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The stoichiometry of particulate nutrients in Lake Tanganyika – implications for nutrient limitation of phytoplankton

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Abstract

We studied the potential nutrient limitation of phytoplankton by means of seston nutrient stoichiometry and nutrient enrichment bioassays in the epilimnion of Lake Tanganyika. In most cases, the particulate carbon to phosphorus (C:P) ratio was high and indicated moderate P deficiency, while the respective C:N ratio mainly suggested moderate N deficiency. The N:P ratios of seston indicated rather balanced N and P supply. In three two-day enrichment bioassays in April–May 1995, a combined addition of P, N and organic carbon (glucose) always increased primary production in comparison to untreated controls. Primary production also slightly increased after the addition of phosphate-P, while the additions of single ammonium-N and glucose had no effect. Although the measured turnover time of P was short and our few nutrient enrichment experiments suggested that P may be the most limiting single nutrient, the particulate nutrient ratios and the strong stimulation of primary production after the combined addition of P and N mostly suggest that in the upper epilimnion of Lake Tanganyika plankton experience a restricted, but approximately balanced nutrient supply.

Introduction

In freshwaters, phosphorus (P) has been regarded as the nutrient most likely to limit phytoplankton growth (Hecky & Kilham, 1988). Recent studies (e.g. Hecky & Kilham, 1988; Elser et al., 1990; Hecky et al., 1993) have indicated, however, that a wide variety of conditions exists in lakes, including P and N deficiency, as well as P and N sufficiency. According to the literature survey by Henry et al. (1985), many tropical lakes seem to be N-limited. Hecky et al. (1993) found that tropical lakes generally have severely P or N deficient seston, but in some cases they can be P and N sufficient. In Lake Tanganyika, the ratios of inorganic nutrients are close to the Redfield proportions suggesting that strong nutrient limitation of primary production is unlikely (Hecky, 1991; Edmond et al. 1993). However, owing to the hydrology and nutrient chemistry of the lake, the productivity of Lake Tanganyika has been suggested most likely to be N limited (Hecky & Kilham, 1988; Edmond et al., 1993).

The chemical evaluation of the limiting nutrient is often based on the comparison of observed nutrient ratios to the C:N:P ratio of 106:16:1 by atoms; or 41:7:1 by mass (Redfield, 1958). Nutrient limitation has also been studied by means of nutrient enrichment bioassays (Hecky & Kilham, 1988). Primary production of Lake Tanganyika is assessed in connection of the FAO/FINNIDA project 'Research for the Management of the Fisheries on Lake Tanganyika', elucidating the biological basis of fish production in the lake (Salonen & Sarvala, 1994). As a part of these studies, we studied the role of P, N and C for plankton growth in Lake Tanganyika, applying both the particulate nutrient ratio approach and nutrient enrichment bioassays.

Study area, material and methods

The study was carried out at Lake Tanganyika during the wet season in November–December 1994 and during two cruises aboard *R/V Tanganyika Explorer* at the beginning of the dry season on 28 April–5 May 1995 and towards the end of the wet season in March–April 1998. Lake Tanganyika is the largest and deepest and probably oldest, of ancient African lakes (Coulter, 1991). The lake is permanently meromictic and anoxic below 150 m depth (Hecky et al., 1991; Edmond et al., 1993). As a result, the pelagic ecosystem is isolated from the deep nutrient-rich water (Hecky, 1991; Edmond et al., 1993) and the production in the lake is dependent on internal nutrient cycling (Hecky & Kilham, 1988). Most of the organic carbon originates from the pelagic ecosystem of the lake, which also is characterized by high fish production and few zooplankton taxa (Hecky, 1991). The general features of Lake Tanganyika and its life are described in detail by Coulter (1991).

Particulate nutrient ratios and chlorophyll *a*

Samples for the vertical distribution of particulate nutrients (C, N, P) and chlorophyll *a* were taken from the surface to the depth of 100 m at 10 m intervals with a darkened 1 m long tube sampler (Limnos Ltd, Finland). During the rainy season, in December 1994, one vertical profile was taken off Kigoma, Tanzania (Figure 1). During the cruise on *R/V Tanganyika Explorer* in April–May 1995, samples were taken at six sampling stations in different parts of the lake (Figure 1). Additional 20 vertical profiles for the particulate N and P distribution were taken from the surface to the depth of 50–100 m in March 1998. At the time of sampling in 1995, the thermocline usually located at the depth of 40–50 m (Huttula, unpubl.). One to two litres of water was filtered through preignited Whatman GF/F or GF/C (1998 cruise) glassfibre filters. During the 1995 cruise, the filters were dried in a desiccator and stored in darkness in small plastic dishes at 2–6 °C, which was the coldest temperature available on board, while in 1998 they were stored at −20 °C in a freezer.

In Finland, four pieces of known area were punched from each filter for the determination of chlorophyll *a* and particulate organic carbon (POC). Chlorophyll was extracted in 7 ml of 96% ethanol and determined with a Hitachi F-4000 Fluorescence

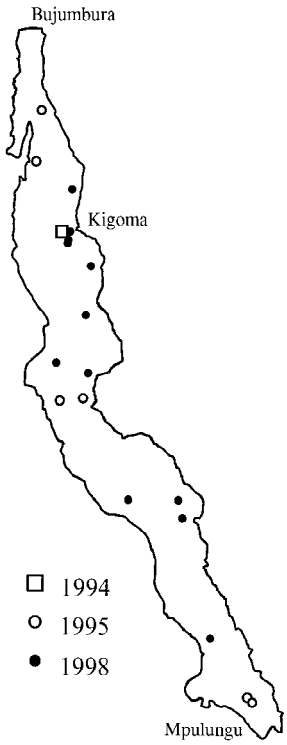

Figure 1. Vertical sampling stations for particulate nutrients and chlorophyll *a* in Lake Tanganyika during the study.

Spectrophotometer (excitation at 430 nm, emission at 671 nm) calibrated against pure chlorophyll *a* (Sigma). POC was determined with the high temperature combustion method of Salonen (1979). Possible carbonates were not removed before the determination. Total particulate P and N were determined from the rest of the filter using a wet oxidation method (Koroleff, 1983). The background nutrient concentration of the filters was subtracted from the final results. The results were not corrected for detrital contribution, since African great lakes with low particulate concentrations seem to be relatively free of significant inputs of terrestrial and atmospheric particulate material (Hecky et al., 1993).

Nutrient enrichment bioassays

Three nutrient enrichment bioassays were carried out during the cruise in April–May 1995. An integrated sample, representing the upper part of the productive layer of the lake, was taken from the depths of 0, 5, 10 and 20 m with a 1 m long darkened tube sampler (Limnos Ltd, Finland) into a darkened 15 l polyethylene container. For the first (30 April) and second (2 May)

experiment sample water was collected around 14:00 and 16:00 (Burundi time: GMT+2), respectively, from the southern basin of the lake near Mpulungu, Zambia (latitudes 08° 30.10′ S and 08° 32.16′ S). For the third experiment (3 May) sample water was collected around 15:00 from the central basin of the lake (latitude 06° 11.00′ S).

In the laboratory of the research vessel, two 20 ml acid-washed and preignited glass liquid scintillation vials for each treatment were filled with sample water and kept in darkness to avoid photodamage of phytoplankton. Finally, phosphate-P, ammonium-N and organic C (D(+)-α-glucose) were added separately or combined (PNC) to final concentrations of 0.8 μmol P l^{-1}, 12.5 μmol N l^{-1} and 20.8 μmol C l^{-1} from autoclaved stock solutions of KH_2PO_4, NH_4Cl and $C_6H_{12}O_6$, respectively. A combined addition of P and N in the PNC treatment followed the Redfield N:P ratio of 16:1 (by atoms).

Primary production of phytoplankton was measured with the radiocarbon method (Steemann Nielsen, 1952), using acidification instead of filtration (Schindler et al., 1972), but no bubbling (Niemi et al., 1983). After nutrient additions, 100 μl (0.11 MBq [3 μCi]) of radiocarbon solution ($Na_2{}^{14}CO_3$) was added into each vial. Samples were incubated for 2 d under continuous light in the on-board incubator. During incubations, we could not follow a daily light period of ca. 12 h light and 12 h dark, since the enrichment experiments as well as the other ongoing primary production measurements were started at different times of the day. In the first two experiments, light intensity inside the incubator was adjusted to 211 μE m^{-2} s^{-1} with neutral density screening. In the third experiment, we used higher illumination (511 μE m^{-2} s^{-1}). The selected light intensities were probably high enough to saturate photosynthetic system of Tanganyika phytoplankton; the mean daily (24 h) light exposure of phytoplankton approximates 130 μE m^{-2} s^{-1} during wet season stratification (Hecky, 1991). Water temperature was held constant inside the incubator with a throughflow of lake water. The outflow water was slightly warmer (29–30 °C) than in the surface layers of the lake (27–27.5 °C).

Incubation was terminated by 1 ml of filtered 40% formaldehyde. After mixing, the 6 ml subsamples were pipetted into 20 ml plastic scintillation vials. One drop of orthophosphoric (H_3PO_4) acid was added into the vials to remove inorganic ^{14}DIC by exchange with air (Niemi et al., 1983). The samples were transported to Finland, where vials were still kept open for 2 d to ascertain that all traces of inorganic radiocarbon were removed from the samples. Then, 9 ml of Wallac HiSafe 3 Scintillation Fluor was added to the vials and mixed thoroughly. The radioactivity was measured with a Wallac 1409 Liquid Scintillation Counter.

Dissolved inorganic carbon (DIC) in water was determined in Finland from unpreserved samples with a carbon analyser (Salonen, 1981). High pH (ca. 9 at 0–40 m depth; Edmond et al., 1993) and alkalinity of Tanganyika water make the proportion of free CO_2 low, wherefore the rather long storage time does not markedly affect the concentration of DIC. The concentration was very similar in all experiments (mean 72.4 g m^{-3}; range 71.4–72.8 g m^{-3}). The final results of primary production were calculated from the measured radioactivity above background and DIC. The carbon fixation in light was not corrected for the dark CO_2 uptake simply because we had to omit dark vials due to the limited space of the on-board incubator. With few exceptions (30 April: control and PNC treatment; 2 May: PNC treatment), primary productivities in the duplicate vials were in full agreement.

Samples for the determination of inorganic P uptake were taken with a darkened 1 m long tube sampler (Limnos Ltd, Finland) and all further treatments were made inside the laboratory of the research vessel to avoid potential harmful effects of ultraviolet solar radiation. 5 μl of carrier free ^{33}P-phosphate (ca. 30 000 dpm) was introduced into each 10 ml water samples and then 1 ml portions of sample water were filtered on 0.2 μm Nuclepore filters after sequentially increasing time intervals. Between these samplings, the samples were kept in an incubator with a throughflow of water from the lake. Similar samples, but poisoned with 0.5 ml of 40% formaldehyde were used as a control. Two 1 ml subsamples were also taken to determine the total radioactivity used in the determination. The radioactivities of filters and total samples were measured in the field with a Hidex Triathler liquid scintillation counter. The turnover time of P was calculated as the reciprocal of the slope of the natural logarithmic decrease of the percentage of P remaining in filtrate. Soluble reactive phosphorus (SRP) was determined with an AKEA autoanalyzer according to Murphy & Riley (1962).

Results

In April–May 1995, the ratio of POC to chlorophyll *a* (C:Chl *a*) varied between 6.7 and 36 (μmol μg^{-1})

Table 1. Particulate C, N and P concentrations (μmol l^{-1}), and elemental composition ratios of C:N, N:P, C:P (μmol μmol^{-1}) and C:Chl *a* (μmol μg^{-1}) in Lake Tanganyika water. Indication of nutrient deficiency after Healey & Hendzel (1980): P – P deficiency; N – N deficiency; g – general nutrient deficiency; a single symbol – moderate deficiency; double symbols – severe deficiency

Sample	n		C	N	P	C:N	C:P	N:P	C:Chl *a*
December 1994									
0 – 100 m	9	Mean	9.6	0.8	0.06	16.3^{NN}	176 ^{P}	12	22.9 ^{gg}
		Median	10.0	0.8	0.06	10.6^{N}	145^{P}	13	14.2 ^{gg}
		Min	5.2	0.3	0.03	8.5 ^{N}	113	8	8.8 ^{gg}
		Max	15.5	1.7	0.14	57.5 ^{NN}	445^{PP}	15	100.6 ^{gg}
0 – 40 m	5	Mean	13.6	1.1	0.08	9.8^{N}	134 ^{P}	14	12.8 ^{gg}
		Median	10.8	1.1	0.08	9.6 ^{N}	125	14	14.2 ^{gg}
		Min	6.8	0.8	0.06	8.5 ^{N}	113	12	8.8 ^{gg}
		Max	15.5	1.7	0.14	11.3 ^{N}	168^{P}	15	16.3 ^{gg}
April-May 1995									
0 – 100 m	57	Mean	8.9	1.0	0.06	8.8^{N}	180^{P}	21	27.1 ^{gg}
		Median	7.4	1.1	0.05	8.6 ^{N}	167^{P}	19	13.6 ^{gg}
		Min	2.8	0.3	0.01	5.2	89	13	6.7 ^{g}
		Max	29.1	2.6	0.16	14.9 ^{NN}	396^{PP}	50^{PP}	143.3 ^{gg}
0 – 40 m	28	Mean	12.8	1.4	0.08	8.9^{N}	168 ^{P}	19	15.2 ^{gg}
		Median	12.5	1.3	0.08	8.8 ^{N}	153^{P}	17	12.3 ^{gg}
		Min	6.3	0.9	0.03	6.0	108	13	6.7^{g}
		Max	29.1	2.6	0.16	12.9^{N}	396^{PP}	41^{PP}	35.6^{gg}
March 1998									
0 – 100 m	156	Mean		0.6	0.04			17	
		Median		0.6	0.04			16	
		Min		0.1	0.01			5	
		Max		1.8	0.12			62^{PP}	
0 – 40 m	100	Mean		0.7	0.05			17	
		Median		0.7	0.04			16	
		Min		0.2	0.01			5	
		Max		1.8	0.12			36^{PP}	

at the depth of 0–50 m (Figure 2). At greater depths, the ratio often steeply increased due to very low concentrations of chlorophyll suggesting that in the uppermost 50 m water column algae contributed much more to the organic matter pool (Figure 2, Table 1).

In April–May 1995, the vertical distribution of the particulate C:N ratio showed a rather clear pattern (Figure 2). At the upper 30 m of the water column, the values were generally higher than the Redfield ratio. At the depth of 40–60 m, N was proportionally higher, but again in deeper water the C:N ratio started to increase. The vertical distribution of the particulate C:P ratio followed a similar course (Figure 2, Table 1). The vertical distribution of the particulate N:P ratio was even down to 60 m and indicated balanced availability of P and N. A comparison of the N:P ratios between the study years reveals, however, that in 1995 the mean N:P ratio (19.3, n=39) at 0–60 m depth was significantly higher (Student's t-test, p-value 0.003) than in 1998 (16.2, n=139) (see also Table 1). In 1995, the average atomic C:N:P ratio was 168:19:1 in the productive layer (0–40 m).

In the 2-d nutrient enrichment bioassays, primary production of phytoplankton varied between 10–72 mg C m^{-3} d^{-1} in different treatments. In all experiments, a combined addition of P, N and glucose

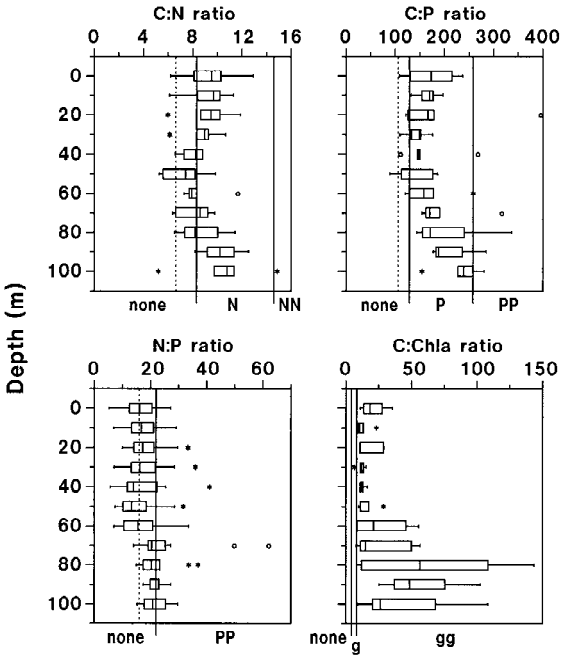

Figure 2. Box plot presentation of the particulate nutrient stoichiometry (μmol μmol^{-1}), and the POC: chlorophyll *a* ratios (μmol μg^{-1}) in Lake Tanganyika in April–May 1995. Indication of nutrient deficiency as in Table 1. n=5–6, except for the N:P ratio also including the results of the 1998 cruise (0–60 m: n=25–26, 70–100 m: n=10–13). Dotted line – the Redfield ratio (by atoms). Explanation of the box plot: Vertical line – median; Ends of the box split the remaining halves in half again forming a midrange box; Horizontal bars (whiskers) show the range of values which fall within 1.5 midrange width of the ends of the box; Values outside the horizontal bars are shown either as asterisks and empty circles according to their distance from the median.

Table 2. Concentrations of soluble reactive P (μmol l^{-1}) in some vertical samples in Lake Tanganyika in March–April 1998. Values of <0.01 μmol l^{-1} were below the detection limit of the molybdate method

Depth (m)	Soluble reactive P (μmol l^{-1})		
	Off Kigoma 25 March 1998	Off Kigoma 14 April 1998	Malagarazi estuary 15 April 1998
0	<0.01	<0.01[a]	<0.01
10	<0.01	<0.01	<0.01
20	<0.01	<0.01	0.56[a]
30	<0.01	<0.01	0.38[a]
40	<0.01	<0.01	<0.01[a]
50	<0.01	<0.01	0.78[a]
60	<0.01[a]	1.79	3.29[a]

[a] A mean of 2–4 replicate determinations.

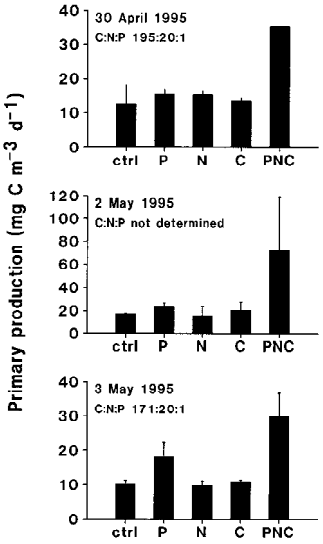

Figure 3. Responses of phytoplankton primary production (mean with the range of two replicates) to single (P, N or glucose; C) or combined (PNC) nutrient enrichments in Lake Tanganyika water (0–20 m). The results of 2 d incubations are shown as a daily rate. The particulate C:N:P ratios of the sample water were determined at the beginning of the experiment. ctrl – control.

(C) increased primary production (Figure 3). Single P enrichments also possibly slightly increased primary production, while single additions of N and C had little or no effect on primary production. The stimulation of primary production by the PNC treatment on 2 May was probably too high, since one of the PNC enriched vials showed exceptionally high primary productivity. In the other replicate, the increase in primary production after PNC enrichment was of the same order as in the other two bioassays. The particulate C:P and C:N ratios of the sample water at the beginning of the experiments on 30 April and 3 May suggested moderate co-limitation by P and N (Figure 3), while the particulate N:P ratios of 20:1 implied rather balanced P and N supply.

During the first two weeks of April 1998, the median turn-over time of P was 19 min (range, excluding one outlier value, 7–35 min, n=14) at the depth of 10–20 m in Lake Tanganyika. At the surface, the turn-over times were generally longer, probably due to inhibition by solar radiation, and thus do not yield realistic turnover times of P in the whole water column. At the same time, the concentration of SRP was mainly below detection in the uppermost 50 m of the water column (Table 2).

Discussion

The particulate elemental composition ratios observed in our study were within the range of reports from other deep African lakes with the closest resemblance to those from Lake Malawi (Hecky et al., 1993: 715, Table 6). Using the criteria of Healey & Hendzel (1980), particulate composition ratios usually suggested no severe single P or N limitation of plankton in epilimnetic waters of Lake Tanganyika (see Figure 2, Table 1). In contrast, the C:N:P ratios generally indicated simultaneous moderate P and N deficiency.

The growth rates of natural phytoplankton communities can be maximal under nutrient sufficiency, corresponding to chemical composition of phytoplankton close to the Redfield ratio (Goldman et al., 1979; see also Harris, 1986). The observed atomic C:P ratios of <200 and N:P ratios of <30 suggest high relative growth rates ($>0.8\ \mu_{max}$; Goldman et al., 1979) for Tanganyika phytoplankton, which is in line with earlier observations (Hecky, 1991). This would mean an algal community composed of species that can rapidly take up nutrients from a nutrient pulse and immediately utilize the nutrients for growth (cf. Kilham & Hecky, 1988). This could be a likely strategy in Lake Tanganyika with irregular mixing and upwelling patterns and where phytoplankton is most likely to rely on nutrients regenerated by zooplankton. In contrast, the observed C:Chl *a* ratios were more suggestive of low relative growth rates, in which case a severe nutrient limitation frequently occurs (Goldman, 1980).

Some caution is needed, however, when intepreting our particulate nutrient data from Lake Tanganyika. First, the storage of filters might have resulted in losses in chlorophyll concentrations (cf. Riemann et al., 1993), and consequently higher values of the C:Chl *a* ratio. By assuming a constant chlorophyll *a*: *in vivo* fluorescence ratio, a comparison of the 1995 and 1998 data (in 1998 the filters were stored at –20 °C) suggests a possible loss of 17–20% of chlorophyll in the desiccator-dried filters stored at 2–6 °C. However, even if the chlorophyll results were corrected for the possible loss, the C:Chl *a* ratios would still indicate severe general nutrient limitation (data not shown). In any case, due to very low concentrations of chlorophyll in Lake Tanganyika, one should be careful when interpreting the results of the C:Chl *a* ratios. Second, there is a possibility that detrital material and heterotrophic plankton accounted for the values of particulate nutrients. Since most of the organic carbon originates from the pelagic ecosystem of the lake (Hecky, 1991), the role of allochthonous detritus is probably slight in the pelagial of Lake Tanganyika (Hecky et al., 1993). Conversely, autochthonous detritus may be of some importance to the particulate nutrient pool. Considering the heterotrophic community, the larger zooplankton, which usually locate at the depth of >40 m during day (= sampling) time (Vuorinen et al., 1995), should not hamper the results of the particulate nutrients at least at the upper parts of the epilimnion. On the other hand, protozoans are a prominent feature of the Tanganyika plankton and their biomass is often comparable to that of phytoplankton (Hecky, 1991). Particularly, *Strombidium* species, with zoochlorellae present in their cell, can be abundant during April–May, despite their biomass maxima occur in October–November (Hecky, 1991). This suggests that the particulate nutrient data (and chlorophyll data due to zoochlorellae) is affected at least to some extent by heterotrophs. In April–May 1995 data, 75% of the variance in POC is explained on the basis of a linear relationship with the chlorophyll (adjusted r^2=0.754, p-value=0.000, n=57), suggesting that a large proportion of the organic C in the particulate material was in autotrophs (including protozoans with autotrophic symbionts).

In our study, the results of the nutrient enrichment bioassays were mostly parallel with the results of the particulate composition ratios and mainly suggested co-limitation of N and P in April–May 1995 in the upper epilimnion (0–20 m) of Lake Tanganyika. Notwithstanding, the slight stimulation of primary production by single P enrichments indicated that P most potentially might limit primary production. Thus, the results of the bioassays did not confirm the literature suggestions, based primarily on the inorganic nutrient stoichiometry of water, that N most likely limits phytoplankton in Lake Tanganyika (cf. Hecky et al., 1991; Edmond et al., 1993). The rapid turn-over of P in the productive layer of Lake Tanganyika and undetectable concentrations of SRP also suggest that P may be the limiting nutrient at least at certain times of the year. However, this does not necessarily indicate that only P was limiting.

The nutrient enrichment bioassays were carried out in a small volume of water without the removal of large zooplankton, which might affect the outcome of the experiments (e.g. Gerhart & Likens, 1975; Elser & Kimmel, 1986). However, as already earlier mentioned, the sample water for the experiments was collected during daylight hours from the uppermost

20 m of the lake, which is at that time of the day mostly devoid of zooplankton due to their avoidance of fish predation (Vuorinen et al., 1995). In any case, the sample water inside the vials was isolated from fluctuations normally occurring in the pelagial, which probably enhanced potential nutrient limitation of phytoplankton during 2 d incubations (e.g. Elser & Kimmel, 1986). For instance, the cellular stores of nutrients (mainly P) may run empty (Harris, 1986). Further, it is likely that a competition existed between algae and bacteria for the uptake of regenerated P during incubations. This might even explain the observed moderate algal P limitation in the bioassays, since bacterioplankton are considered superior competitors for P (e.g. Currie & Kalff, 1984) and may also be sinks of P (Vadstein et al., 1993). The latter might be particularly true in our long incubations in light, which might have accumulated excreted organic C from phytoplankton under the depletion of nutrients. Additions of nutrients in the bioassays were several-fold higher than reported values from the epilimnion of Lake Tanganyika (PO_4-P: 0.05–0.16 μM; dissolved inorganic N: not detectable–0.31 μM; Edmond et al., 1993). These relatively high additions of nutrients alone might, at least partly, have forced the observed co-limitation by P and N in the PNC enriched water (cf. Schelske et al., 1986).

To conclude, our data suggest that in Lake Tanganyika phytoplankton development closely traces the abundance of available nutrients, which may lead to approximately similar, moderate to severe, nutrient limitation probably throughout the year. This may result from strong irradiance and heavy predation pressure on algal grazers by fish. Thus, in planktivore-dominated Lake Tanganyika, zooplankton are probably not able to control phytoplankton, and therefore, resource competition may be common among the latter. The results of particulate composition ratios and enrichment bioassays both seem to confirm that in Lake Tanganyika phytoplankton are confronted with an approximately balanced, but restricted nutrient supply, as earlier suggested by Edmond et al. (1993) and Hecky et al. (1993). As a result, phytoplankton production is likely to track closely various mixing events bringing hypolimnetic nutrients to the euphotic zone.

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