry season. Whether such an estimate is valid is debatable, as these high chl events are typically related to surface blooms of *Anabaena* sp., which tend to collapse quickly. Therefore, the difference in productivity estimates from the two studies might not be as large as it appears.

Another possibility is that the observed difference is further evidence of a decrease in primary production in Lake Tanganyika over recent decades, as proposed by Verburg *et al.* (2003), based on limnological and planktological evidence. On the one hand, the very low daily production rates we often measured in the rainy season could be the result of the increased surface temperature, which induces stronger stratification and reduced nutrient supply to the euphotic zone, leading to stronger nutrient limitation and lower chl-*a*. In addition, relatively high chl maxima related

to surface blooms might occur more rarely nowadays and be of shorter duration than in the past (R.E. Hecky, pers. comm). This could be related to reduced dry season winds, which play a key role in supplying nutrients to the surface layers. For instance, *Anabaena* surface blooms are typically observed in Lake Tanganyika at the dry season–rainy season transition, when the lake re-stratifies, favouring buoyant, nitrogen-fixing filamentous cyanobacteria. Obviously, the combination of reduced primary production minima and maxima would explain the lower annual rates we estimated from our data. We remain, however, relatively cautious because, if there are differences in chl-*a* concentration between our 2002–2004 study and that from the 1970s do exist, they might stem from differences in analytical techniques and sampling design. (Descy *et al*., 2005). Nevertheless, we do agree with Verburg, Hecky & Kling (2006) that there is compelling evidence of a decrease in pelagic primary productivity in Lake Tanganyika over recent decades, based on data on water transparency, silica concentration in the surface waters, and C isotopic ratios in the sediment. Our primary production measurements and estimates are in line with these conclusions.

By contrast, the primary production estimates of this study are definitely very different from those of the FAO-FINNIDA LTR (Lake Tanganyika Research) project (Sarvala *et al*., 1999), which reported data from measurements carried out in 1995–1996. Indeed, lake annual primary production according to this study was 426–662 g C m^{-2} $year^{-1}$, despite the fact that the range of chl-*a* was broadly similar in both studies (Salonen *et al*., 1999; Langenberg *et al*., 2003). Two explanations for the high figures were offered by Sarvala *et al*. (1999). First, ^{14}C uptake by phytoplankton was measured on liquid samples after removal of unassimilated radiocarbon, so that the measurements accounted not only for phytoplankton particulate production, but also for some of the dissolved production, some of which would be re-assimilated by heterotrophic bacteria during the incubation. Despite this difference in sample treatment, the photosynthetic capacity measured by LTR was in a range similar to ours [2.4–6.4 mg C (mg chl-*a*)$^{-1}$ h^{-1})]. Moreover, average daily production measured by Sarvala *et al*. (1999) at the same sites was quite similar to our measurements (*c*. 0.5 g C m^{-2} day^{-1}; Sarvala *et al*., 1999, Fig. 6). However, the high annual rates put forward by LTR were based on averaging production from three distant sites, including in the calculation the more productive Bujumbura basin, where measured primary production ranged between 1 and 4 g C m^{-2} day^{-1}. Hence, the discrepancies in annual rates may stem more from differences in calculations than in the measurements themselves. We believe that our approach based on determining the parameters of the photosynthesis-light curve from measurements at different seasons, to re-calculate phytoplankton production at a given site at regular time intervals, is more reliable, and may provide realistic annual rates at this site, without attempting to assess whole-lake productivity. Another important point to stress here is that none of the studies conducted so far really accounted for the spatial and temporal variability of phytoplankton biomass and production expected in this large lake. In this respect, estimates based on satellite imagery (Bergamino *et al*., 2007), involving assessment of surface chl-*a* and water transparency, should lead to improved whole-lake estimation of phytoplankton production.

The phytoplankton growth rates we calculated from primary production rates in Lake Tanganyika are in a range commonly cited for phytoplankton growth rates in freshwaters (Reynolds, 1984), but are much lower than those published by Hecky & Fee (1981) for Lake Tanganyika. Using very similar methods, Hecky & Fee (1981) calculated high phytoplankton growth rates (mean 0.9 day^{-1}), potentially explaining why high secondary production could be supported by low phytoplankton biomass with high turnover rate. However, the growth rates they determined were based on a single and low estimate of phytoplankton carbon (0.6 g C m^{-2}) obtained from phytoplankton biovolume, not from chl-*a* converted to carbon. C : chl-*a* ratios are typically high in oligotrophic waters (Cloern *et al*., 1995; Geider, Macintyre & Kana, 1997), because of low chl content of algal cells at high light, and are also sensitive to nutrient deficiency (Healey & Hendzel, 1979; Guildford *et al*., 2003). In nutrient addition experiments conducted in Lake Malawi, Guildford *et al*. (2003) measured POC and chl-*a* in the lake water in initial conditions. C : chl-*a* ratios calculated from these measurements vary from approximately 70–300, with a mean of 165 (not taking into account non-phytoplankton carbon). As nutrient availability, light penetration and chl-*a* concentration are similar in Lake Malawi and Tanganyika, we believe that our determination of a C : Chl *a* ratio of

120 for Lake Tanganyika phytoplankton is realistic. On the basis of this mean ratio, Pirlot (2006) estimated total phytoplankton biomass in the water column between 3.0 and 4.4 g C m^{-2}, depending on season and site, and independent epifluorescence and cytometry counts indicated that picophytoplankton biomass amounted to 1.5 g C m^{-2} (Pirlot, 2006). Seemingly, Hecky & Fee (1981) underestimated phytoplankton biomass as carbon, which led them to overestimate algal growth rates. The growth rates we calculated correspond to average total phytoplankton doubling times of 4–6 days (minimum 2.5 days), but obviously Lake Tanganyika phytoplankton comprises different populations, probably with very different growth and loss rates, which should be estimated using adequate methods.

Moreover, growth rates of phytoplankton may be further reduced by a moderate nutrient limitation, most probably by P, especially during the stratified conditions of the rainy season, as evidenced by the C : P increase in the seston during this season at both study sites. Järvinen *et al.* (1999) reached similar conclusions. Our data also indicate a probable more frequent occurrence of moderate N limitation at the northern site than at the southern site. In a parallel study (De Wever, 2006), multiple nutrient enrichment bioassays using addition of iron and combined addition of N and P were carried out at the same study sites in 2003 and 2004 to compare the response of different phytoplankton groups to the nutrient additions. The results confirm moderate macronutrient limitation of Lake Tanganyika phytoplankton, as we observed in our study solely based on seston stoichiometry. Furthermore, De Wever's study (2006) suggests co-limitation by N, P and Fe, with a differential response among phytoplankton groups and, in particular, with a strong response of picocyanobacteria to Fe additions. Data are lacking, however, to examine whether the extent of nutrient limitation of phytoplankton has changed in Lake Tanganyika as a result of the warming trend of the past decades.

Finally, caution is needed in attempts to estimate the climate impact on consumer production resulting from decreased primary production, notably because phytoplankton community structure matters in the carbon transfer processes through the food web. Indeed, the trophic fate of the different phytoplankton fractions, comprising very small *Synechococcus*, single-celled or colonial diatoms or green algae, and large filaments or colonies of cyanobacteria, may be very different. In any case, one may expect that only the nanoplankton (perhaps half of phytoplankton biomass) is directly grazed by the calanoid and cyclopoid copepods that constitute the major trophic link between phytoplankton and fish. By contrast, the smaller phytoplankton is grazed by heterotrophic nanoflagellates and by ciliates (Unrein & Sarmento, 2005), which in turn may be preyed upon by copepods. This is one more reason to take into account heterotrophic plankton production to explain the fishery yield in the oligotrophic Lake Tanganyika, as previously highlighted by Hecky & Fee (1981). Recent studies have confirmed this view, showing that heterotrophic plankton biomass may approach or even exceed autotroph biomass in the lake (Pirlot *et al.*, 2005; Pirlot, 2006). In addition, the trophic role of heterotrophic bacteria in the food web has recently been evaluated: Pirlot (2006) estimated that bacterial production is on average about half of phytoplankton production, and that a significant fraction of bacterial production is transformed into protozoan production that becomes available to larger zooplankton. The picture that may emerge from these recent studies is that the combination of different carbon transfer pathways helps sustain metazooplankton and fish production, so that simple models based on relationships between primary production and fish production will be insufficient to predict the impact of environmental changes on lake productivity.

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References

Bergamino N., Loiselle S.A., Cozar A., Dattilo A.M., Bracchini L. & Rossi C. (2007) Examining the dynamics

of phytoplankton biomass in Lake Tanganyika using empirical orthogonal functions. *Ecological Modelling*, **204**, 156–162.

Cloern J., Grenz C. & Vidergar-Lucas L. (1995) An empirical model of the phytoplankton chlorophyll: carbon ratio – the conversion factor between productivity and growth rate. *Limnology and Oceanography*, **40**, 1313–1321.

Cocquyt C. & Vyverman W. (2005) Phytoplankton in Lake Tanganyika: a comparison of community composition and biomass off Kigoma with previous studies 27 years ago. *Journal of Great Lakes Research*, **31**, 535–546.

Cohen A., Lezzar K., Cole J., Dettman D., Ellis G., Gonneea M, Plisnier P.-D., Langenberg V., Blaauw M. & Zilifi D. (2006) Late Holocene linkages between decade-century scale climate variability and productivity at Lake Tanganyika, Africa. *Journal of Paleolimnology*, **36**, 189–209.

Coulter G.W. (1991) *Lake Tanganyika and its Life*. Oxford University Press, Oxford.

De Wever A. (2006) *Spatio-Temporal Dynamics in the Microbial Food Web in Lake Tanganyika*. PhD Thesis, University of Ghent, Ghent, Belgium.

Descy J.-P., Higgins H., Mackey D., Hurley J. & Frost T. (2000) Pigment ratios and phytoplankton assessment in northern Wisconsin lakes. *Journal of Phycology*, **36**, 274–286.

Descy J.-P., Hardy M.-A., Stenuite S., Pirlot S., Leporcq B., Kimirei I., Sekadende B., Mwaitega S.R. & Sinyenza D. (2005) Phytoplankton pigments and community composition in Lake Tanganyika. *Freshwater Biology*, **50**, 668–684.

Falkowski P.G. & Raven J.A. (1997) *Aquatic Photosynthesis*. Nick Mann, Warwick.

Geider R.J., Macintyre H.L. & Kana T.M. (1997) Dynamic model of phytoplankton growth and acclimation: responses of the balanced growth rate and the chlorophyll *a* : carbon ratio to light, nutrient-limitation and temperature. *Marine Ecology Progress Series*, **148**, 187–200.

Guildford S.J. & Hecky R.E. (2000) Total nitrogen, total phosphorus, and nutrient limitation in lakes and oceans: is there a common relationship? *Limnology and Oceanography*, **45**, 1213–1223.

Guildford S.J., Hecky R.E., Taylor W.E., Mugidde R. & Bootsma H.A. (2003) Nutrient enrichment experiments in tropical Great Lakes Malawi/Nyasa and Victoria. *Journal of International Great Lakes Research*, **29**, 89–106.

Harris G.P. (1984) Phytoplankton productivity and growth measurements: past, present and future. *Journal of Plankton Research*, **6**, 219–237.

Healey F.P. & Hendzel L.L. (1979) Indicators of phosphorus and nitrogen deficiency in five algae in culture. *Journal of the Fisheries Research Board of Canada*, **36**, 1364–1369.

Hecky R.E. (1991) The pelagic ecosystem. In: *Lake Tanganyika and its Life* (Ed. G.W. Coulter), pp. 90–110. Oxford University Press, Oxford.

Hecky R.E. & Fee E.J. (1981) Primary production and rates of algal growth in Lake Tanganyika. *Limnology and Oceanography*, **26**, 532–547.

Järvinen M., Salonen K., Sarvala J., Vuorio K. & Virtanen A. (1999) The stoichiometry of particulate nutrients in Lake Tanganyika – implications for nutrient limitation of phytoplankton. *Hydrobiologia*, **407**, 81–88.

Jeffrey S.W., Mantoura R.F.C. & Wright S.W. (1997) *Phytoplankton Pigments in Oceanography*. SCOR – UNESCO, Paris, France, 661 p.

Kirk J.T.O. (1983) *Light and Photosynthesis in Aquatic Ecosystems*. Cambridge University Press, Cambridge, UK.

Langenberg V.T., Sarvala J. & Roijackers R. (2003) Effect of wind induced water movements on nutrients, chlorophyll-*a*, and primary production in Lake Tanganyika. *Aquatic Ecosystem Health & Management*, **6**, 279–288.

O'Reilly C., Dettman D. & Cohen A.S. (2005) Paleolimnological investigations of anthropogenic environmental change in Lake Tanganyika: VI. Geochemical indicators. *Journal of Paleolimnology*, **34**, 85–91.

O'Reilly C., Hecky R.E., Cohen A.S. & Plisnier P.-D. (2002) Interpreting stable isotopes in food webs: recognizing the role of time averaging at different trophic levels. *Limnology and Oceanography*, **47**, 306–309.

O'Reilly C., Allin S., Plisnier P.-D, Cohen A. & McKee B. (2003) Climate change decrease aquatic ecosystem productivity of Lake Tanganyika, Africa. *Nature*, **424**, 766–768.

Pandolfini E., Thys I., Leporcq B. & Descy J.-P. (2000) Grazing experiments with two freshwater zooplankters: fate of chlorophyll and carotenoid pigments. *Journal of Plankton Research*, **22**, 305–319.

Peterson B.J. (1978) Radiocarbon uptake: its relation to net particulate carbon production. *Limnology and Oceanography*, **23**, 179–184.

Pirlot S. (2006) *The Bacterioplankton of Lake Tanganyika: Biomass, Production and Trophic Fate*. PhD Thesis, University of Namur, Namur, Belgium.

Pirlot S., Vanderheyden J., Descy J.-P. & Servais P. (2005) Abundance and biomass of heterotrophic microorganisms in Lake Tanganyika. *Freshwater Biology*, **50**, 1219–1232.

Plisnier P.-D. & Coenen E.J. (2001) Pulsed and dampened annual limnological fluctuations in Lake Tanganyika. In: *The Great Lakes of the World (GLOW): Food-Web, Health and Integrity* (Eds M.H. Munawar &

R.E. Hecky), pp. 83–96. Backhuys, Leiden, The Netherlands.

Plisnier P.-D. & Descy J.-P. (2005) *CLIMLAKE: Climate Variability as Recorded in Lake Tanganyika*. Final report (2001–2005). Science Policy Office, Bruxelles, Belgium.

Plisnier P.-D., Chitamwebwa D., Mwape L., Tshibangu K., Langenberg V. & Coenen E. (1999) Limnological annual cycle inferred from physical–chemical fluctuations at three stations of Lake Tanganyika. *Hydrobiologia*, **407**, 45–58.

Reynolds C.S. (1984) *The Ecology of Freshwater Phytoplankton*. Cambridge University Press, Cambridge.

Salonen K., Sarvala J., Järvinen M., Langenberg V., Nuottajärvi M., Vuorio K. and Chitamwebwa D.B.R. (1999) Phytoplankton in Lake Tanganyika – vertical and horizontal distribution of *in vivo* fluorescence. *Hydrobiologia*, **407**, 89–103.

Sarvala J., Badende S., Chitamwebwa D., Juvonen P., Mwape L., Molsa H., Mulimbwa N., Salonen K., Tarvainen M. & Vuorio K. (2003) Size-fractionated δ15N and δ13C isotope ratios elucidate the role of the microbial food web in the pelagial of Lake Tanganyika. *Aquatic Ecosystem Health & Management*, **6**, 241–250.

Sarvala J., Langenberg V., Salonen K. *et al.* (2006) Fish catches from Lake Tanganyika mainly reflect changes in fishery practices, not climate. *Verhandlungen – Internationale vereinigung für theoretische und angewandte Limnologie*, **29**, 1182–1188.

Sarvala J., Salonen K., Jarvinen M. *et al.* (1999) Trophic structure of Lake Tanganyika: carbon flows in the pelagic food web. *Hydrobiologia*, **407**, 140–173.

Steeman-Nielsen E. (1952) The use of radio-active carbon (^{14}C) for measuring organic production in the sea. *Journal du Conseil International pour l'Exploration de la Mer*, **18**, 117–140.

Unrein F. & Sarmento H. (2005) El Lago Tanganyika. *Investigacion y Ciencia*, Julio **346**, 38–39.

Verburg P., Hecky R.E. & Kling H. (2003) Ecological consequences of a century of warming in Lake Tanganyika. *Science*, **301**, 505–507

Verburg P., Hecky R.E. & Kling H.J. (2006) Climate warming decreased primary productivity in Lake Tanganyika, inferred from accumulation of dissolved silica and increased transparency. Comment to Sarvala *et al.* 2006 (Verh. Internat. Verein. Limnol. 29, p. 1182–1188). *Verhandlungen - Internationale. Vereinigung für thearetische and angewandte Limnologie.*, **29**, 2335–2338.

Vollenweider R.A. (1965) Calculations models of photosynthesis-depth curves and some implications regarding day rate estimates in primary production measurements. *Memorie dell'Istituto Italiano di Idrobiologia*, **18**, 425–457.

Vollenweider R.A. (1974) *A Manual on Methods for Measuring Primary Production in Aquatic Environments*. Blackwell Scientific Publications, Oxford.

Vuorio K., Nuottajarvi M., Salonen K. & Sarvala J. (2003) Spatial distribution of phytoplankton and picocyanobacteria in Lake Tanganyika in March and April 1998. *Aquatic Ecosystem Health & Management*, **6**, 263–278.

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