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ORIGINAL PAPER

Seasonal variation in primary production of a large high altitude tropical lake (Lake Tana, Ethiopia): effects of nutrient availability and water transparency

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Abstract Primary production rates, chlorophyll and phytoplankton biovolume were measured monthly from April 2003 to November 2004 in Lake Tana, a large tropical lake in the highlands of Ethiopia. The lake is characterised by low nutrient concentrations, and a low water transparency due to high silt load of the inflowing rivers during the rainy seasons (May–November) and daily resuspension of sediments in the inshore zone. The mean chlorophyll-*a* concentrations varied seasonally and ranged from 2.6 mg m^{-3} to 8.5 mg m^{-3} (mean: 4.5 mg m^{-3}) in the offshore zone. Primary production was measured using the light–dark bottles technique. We incubated only at three depths, i.e. 0.6, 1.2 and 1.8 m. Therefore, we may have missed a substantial part of the depth production profile and probably also frequently missed P_{max}. Gross primary production in the openwater averaged 2.43 g O_2 m^{-2} d^{-1} and ranged between 0.03 g O_2 m^{-2} d^{-1} and 10.2 g O_2 m^{-2} d^{-1}; production was significantly higher in the inshore zone. The highest production rates were observed in the post-rainy season (Oct–Nov), which coincided with a bloom of *Microcystis* and higher chlorophyll levels. This seasonal high production is probably caused by a relatively high nutrient availability in combination with favourable light conditions. The gross primary production rates of L. Tana are among the lowest compared with other tropical lakes. This will be partly the result of our underestimation of gross primary production by often missing P_{max}. Another cause is the oligotrophic nature of the lake in combination with its relatively low water transparency. The gross primary production per unit chlorophyll in the openwater zone was in the same range as in 30 other tropical lakes and reservoirs. The higher primary production in the inshore zone is probably the result of the daily water column mixing ($Z_{mix} \geq Z_t$) in this area, enhancing nutrient recycling. A large proportion of the annual primary production is realised in one of the four seasons only. This productive post-rainy season is relatively short (2 months) and therefore efficiency of transfer of matter between the first and second trophic level of the Lake ecosystem will be poor.

Keywords Silt load · Mixing depth · Euphotic depth · Chlorophyll-*a* · Tropical limnology · Africa

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Introduction

Lake Tana (altitude 1,830 m), Ethiopia, has emerged as one of the global top 250 lake regions most important for biological diversity (Lake Net 1999). It is located in northeastern Africa, and is with a surface area of 3,200 km^2 and a catchment's area of 16,500 km^2 the largest lake in Ethiopia. In this Lake 15 large barb species (*Labeobarbus*) compose a world unique concentration of endemic cyprinid fish (Nagelkerke et al. 1994; Nagelkerke and Sibbing 2000). The fish community contains furthermore three endemic diploid species of small barbs (*Barbus* spp.) (Dejen et al. 2002) and at least two endemic *Garra* species (Getahun 2000). This speciation was possible because the Lake has been isolated for at least 10,000 years from the lower Blue Nile basin by 40 m high falls, 30 km downstream from the Blue Nile outflow (de Graaf et al. 2000a, b; Nagelkerke and Sibbing 2000). Recently, a dramatic decline of the endemic labeobarb stocks by overfishing (Nagelkerke et al. 1995; de Graaf et al. 2004) raised the question about the carrying capacity of the lake. Although the fish and zooplankton communities of Lake Tana have been intensively studied during the last 20 years, the phytoplankton composition and its primary production was never studied before (de Graaf 2003; Dejen et al. 2004).

The study of primary production in lakes is fundamental to understanding both water quality and fisheries. Primary production is the basic food source for the zooplankton, which themselves are important food items for the fish community.

In this study, we measured the primary production of Lake Tana and related it to selected environmental parameters such as nitrate, phosphate, silicate, water temperature, underwater light conditions and mixing depth. We addressed four questions: (a) What is the gross annual primary productivity in the lake and are there differences in production rates between inshore and openwater zones? (b) How does the annual primary productivity in the openwater zone of Lake Tana compare with other tropical lakes? (c) Is the primary production per unit chlorophyll-*a* in the euphotic zone in the openwater of Lake Tana similar to that in other tropical lakes and reservoirs? (d) Is primary production mainly regulated by light conditions and mixing depth or also by nutrient availability?

Material and methods

Study area

Lake Tana basin lies between latitude 10°58′–12°47′ N and longitude 36°45′–38°14′ E. About 1,430 km^2 of land is seasonally flooded and forms an extensive wetland, e.g. the Fogera plain on the east side (Fig. 1: Site 4), Dembia plain in the north (Fig. 1: Site 5), and the Kunzila plain in the southwest (Fig. 1: Site 6) where the Gilgel Abbay river delta is located. This land is mainly used for agriculture and cattle grazing. The only extensive areas of dense forest (1,347 ha) is on the Zegie Peninsula (Fig. 1: Site 2) on the southwestern part of the lake.

Lake Tana is shallow (average depth 8 m; Z_{max} 14 m). It is well mixed and does not have any lengthy period with thermal stratification (Dejen et al. 2004)—all water masses stratify over short periods of time, however, not all have stable thermal stratification. The catchment area of the lake has a dendritic type of drainage network. Five major permanent rivers, the largest of which is the Gelgel Abbay (Small Blue Nile), feeds the lake. Montmorillonite rich clay soils dominate the northern and eastern shores where most inflowing rivers originate and flood the lake during the rainy season (Hurni 1996). Inflowing rivers carry a heavy silt load into the lake during the rainy season, and annual soil loss in the Lake Tana catchment area ranges from 31 to 50 tons per hectare. This has been increasing substantially during recent years (Teshale et al. 2001).

Recently, Lake Tana has been used for the generation of hydroelectric power, about 30 km downstream where the Blue Nile originates. The 78 Megawatts power plant now diverts a large proportion of the inflowing river water through its turbines.

The study was carried out from April 2003 to November 2004. The following parameters were measured at monthly intervals at six sampling sites: dissolved oxygen, water temperature, water transparency, nutrient concentrations and

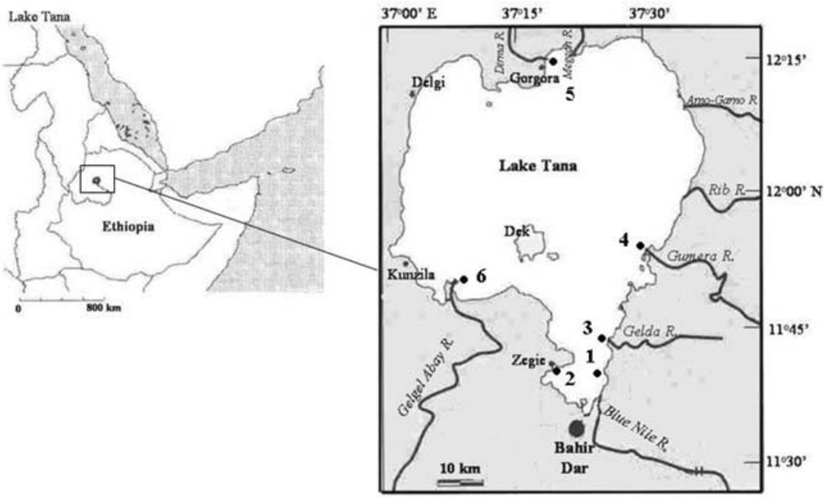

Fig. 1 Map of Lake Tana, showing its main contributories, sampling and incubation sites for primary production measurements. Sampling sites are: 1 = Gumietirs, 2 = Zegie, 3 = Gelda, 4 = Gumera, 5 = Dirma and 6 = Gelgel Abay. At each site there were two sampling stations one inshore and one in the offshore zone. Primary production was measured only in Gelda

chlorophyll-*a* (Fig. 1). At each sampling site two sampling stations were located, one in the inshore zone, ca. 250 m from the shore, depth <3.5 m, and one in the openwater, ca. 1,500 m from the shore, depth >4 m. Primary production was measured at one site only (Gelda, Site 3).

Climate

The climate of L. Tana is characterised roughly by four seasons: (1) A main-rainy season with heavy rains during July–September, (2) A dry season during December–April, (3) A pre-rainy season during May–June and (4) A post-rainy season during October–November (Fig. 2a, b).

Hydrology

The Bureau of Water Resources in Bahir Dar provided information about water level fluctuations and rainfall data was provided by the National Meteorological Service Agency collected from Gorgora, Dera Hamusit and Bahir Dar stations. Evaporation losses during October to June exceed input via rainfall (Molla and Menelik 2004). Water use for hydroelectric power generation is especially high during the dry season (Dec.–April). The complex pattern of water losses and inputs can cause large daily and seasonal water level fluctuations (Fig. 2b). The average retention time of the water in the lake, in the time before the electric power plant was in operation, was 6.1 years (Wudneh 1998).

Total annual rainfall at Bahir Dar was higher in 2003/2004 than in previous years (Fig 2a, b). During our study there was only one rainfall peak per year during July–August, which is usually the case (Fig. 2a, b). Generally, water levels were highest at the end of the main-rainy season and during the post-rainy period, slowly decreasing to a minimum around the end of the dry season (Fig. 2b).

Mixing of the water column

Wind speeds did not vary much during the year, where the mean monthly values based on one daily observations in the morning, ranged between 0.8 m s^{-1} and 1.4 m s^{-1} with highest wind speeds in June and lowest during Aug.–Dec. (data provided by the National Meteorological Service Agency in Bahir Dar: Fig. 2c). Predominantly southerly winds prevail from January to July, but northerly from August until November (Gasse 1987). The maximum fetch (Scheffer 1998) is 103 km, whereas the fetch in Gelda, the site where primary production was measured, varied between 5 km and 75 km depending on the wind direction. The lake is exposed to the winds since it is shallow and not protected by vegetation, except on the southwest side, which is forested (Zegie Peninsula: Site 2). Wind speeds show a pronounced diurnal pattern, during the night and morning wind speed is generally below 1.5 m s^{-1}, but in the afternoon starting at noon and going on until the evening (7 pm) wind speeds are gener-

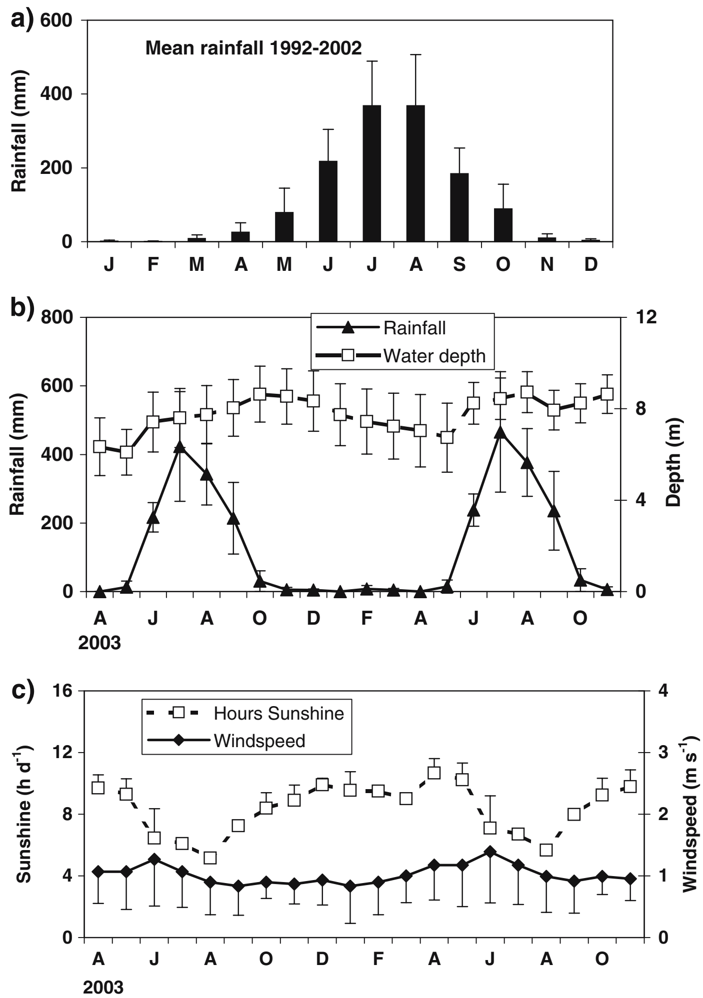

Fig. 2 Mean monthly rainfall (mm) and water depth (m) in Lake Tana: (**a**) average rainfall for the 10-year period 1992–2002, (**b**) monthly rainfall and water depth and (**c**) mean hours of daily sunshine per month and wind speed (m s^{-1}) from April 2003 to November 2004. Error bars represent 1 SD

ally between 3.0 m s^{-1} and 4.8 m s^{-1}. Using different scenarios of afternoons with wind speeds of 3.0, 4.0 and 4.8 m s^{-1}, respectively, and a fetch of 5 km and 75 km (see above) we calculated the maximum mixing depth per day using the mixing model of Scheffer (1998). The model calculations showed that the maximal mixing depth per day varied between 4 m and 21 m which invariably causes mixing of the whole water column in the shallow inshore zone (0–4 m) but not every day in the openwater (4–14 m). The model calculations also showed that the mixing depth in Gelda during night and morning generally varied between 0.7 m and 3.6 m, which will only cause total mixing in the shallowest parts of the inshore zone but rarely in the openwater region. Although a stable thermocline is lacking (Dejen et al. 2004), a thermal stratification of short duration (i.e. several hours) may occur especially during the dry season (this supports the comments made on thermal stratification in ''Study area'').

Environmental conditions

The physico-chemical parameters were measured between 09:30 and 13:30 at six sampling sites in the openwater zone of L. Tana (Fig. 1). All measurements and water samples were collected just below the surface at a depth of ca. 0.5 m. Water temperature was determined to the nearest 0.1°C using a mercury thermometer and the conductivity using a WTW LF 56 conductivity meter, which was calibrated for the temperature effect to 25°C according to Golterman et al. (1978). Dissolved oxygen was measured with YSI 58 portable oxygen-meter. Light penetration in the water column was determined with a standard Secchi-disk (25 cm in diameter). Major dissolved nutrients (nitrate, phosphate and silicate) were determined in GF/C (Whatman) filtered lake water samples in the field using a portable spectrophotometer (Hach kit, DR/2010). Nitrate was measured by cadmium reduction method using Nitraver 5 nitrate reagent powder pillow. Soluble reactive phosphate was measured by molybdenum blue ascorbic acid spectrophotometric method (Murphy and Riley 1962). Silica (SiO_2) was measured by heterotrophy blue method (Lind 1979). The depth of the euphotic zone (Z_{eu}) was assumed equivalent to the depth where 1% of the surface light level reaches, and was estimated by multiplying the Secchi-disk depth (Z_{sd}) by a factor 3 ($Z_{eu} = Z_{sd} \times 3$). This factor has been frequently employed for productivity estimates in African lakes (Talling and Lemoalle 1998; Wetzel 2001).

Phytoplankton

Phytoplankton was sampled at six sampling sites (Fig. 1) at monthly intervals. At each station samples were taken at 0.5, 1.5 and 2.5 m depth with a 3-l bottle sampler and pooled afterwards. Equal subsamples of samples collected at each station were pooled and fixed with Lugol's Iodine of which 100 ml was allowed to settle in a graduated cylinder overnight and the supernatant was siphoned till 10 ml remained. Of this concentrated sample 1 ml was used in a Sedgwick—Rafter cell of which 20 fields were counted. Because of the relatively short settling time of ca. 20 h (Nauwerck 1963), we probably underestimated the contribution of the small algal species in the community.

Phytoplankton biovolume was estimated for the different phytoplankton taxa usually at the genus level using Prescott (1962). Calculation of biovolume of taxa represented by single cells was made from mean cell diameters reported in literature (Prescott 1962) assuming that its form corresponded roughly to simple geometric solids, whereas filamentous and large colonial algae were measured individually.

Primary production and chlorophyll-*a*

The primary production was measured at Gelda (Site 3) (Fig. 1) at two stations, one inshore and one in the openwater. Light–dark bottles technique (Winkler's method) was used to measure oxygen production at different depths. Winkler bottles (300 ml) were suspended at three different depths (0.6, 1.2 and 1.8 m) for 3–4 h during middle of the day (10.30–2.30 h). Three replicate light and dark bottles were filled with water from corresponding depths using a 3-l Ruttner sampler. Dark bottles were wrapped in aluminium foil and kept in lightproof bags. A metal wire frame kept the bottles in vertical position 25 cm from one another to avoid self-shading. After 3–4 h incubation the bottles were hauled up and the contents fixed immediately with Winkler's reagents. Thereafter they were acidified and thoroughly mixed before titration in the laboratory, 3–4 h after collection.

Water samples for chlorophyll-*a* estimates were collected at six inshore and six openwater stations (Fig. 1). Samples were taken at three different depths at each station in the euphotic zone and pooled before filtration. For chlorophyll-*a* measurements, 250–1,000 ml of lake water were filtered through Whatman GF/C filters, and filters with phytoplankton were transported to the laboratory in a cool-box and stored in a freezer for not more than one day. As extraction solvent we used acetone; the absorbance of the centrifuged extract was then measured spectrophotometrically before and after acidification (ISO 1992).

Calculations of gross and net photosynthetic rates and respiration rates were based on the changes in the oxygen content in the light and dark bottles and the initial O_2 concentration (Vollenweider 1974): Gross photosynthetic rate = $(L - D)/3$ h = mg O_2 l^{-1} h^{-1}; net photosynthetic rate = $(L - I)/3$ h = mg O_2 l^{-1} h^{-1}; and respiration rate = $(I - D)/3$ h = mg O_2 l^{-1} h^{-1} (L = O_2 concentration in the light bottle after incubation for 3 h, D = O_2 concentration in the dark bottle after incubation for 3 h and I = initial

O_2 concentration). The gross photosynthetic rates and gross respiration rates were plotted as linear rate-depth diagrams. The areas were determined using planimetry and from the depth integral the areal, photosynthetic rates were expressed as g O_2 m^{-2} d^{-1}. The depth-integral of gross production per day (ΣGPP) was calculated over the euphotic zone (Z_{eu}), and the day length was taken at 10 h. The depth integral respiration per day (ΣR) was calculated for the entire water column for a 24 h period assuming that respiration rate per unit time at night was the same as during the day. Chlorophyll-*a* was used as a measure of algal biomass (*B*), biomass integrated over the euphotic zone (Σ*B*, mg Chl m^{-2}) was calculated using the measured chlorophyll-*a* concentration. The production per unit chlorophyll was calculated per unit area of euphotic zone (ΣGPP/Σ*B*, in mg O_2 per mg Chl-a^{-1} h^{-1}).

Data analyses

Spatial and temporal variations of chlorophyll-*a* and primary production were tested with the Kruskal–Wallis test, whereas the Mann–Whitney *U*-test was used for pair wise comparisons. For most data analyses the SPSS version 10.0 was used, but in a in a few cases analyses were carried out with Statistica.7 software (Statsoft).

Results

Environmental parameters

Mean dissolved oxygen concentration and temperature varied only within a narrow range. Conductivity was lowest in the main-rainy season and highest in dry and pre-rainy seasons (Table 1).

Water transparency measured as Secchi-disk depth varied from 5 cm to 80 cm in the inshore zone (mean: 35.4 cm) and from 10 cm to 100 cm in the openwater zone (mean: 43.3 cm) (Fig. 3). In both zones water transparency followed the same seasonal trend. The highest water transparencies were recorded in the dry season (mean 42.9 cm for inshore and 52.9 cm for openwater zone), the lowest in the main-rainy season (mean 27.0 cm for inshore and 30.9 cm for openwater). Differences in water transparency between dry season and main-rainy season were highly significant for both inshore and openwater zone (Mann–Whitney *U*-test: $P < 0.001$). Water transparency was significantly lower in the inshore zone than in the openwater (Mann–Whitney *U*-test: $P < 0.001$).

In the inshore zone, water transparency in the dry season was significant higher than in the pre-rainy season (Mann–Whitney *U*-test: $P < 0.05$) and post-rainy season (Mann–Whitney *U*-test: $P < 0.05$), whereas water transparency in the main-rainy season was significantly lower than in the pre-rainy season (Mann–Whitney *U*-test: $P < 0.01$) and post-rainy season (Mann–Whitney *U*-test: $P < 0.001$). In the openwater zone, transparency in the dry season did not differ from the pre-rainy season (Mann–Whitney *U*-test: $P = 0.61$), but was significantly higher compared with the post-rainy season (Mann–Whitney *U*-test: $P < 0.001$), whereas water transparency in the main-rainy season was significantly lower than in the pre-rainy season (Mann–Whitney *U*-test: $P < 0.001$) and post-rainy season (Mann–Whitney *U*-test: $P < 0.001$).

In the inshore zone, water transparency differed amongst stations during the dry season. At the two wind-exposed stations (Sites 1 and 5) transparencies were significantly lower (Mann–Whitney *U*-test: $P < 0.05$) than in two wind-protected stations (Sites 2 and 6) (for location of sites see Fig. 1). The transparency differences among stations are most probably due to differences in wind-induced resuspension of bottom sediments.

The concentrations of silicate (expressed as: SiO_2), soluble reactive phosphate (PO_4^{-3}) and nitrate (NO_3-N) showed pronounced seasonal variations, but the variation patterns differed (Fig. 4). Silicate concentrations were low in the dry season, but high during the rest of the year. Phosphate concentrations were very low during the first part of the dry season (Dec.–Feb.), whereas nitrate showed a maximum during the second part of the rainy season and the post-rainy season, and low concentrations during the rest of the year. The concentrations of both silicate and phosphate did not show any significant

Table 1 Environmental parameters of the openwater zone of Lake Tana from April 2003 to November 2004, means per season ±1 SD

	MRS	PORS	DS	PRS
N	16	8	12	4
Temperature (°C)	23.5 ± 1.8	23.4 ± 1.2	22.5 ± 1.4	22.5 ± 1.4
Dissolved oxygen (mg $l^{-1)}$	7.16 ± 0.7	6.38 ± 0.2	6.55 ± 0.8	6.98 ± 0.3
Conductivity (μ S cm^{-1})	142.19 ± 14.1	160.57 ± 4.3	181.83 ± 27.6	183.63 ± 29.8

Abbreviations used: MRS = main-rainy season (July–Sept.), PORS = post-rainy season (Oct.–Nov.), DS = dry season (Dec.–Apr.), PRS = pre-rainy season (May–June). All water samples and measurements were collected just below the surface at a depth of ca. 0.5 m

relationship with chlorophyll-*a* concentrations or primary production rates. A positive relationship was found between nitrate and gross primary production ($r^2 = 0.50$, $P < 0.001$, $N = 20$) and between nitrate and chlorophyll-*a* ($r^2 = 0.33$, $P < 0.01$, $N = 20$).

Phytoplankton

The phytoplankton was dominated by Cyanobacteria and Bacillariopyceae, Chloropyta were subdominant (Fig. 5). Cyanobacteria were dominant in de post-rainy season (October–November), whereas diatoms were dominant during the dry (December–April) and the pre-rainy season (May–June). Cyanobacteria were dominated by two *Microcystis* species of which *M. flosaqua* was the most abundant. Diatoms were dominated by six species of *Aulacoseira* (formerly named *Melosira*): *A. assizi, A. ambigua, A. granulata, A. muzzanensis, A. varians* and *A. distans*, of which *A. granulata* was the most dominant (>50% of *Aulacoseira* spp. combined). *Staurastrum triangularis* dominated the Chlorophyta.

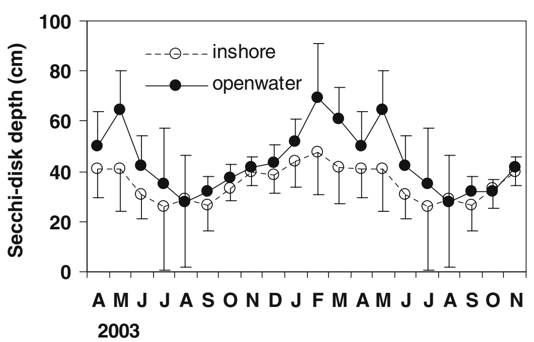

Fig. 3 Seasonal variations in water transparency in inshore and openwater stations of Lake Tana measured as Secchi-disk depth (cm) for the period April 2003–November 2004. Error bars represent +1 SD for openwater and –1 SD for inshore zone. Sampling at six sites, at each site two sampling stations were located, one in the inshore zone, ca. 250 m from the shore, depth <3.5 m, and one in the openwater, ca. 1,500 m from the shore, depth >4 m. Number of observations per sampling date per habitat: $N = 6$

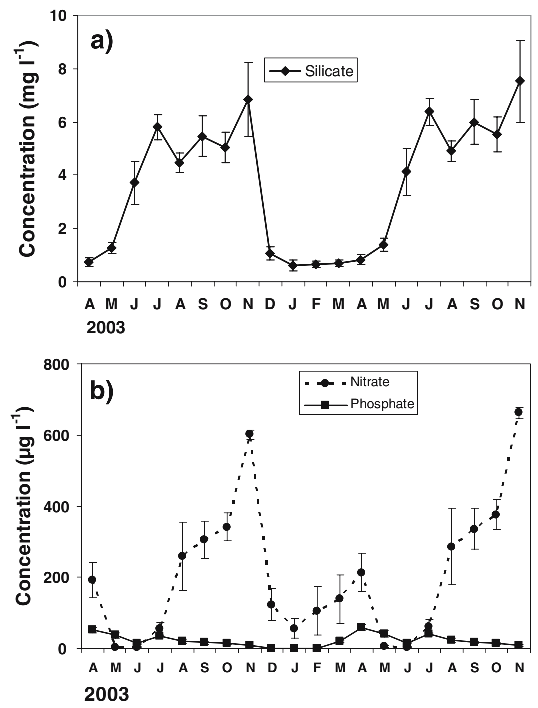

Fig. 4 Seasonal variation in the concentrations of (**a**) silicate (mg l^{-1}) and (**b**) soluble reactive phosphate (µg l^{-1}) and nitrate (µg l^{-1}) in the openwater of Lake Tana. Error bars represent ±1 SD and denote variation among sampling stations. Water samples were collected at monthly intervals just below the surface at a depth of ca. 0.5 m. Sampling at six sites in the openwater, ca. 1,500 m from the shore, depth >4 m. Number of observations per sampling date per habitat: $N = 6$. Note that in case of phosphate error bars are smaller than data points

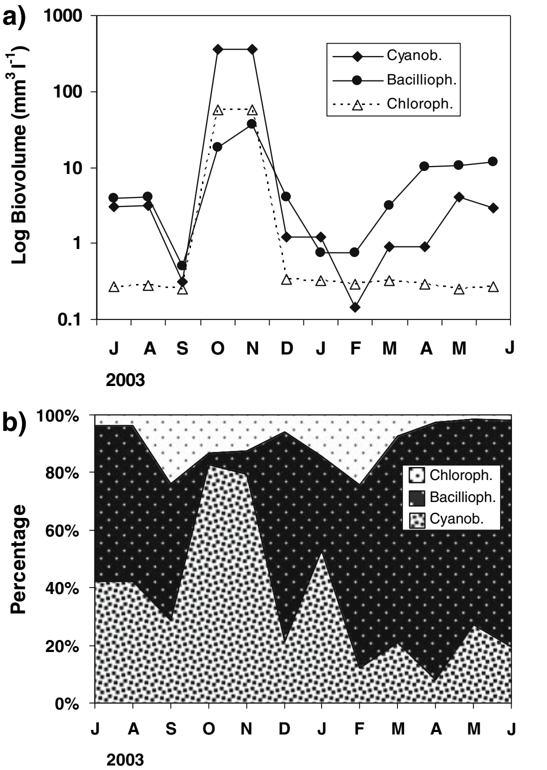

Fig. 5 Seasonal variation in the phytoplankton composition in the openwater of Lake Tana for the period July 2003–June 2004. Shown are: (**a**) the absolute biovolume ($mm^3\ l^{-1}$) and (**b**) the relative biovolume (%) of the main groups: Cyanobacteria, Bacillariophycea and Chlorophyta. Phytoplankton was sampled at six sampling sites at monthly intervals. At each station samples were taken at 0.5, 1.5 and 2.5 m depth with a bottle sampler and pooled afterwards

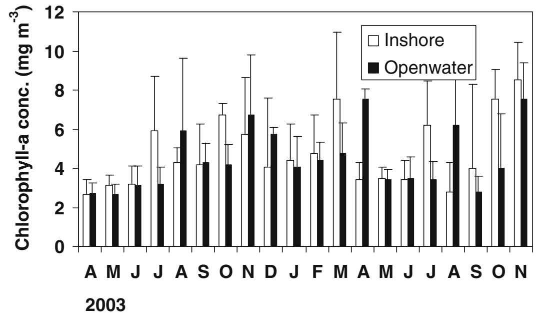

Fig. 6 Seasonal variation in chlorophyll-*a* concentration ($mg\ m^{-3}$) in inshore and openwater stations. Error bars represent 1 SD. All samples were collected at three different depths within the euphotic zone. Sampling at six sites, at each site two sampling stations were located, one in the inshore zone, ca. 250 m from the shore, depth <3.5 m, and one in the openwater, ca. 1,500 m from the shore, depth >4 m. Number of observations per sampling date per habitat: $N = 6$

Primary production and chlorophyll content

The mean chlorophyll-*a* concentrations per sampling date varied seasonally and ranged from 2.6 $mg\ m^{-3}$ to 8.5 $mg\ m^{-3}$ (mean: 4.8 $mg\ m^{-3}$) in the inshore zone and from 2.6 $mg\ m^{-3}$ to 7.6 $mg\ m^{-3}$ (mean: 4.5 $mg\ m^{-3}$) in the offshore zone (Fig. 6). The highest chlorophyll concentrations were observed in the post-rainy season. Chlorophyll-*a* concentrations were often higher in the inshore zone than in openwater zone. These differences between inshore and offshore stations were marginally significant (Mann–Whitney *U*-test, $P = 0.059$). In the openwater zone no relationship between the chlorophyll-*a* concentration and water transparency was observed ($r^2 = 0.019$, $P = 0.56$, $n = 20$), which implies that water transparency was only controlled by the concentration of suspended silt, rather than the phytoplankton.

Gross primary production rate varied seasonally between 0.03 and 12.0 g $O_2\ m^{-2}\ d^{-1}$. Net primary production was ca. 35% of gross primary production and followed the same seasonal pattern as that of the gross primary production (Table 2). Production profiles differed between seasons, probably as a result of the varying silt load. During the post-rainy season the relatively high silt load resulted in a lower water transparency and a sharp decrease of the production rate with depth (Figs. 3, 7b), whereas in the dry season production rate remained relatively high until intermediate depth (Fig. 7a). Respiration rate was independent of the photosynthetic rate. In the post-rainy season it was constant independent of depth, in the dry season it increased at a depth of ca. 2 m. The highest gross primary production was observed during the post-rainy season (Kruskal–Wallis test, $P < 0.001$). The primary production rates in dry, main-rainy and pre-rainy seasons were very similar (Fig. 8) and did not significantly differ from each other (Kruskal–Wallis test, $P > 0.05$). The highest primary production was recorded in both years during October and November, which coincided with a bloom of Cyanobacteria (Fig. 5). Gross primary production

Table 2 Summary of photosynthesis, algal chlorophyll-*a*, algal respiration and derived parameters for Lake Tana over the research period (April 2003–November 2004) for different seasons in the inshore zone (I) and in the openwater (O) (mean ± 1 SD)

	MRS		PORS		DS		PRS	
	I	O	I	O	I	O	I	O
N_d	8	8	4	4	6	6	4	4
Z_t	3.0 ± 0.3	8.0 ± 0.3	3.0 ± 0.5	8.0 ± 0.5	2.0 ± 0.7	6.0 ± 0.7	2.0 ± 0.3	6.0 ± 0.3
Z_{eu}	0.81 ± 0.3	0.95 ± 0.3	1.0 ± 0.5	1.14 ± 0.5	1.27 ± 0.7	1.63 ± 0.7	1.08 ± 0.3	1.60 ± 0.3
ΣB	4.42 ± 3.3	2.86 ± 2.4	7.32 ± 5.9	5.68 ± 3.5	8.53 ± 5.8	6.22 ± 4.6	7.93 ± 1.6	5.95 ± 1.6
ΣGPP	1.95 ± 0.5	1.7 ± 0.6	7.91 ± 4.7	7. 35 ± 3.0	5.36 ± 3.8	2.27 ± 3.6	4.70 ± 0.5	1.9 ± 0.1
ΣNPP	0.27 ± 0.4	0.53 ± 0.5	5.13 ± 3.4	4.2 ± 1.6	3.45 ± 2.6	1.4 ± 1.9	2.68 ± 0.6	1.45 ± 0.3
ΣR	1.52 ± 0.5	1.00 ± 2.0	4.51 ± 5.8	5.96 ± 2.6	3.83 ± 6.4	1.05 ± 2.6	1.18 ± 0.2	1.3 ± 0.8
$\%R/\Sigma$GPP	78.0 ±	58.8 ±	57.0 ± 4.2	81.1 ±	71.5 ±	46.3 ±	25.1 ±	68.4 ±
P_{max}	0.12 ± 0.1	0.05 ± 0.04	1.98 ± 0.9	0.94 ± 0.7	0.34 ± 0.4	0.07 ± 0.03	0.2 ± 0.05	0.12 ± 0.02
ΣGPP/ΣB	44.1 ± 9.6	59.4 ± 8.5	108.0 ± 16.6	129.4 ± 10.2	62.8 ± 22.4	36.5 ± 4.3	59.3 ± 8.0	31.9 ± 0.9

Abbreviations used: DS = dry season (Dec.–Apr.), MRS = main-rainy season (July–Sept.), PRS = pre-rainy season (May–June), PORS = post-rainy season (Oct.–Nov.), N_d = number of sampling dates per season, Z_t = total depth (m), Z_{eu} = euphotic depth (m), ΣB = depth integrated chlorophyll-*a* content over Z_{eu} (mg Chl m^{-2}), ΣR = depth integrated respiration over Z_t for 24 h (g O_2 m^{-2} d^{-1}), ΣGPP = depth integrated gross primary production over Z_{eu} for 10 h (g O_2 m^{-2} d^{-1}), % R = depth integrated respiration as percentage of total GPP, ΣNPP = depth integrated net primary production (g O_2 m^{-2} d^{-1}), P_{max} = photosynthetic rate at optimum depth (mg O_2 m^{-3} h^{-1}), ΣGPP/ΣB = production per unit chlorophyll over Z_{eu} per unit area (mg O_2 mg Chl^{-1} h^{-1})

in inshore and offshore zone was not correlated with temperature (inshore zone: $r^2 = 0.046$, $P = 0.36$, $n = 20$; offshore zone: $r^2 = 0.004$, $P = 0.78$, $n = 20$). The gross primary production in the inshore stations was significantly (Mann–Whitney *U*-test, $P < 0.001$) higher than in the openwater stations (Table 2). The inshore zone showed a significantly higher gross primary production per unit of chlorophyll over the euphhotic zone than the offshore zone (Mann–Whitney *U*-test, $P < 0.01$) (Table 2).

Community respiration as a percentage of gross primary production showed seasonal variation (Kruskal–Wallis test, $P < 0.05$). It was relatively high during the main-rainy season and the dry season (Mann–Whitney *U*-test, $P < 0.01$), but did not differ between inshore and offshore zones (Mann–Whitney *U*-test, $P = 0.48$) (Table 2). The measured euphotic depths (Z_{eu}) were generally shallow and in the inshore zone approximately only one-quarter of the maximum water depths. This depth was generally deeper during dry season and shallowest during the main-rainy season. The photosynthetic rate at optimum depth (P_{max}) was significantly higher in the inshore stations than in the openwater (Mann–Whitney *U*-test, $P < 0.01$) (Table 2).

We calculated the chlorophyll specific GPP over the euphotic zone in the openwater zone for 20 sampling dates. Specific production rates generally varied between 0.18 and 1.13 g O_2 mg chl^{-1} d^{-1} (average 0.61 g O_2 mg chl^{-1} d^{-1}); we did not observe any seasonal trends. There was a strong linear relationship between the depth-integrated GPP and the chlorophyll-*a* content in the euphotic zone ($r^2 = 0.77$, regression coefficient = 0.39, $P < 0.001$, $n = 20$).

Discussion

We incubated only at three depths, i.e. 0.6, 1.2 and 1.8 m, excluding the surface sample. Therefore, we may have missed a substantial part of the depth production profile and probably also frequently missed P_{max}, which can be clearly seen in Fig. 7b (GPP in post-rainy season). This probably lead to underestimation of the primary production, especially in the main-rainy season where $Z_{eu} < 1$ m. The problem of such measurements was clearly shown by Grobbelaar (1985). If we missed P_{max} in our measurements, we would substantially underestimate productivity and also finding relationships with other factors would be seriously impaired.

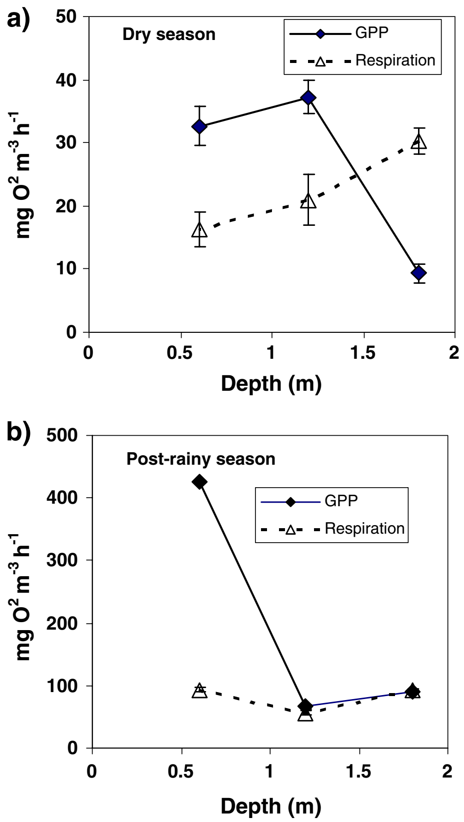

Fig. 7 Two examples of gross primary production (GPP, mg O^2 m^{-3} h^{-1}) and respiration (R, mg O^2 m^{-3} h^{-1}) profiles for the openwater of Lake Tana in two contrasting seasons: (**a**) 15 December 2003 (dry season) and (**b**) 15 October 2004 (post-rainy season). Note that error bars may be smaller than data points

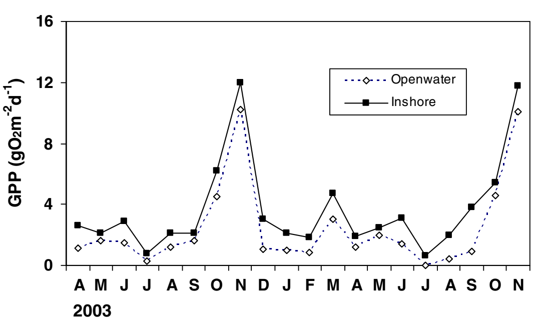

Fig. 8 Seasonal variation in the depth integral of gross primary production per day (g O^2 m^{-2} d^{-1}) in inshore and openwater stations

LakeTana exhibits only small seasonal variations in temperature and dissolved oxygen. For a tropical lake, water temperatures were relatively low (range: 20.9–27.7, mean = 23.1°C). Since gross primary production was not affected by temperature it is unlikely that these relatively low temperatures limited primary production. The lake is characterised by its low nutrient concentrations and low water transparency due to high silt loads of the inflowing rivers and daily resuspension of sediments in the inshore zone.

In turbid lakes the conditions for population growth and biomass accumulation of phytoplankton are very delicately balanced by light condition versus nutrient supply. The two main reasons for the lower productivities in turbid waters are the absorption of nutrients on the suspended clay particles (Grobbelaar 1983), rendering them less available, and the reduction in the depth of the euphotic zone. Secchi-disk depth was higher in 2004 than in 2003 because of greater dilution of the lake water due to higher precipitation. Low Secchi-disk depths were recorded during the main-rainy season because of high silt loads from the inflowing rivers together with higher wind speeds during rainy periods. No stable thermal stratification was measured. Our model calculations showed that wind induced mixing during ca. 7 h per day, resulted in the complete mixing of the water column ($Z_m \geq Z_t$), especially in the afternoons. Mixing was more pronounced in the inshore zone but occurred only occasionally in the openwater. Therefore, the significantly lower water transparency in the inshore stations is most likely due to wind-induced resuspension of shallow bottom sediments.

We observed the annual peak in primary production during the post-rainy season (October–November) following the main-rainy period. Rain-induced increases in primary production rates have been observed also in other African lakes (Lemoalle 1975; Melack 1979; Thomas et al. 2000). Probably, the availability of nutrients increased because the inflowing rivers carried fertilisers from the surrounding agricultural lands into the lake. Increased water inflows started in the pre-rainy season, but were highest in the main-rainy season. In the main-rainy season primary production was probably limited by reduced duration and intensity of sunlight and high concentrations of silt reducing water transparency. But, during the post-rainy season light conditions were much better and nutrient availability was still relatively high, leading to the highest seasonal production rates of the year. These conditions favoured *Microcystis.* Through its buoyancy this taxon has an advantage over other algae, resulting in relatively high algal densities and no doubt contributed substantially to the relative high primary production in this season. The high production in the post-rainy season was probably further enhanced by the wind induced turbulence in the afternoon, which is enhancing nutrient recycling by stirring and resuspension of sediments. The conclusion that an increased availability of nutrients are primarily responsible for the high primary production in the post-rainy season is not corroborated by Grobbelaar (1992), who concluded that that the ratio of euphotic to mixing depth was the most important factor affecting overall productivity and that nutrients are of secondary importance.

The gross primary production over the euphotic zone was substantial higher in the inshore zone than in the openwater. This is probably the result of the higher nutrient availability in the inshore as compared to the openwater zone. The lower average light intensity to which the phytoplankton individuals in the openwater zone are exposed may also have contributed to the reduced production rates in this area (see below).

When productivity of turbid systems is considered dark adaptation caused by significantly lower water transparencies may affect primary production (Grobbelaar 1984). Although we did not observe an increase of the integral gross production per unit of cholorophyll with decreasing water transparency over time as observed by Grobbelaar (1992) for a mesotrophic and eutrophic reservoir in South Africa. Since we probably underestimated GPP by frequently missing a substantial part of the production profile (see above in ‘‘Discussion’’) dark adaptation cannot be ruled out. In Lake Tana, the lowest water transparencies and shallowest euphotic zone was observed in the main-rainy seasons, whereas the highest mean integral gross production per unit of cholorophyll was observed in the post-rainy season (but see previous discussion on underestimating GPP in the main-rainy season). To find out if there were indications for dark adaptation we compared the mean gross primary production per unit of chlorophyll in the openwater zone of L. Tana with the chlorophyll specific GPP in the pelagic zone of other tropical lakes and reservoirs (Fig. 9). The data represents 25 tropical African lakes and reservoirs as reviewed by Lemoalle (1981), as well as for five other tropical lakes and reservoirs (Amarasinghe and Vijverberg 2002). The average chlorophyll-specific gross primary production over the euphotic zone in Lake Tana (0.61 g O_2 mg chl^{-1} d^{-1}) lies in the same range as in 30 other tropical lakes and reservoirs, and suggests that dark adaptation does not play a role in the large openwater zone of L. Tana. The average gross primary production in Lake Tana (mean: 2.9 g O_2 m^{-2} d^{-1}), however, belongs to the three lowest values reported (mean 10.0, range: 2.6–23.0 g O_2 m^{-2} d^{-1}). However, we probably underestimated the primary production of L. Tana by using only three depths in such a turbid lake and, therefore, probably often missed P_{max}. Consequently, gross primary production was probably underestimated and dark adaptation cannot be ruled out.

The ratio between depth of the euphotic zone (Z_{eu}) and the mixing depth (Z_{mix}) is a strong driving force for phytoplankton productivity under turbid conditions (Lewis 1987; Grobbelaar 1992). In Lake Tana, Z_{eu} usually varied between

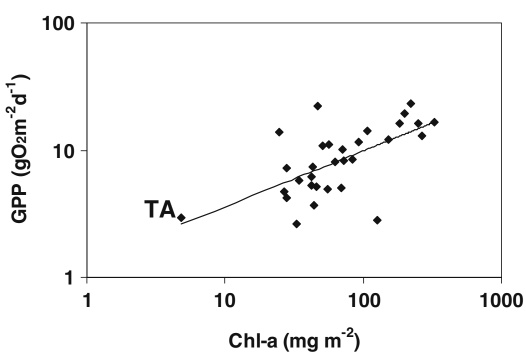

Fig. 9 The mean gross primary production per unit of chlorophyll in Lake Tana (TA, this study) compared with the linear relationship between log chlorophyll-*a* concentration (mg m^{-2}) and the log depth integral of gross daily primary productivity (g O^2 m^{-2} d^{-1}) over the euphotic zone for 27 African tropical lakes, two southeast Asian reservoirs and one tropical lake in South America (r^2 = 0.33, n = 30, P < 0.001)

0.9 m and 1.8 m and, therefore, Z_{mix} generally exceeded Z_{eu} during the whole day. However, in deeper turbid waterbodies the aphotic zone is relatively large compared to the euphotic depth and the ratio of euphotic depth (Z_{eu}) to mixing depth (Z_{mix}) determines the relative time spent in the dark by the phytoplankton. A deep mixing relative to the euphotic depth reduces primary production in two different ways. Firstly, the average light intensity to which the phytoplankton individuals are exposed decreases, secondly since the phytoplankton individuals remain for longer time in the dark, respiration losses will increase. In the deeper openwater zone the limiting influence on primary production of mixing depth in relation to the euphotic depth will be more prominent. Under these conditions, the phytoplankton population are expected to consume more carbon for respiration. Contrary to expectations, we did not find that respiration rates were systematically higher in the openwater as compared with the inshore zone (Table 2). This may be the effect of the respiration of the microbes associated with the detritus and silt particles in the inshore zone, which may have caused overestimation of the phytoplankton respiration rates in this zone. On average respiration was equal to 62% of the oxygen produced by photosynthesis during daytime. This value is similar as found for most other tropical lakes (Amarasinghe and Vijverberg 2002).

Conclusions

The gross primary production rates of L. Tana are among the lowest compared with other tropical lakes. This will be partly the result of our underestimation of GPP by often missing P_{max}. Another cause is probably the oligotrophic nature of the lake in combination with its relatively low water transparency. The higher primary production in the inshore zone is probably the result of the daily deep-water column mixing, enhancing nutrient recycling. A large proportion of the annual primary production is realised in one of the four seasons only. This high production in the post-rainy season is probably caused by a relatively high nutrient availability in combination with favourable light conditions. This productive post-rainy season is relatively short (2 months) and therefore efficiency of transfer of matter between the first and second trophic level of the Lake ecosystem will be relatively poor.

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