Dynamics and limitations of phytoplankton biomass along a gradient in Mwanza Gulf, southern Lake Victoria (Tanzania)

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SUMMARY

1. We investigated how dynamics in phytoplankton biomass are driven through light and nutrient limitations in the Mwanza Gulf, Lake Victoria (Tanzania).

2. We measured light attenuation, chlorophyll *a* and water quality parameters along a phytoplankton biomass gradient in the Mwanza Gulf at six sampling stations in three different seasons from August 2009 to March 2011.

3. We found a higher rate of attenuation of photosynthetic available radiation than in other gulfs of Lake Victoria which could only partially be explained by phytoplankton biomass, measured as chlorophyll *a*. Suspended particulate detritus strongly affected light attenuation, particularly in shallow water.

4. In shallow water in the southern part of the Mwanza Gulf, nutrients were in excess and phytoplankton biomass was limited by light. In deeper water near the entrance of the gulf, light was not limiting when nitrogen probably was, as indicated by the N:P ratio.

5. Low abundance of N-fixing phytoplankton species suggests that N-fixation was low in shallow water. Phytoplankton biomass was lower in Mwanza Gulf than in northern gulfs of Lake Victoria, but might increase in the future as a result of nutrient enrichment caused by an increase in intensive agriculture and rapid growth of the city of Mwanza.

Keywords: eutrophication, lakes, physical environment, phytoplankton, primary production

Introduction

Lake Victoria has undergone major ecological changes since the 1960s. Its faunal composition changed with the introduction of Nile perch, *Lates niloticus* in the 1950s and 1960s, when the dominant endemic haplochromine cichlid fishes declined and hundreds of species went extinct (Witte *et al.*, 1992; Goudswaard, Witte & Katunzi, 2008). An important commercial fishery targeting Nile perch developed and peaked in 1990 with an estimated maximum total yield of 300 000 ton per year. Catches now fluctuate around 230 000 tons per year (Kolding *et al.*, 2008).

In addition to the Nile perch and its fishery, another major driver of change in Lake Victoria is eutrophication, which started gradually from the 1920s onwards and which was caused by an increasing human population around the lake and corresponding degradation of the shorelines (Hecky, 1993). As a result of the increasing nutrient load into the lake, phytoplankton biomass increased and the community shifted from dominance of diatoms to cyanobacteria (Hecky, 1993; Mugidde, 1993; Kling, Mugidde & Hecky, 2001; Verschuren *et al.*, 2002; Stager *et al.*, 2009; Sitoki *et al.*, 2010). The increased primary production fuelled the food web and increased lake productivity and fish catches (Kolding *et al.*, 2008;

Hecky *et al.*, 2010). However, despite ongoing nutrient load into the lake, phytoplankton biomass has not increased since the 1990s (Silsbe *et al.*, 2006; Sitoki *et al.*, 2010) and is now supposedly light-limited in Lake Victoria in both shallow and deep water (Mugidde, 1993; Silsbe *et al.*, 2006; Cózar *et al.*, 2012). In shallow parts of Lake Victoria, light becomes limited through self-shading when phytoplankton biomass is high and in deep water when the mixed depth is greater than the euphotic depth (Hecky, 1993; Guildford *et al.*, 2003; Mugidde *et al.*, 2003; Gikuma-Njuru & Hecky, 2005). Light limitation in shallow water may also be caused by resuspension of detritus and sediment and high concentrations of dissolved organic matter (Gikuma-Njuru & Hecky, 2005; Loiselle *et al.*, 2008). In inshore areas and bays, this organic matter originates mostly from allochthonous sources such as wastewater or run-off from cultivated shorelines whereas, in offshore areas, it originates mostly from decaying plankton (Machiwa, 2010).

When light conditions are good, nitrogen may become limiting in shallow parts of the lake (Guildford *et al.*, 2003), while in deep water nitrogen might become limited under anoxic conditions, stimulating denitrification, which usually occurs in stratified conditions during the rainy seasons (Guildford *et al.*, 2000; North *et al.*, 2008). In turn, nitrogen limitation favours nitrogen-fixing cyanobacteria (Guildford *et al.*, 2003), which now dominate the phytoplankton of Lake Victoria and are responsible for most of the nitrogen load into the lake (Kling *et al.*, 2001; Mugidde *et al.*, 2003). Phosphorus, on the other hand, has increased since the 1960s and is mostly in excess both in shallow and in deep parts of the lake (Hecky, 1993; Mugidde, 2001).

In contrast to the clear bottom-up effects of nutrient loading, no top-down regulation of phytoplankton biomass has been shown in *in situ* experiments, in which micro-crustacean grazing in shallow and deeper parts of lake Victoria apparently had little effect on chlorophyll *a* concentrations (Lehman & Branstrator, 1993). Moreover, the relative abundance of large-bodied grazers was very low and omnivorous cyclopoid copepods dominated the zooplankton of the Mwanza Gulf throughout the year (personal observations) and the rest of the lake (Mwebaza-Ndawula, 1994; Wanink *et al.*, 2002). Therefore, we assumed that limitation of phytoplankton growth by zooplankton is minimal and was not considered in this study.

Most studies on phytoplankton dynamics and limitations have been conducted in northern Lake Victoria, in eutrophic bays with high phytoplankton biomass (Mugidde, 2001; Gikuma-Njuru & Hecky, 2005; Silsbe *et al.*,

2006; Haande *et al.*, 2011). In general, the southern part of the lake has lower seasonal peaks in phytoplankton biomass, however, and they occur 2 months later than in the northern part, possibly because of a lake-wide convective circulation of water (Cózar *et al.*, 2012). It is unclear whether the phytoplankton dynamics in the north, and their drivers, are the same for the whole of Lake Victoria. Furthermore, phytoplankton dynamics have rarely been studied for southern Lake Victoria. The few studies conducted have focussed on large spatial scales between Gulfs or depth strata covering half the lake (Shayo, Lugomela & Machiwa, 2011; Ngupula *et al.*, 2012). Therefore, this study focussed on the dynamics of phytoplankton biomass and water quality on a small spatial scale in the Mwanza Gulf in southern Lake Victoria, covering a depth gradient from 3 m in inshore water in the south to 30 m in offshore water near the entrance of the Gulf. This depth gradient makes Mwanza Gulf an excellent area to study the spatial dynamics and limitations of phytoplankton biomass in detail.

To study the dynamics of phytoplankton biomass and growth limitation, we examined spatial and seasonal dynamics of water quality parameters, light attenuation and chlorophyll *a* concentrations in the Mwanza Gulf from shallow inshore to deep offshore water. We addressed the following questions: (i) How does phytoplankton biomass vary in time and space? and (ii) What are the factors driving this variability: is it light, nutrients or a combination of both?

Methods

Study area

Mwanza Gulf is located in the south of Lake Victoria (Tanzania) and is about 60 km long, 2.5–11 km wide and has a surface area of approximately 500 km^2 (Fig. 1; Witte & Van Densen, 1995). Its irregular shoreline is characterised by a vegetation of papyrus (*Cyperus papyrus*), reeds (e.g. *Phragmites australis*) and water hyacinth (*Eichhornia crassipes*), alternating with rock formations. The bottom consists of soft mud. The catchment area of the Mwanza Gulf is used mainly for agriculture (ranging from 62.9% in the north to 71.8% in the south). Bush land, formerly used for agriculture, covers around 20% of the catchment area. In the south 5.1% consists of natural habitats such as swamps and woodland, whereas this is only 0.7% in the north. Here, urban area covers 16.2% (Mwanza City; Fig. 1). Forests are absent around Mwanza Gulf (Vlieghe, 2000).
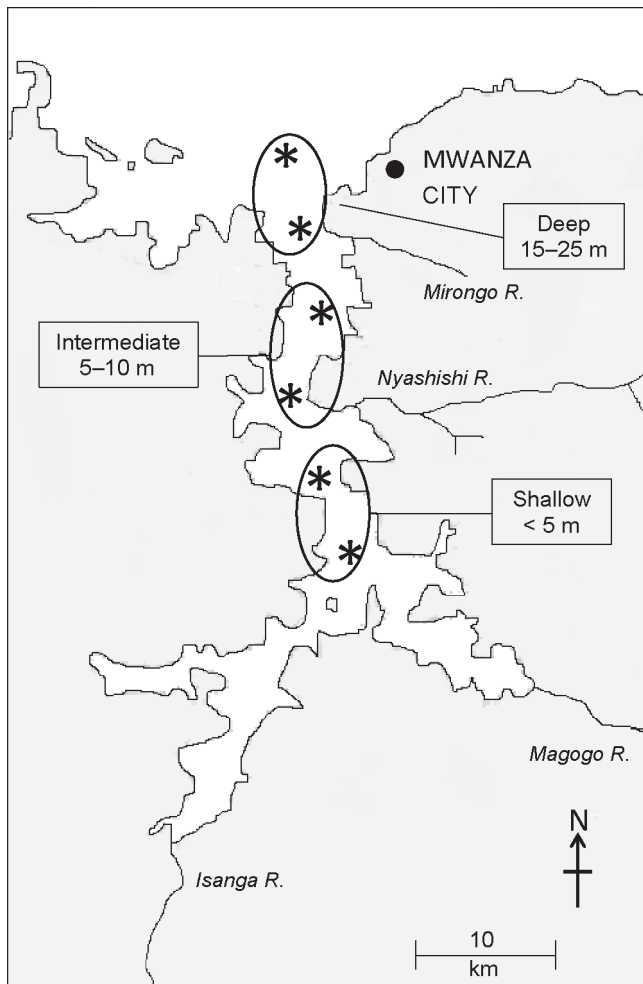
Fig. 1 Map of the Mwanza Gulf with six sampling stations (asterisks). Stations were divided in three areas to facilitate data analyses: (1) shallow = depth range of <5 m, (2) intermediate = depth range of 5–10 m and (3) deep = depth range of 15–25 m.

Whereas most of the water flowing into the Gulf comes from surface run-off, forming seasonal streams during the rainy season, there are also some permanent rivers (Fig. 1). The Isanga River in the south is the largest with a mean annual discharge of 29.8 m^3 s^{-1} and a catchment area of 6812 km^2. The Magogo River has a mean discharge of 8.9 m^3 s^{-1} and a catchment area of 5207 km^2 (Myanza *et al.*, 2005). These rivers collect waste water from fish processing plants and a brewery. Towards the north, the Nyashishi River with a mean annual discharge of 1.7 m^3 s^{-1} and a catchment area of 1565 km^2 flows into the gulf and in Mwanza city in the north, a small river (the Mirongo) collects waste water from the city and industrial plants before flowing into the lake. Compared to other gulfs in the lake, Mwanza Gulf has weak river input and is poorly flushed (Machiwa, 2010).

Climate

There are three seasons in Lake Victoria based on the yearly monsoon cycles. There is a dry season from June to August, when water temperature is low and strong southerly winds keep the water column well mixed, oxygenated and isothermal (Talling, 1966; Akiyama, Kajumulo & Olsen, 1977). In the short rains, from September to December, the water column gradually stratifies as the wind declines, rainfall increases and the surface layer of the water column warms up. During the long rains, from January to May, precipitation is high and stratification is strongest (Talling, 1966). However, both the onset and the timing of rainfall in the Lake Victoria basin are highly variable (Kizza *et al.*, 2009).

Mwanza Gulf had similar seasons during the sampling period from 2009 to 2011, although during the short and long rains, from September 2009 to May 2010, rainfall was twice as much as from September 2010 to May 2011.

Data collection

Data were collected from August 2009 until April 2011 at six sampling stations along a north-south gradient in three areas (Fig. 1). Data from the six stations were pooled for analyses into three areas: shallow (<5 m depth), intermediate (5–10 m depth) and deep water (10–25 m depth; Fig. 1). In 2009–2010, sampling at all stations was done once per season, starting in August 2009 during the dry season and ending in May 2010 during the long rains. In 2010–2011, sampling was done three times per season, starting in June 2010 during the dry season and ending in April 2011 during the long rains. At each station, three locations, separated ca. 500 m from each other, were sampled between 10:00 h and 14:00 h. To minimise direct littoral influences, sampling at each station was done at least 1.5 km from the shore. In May 2012, additional observations were carried out on dissolved organic matter fractions.

A hydrolab DS5 multiprobe (OTT Messtechnik GmbH & Co, Kempten, Germany) collected vertical profiles of temperature, conductivity and chlorophyll *a* from the bottom to the surface. A mounted spherical quantum sensor (LI-COR Biosciences, Lincoln, Nebraska, U.S.A.) measured photosynthetic active radiation. Water samples were taken on three occasions throughout the sampling period for calibration. Conductivity was calibrated by using standards with known conductivity and chlorophyll *a* by using extraction in 80% ethanol at 75 °C for 5 min (Moed & Hallegraef, 1978). Probe measurements

were in general 1.5- to 2-fold lower compared to the extracted chlorophyll *a* analyses. Chlorophyll *a* measurements with the probe were corrected with the extracted calibration analyses of chlorophyll *a*.

At each station, Secchi depth was measured in triplicate with a 25-cm-diameter black and white Secchi disc and was defined as the average depth at which the disc disappeared when lowering it in the water and reappeared when lifting it.

At each sampling station, water samples were taken every metre over the euphotic depth by using a Van Dorn water sampler. Samples were pooled for analyses of the following nutrients: total phosphorus (TP), total nitrogen (TN); particulate fractions: particulate organic carbon (POC) and particulate inorganic matter (PIM); and dissolved fractions: dissolved organic carbon (DOC), chromophoric dissolved organic matter (CDOM) and humic acid. Nutrients were analysed in the laboratory by a digestion and photometric method (Merck KGaA, Darmstadt, Germany). Water was filtered through a glass-fibre C filter (Whatman GmbH, Den Bosch, the Netherlands), and seston was used for analyses of POC and PIM. Particulate organic carbon was analysed with the standard loss on ignition method (American Public Health Association (APHA), 2005), whereby the organic fraction was calculated by the seston mass combusted for 1 h at 550 °C subtracted from the mass dried at 105° for 24 h and divided by 2.5 to get the carbon content. Particulate organic carbon contains carbon derived from mainly phytoplankton and detritus. Detritus was calculated by estimating the carbon content of chlorophyll by using a chlorophyll: dry mass ratio of 1 : 50 (Bailey-Watts, 1974) and a dry mass: carbon ratio of 2 : 1 (Winberg, 1971). This calculated C concentration was subtracted from POC to estimate the carbon concentrations of detritus. For estimating PIM, five unused filters were weighed after combustion at 550 °C for 1 h, and the average mass was subtracted from that of the filters with seston after combustion.

Water for DOC, CDOM and HA was filtered through 0.22 µm pore filter and the filtrate collected for analyses. Dissolved organic carbon was analysed by chemical oxygen demand (American Public Health Association; APHA, 2005). Chromophoric dissolved organic matter and HA were determined by measuring the absorbance at 272 and 465 nm and calibrated gravimetrically (Mazzuoli *et al.*, 2003).

Pooled water samples from the euphotic zone were preserved in glutaraldehyde and sent to the Netherlands Institute of Ecology for analyses with a phyto-PAM fluorometer (Walz, Germany) to differentiate between chlorophytes, diatoms and cyanobacteria. On 1 September 2010 and 4 April 2011, water samples from station 1, 3 and 6 were preserved with lugol, and after sedimentation, phytoplankton was generally classified to the genus or species and abundances estimated. Phytoplankton was counted as number of colonies, but the number of cells per colony was noted and all colonies were classified into size classes.

Estimating physical parameters

Water density was calculated using vertical profiles of temperature and conductivity (Chen & Millero, 1977). Thermal stability of the water column (N^2) was calculated according to the following equation (Langenberg, 2008):

$$N^2 = \frac{-g\Delta\rho}{\bar{\rho}\Delta z} \tag{1}$$

where N is the Brunt-Vaisälä buoyancy frequency, g is the gravitational acceleration (m s^{-2}), ($\Delta\rho/\Delta z$) is the density gradient over a depth interval and $\bar{\rho}$ is the mean density over the water column (kg L^{-1}).

Water temperature (T_{water}) was defined as the mean temperature over the whole water column. Mixed depth (Z_{mix}) was defined as the maximum change in temperature with depth over the water column. The euphotic depth (Z_{euph}) was defined as the depth at which 1% of the surface irradiance remains.

Analysis of spatial and seasonal dynamics

The spatial and seasonal effects on the dynamics of stratification, water quality and light-associated parameters and phytoplankton data were analysed by Kruskal–Wallis tests because normality could not be achieved directly or after log transformations. In case of significant spatial or seasonal effects, *post hoc* pairwise comparisons were performed with adjusted levels for multiple comparisons using a Bonferroni correction.

Analyses of light conditions

The attenuation of photosynthetically active radiation (PAR: 400–700 nm wave length) is caused by optically active components in the water column and expressed by the attenuation coefficient K_{PAR}. K_{PAR} was estimated as the slope of the linear regression of the natural logarithm of PAR on depth of each vertical profile. Regression correlation coefficients of <0.9 and regressions with <15 observations within a single vertical profile, were

excluded from further data analyses. In fresh water, light attenuating components consist mainly of phytoplankton biomass and background attenuation of other components such as coloured CDOM, inorganic sediments, suspended detritus and pure water (Morel, 1988):

$$K_{PAR} = (k_{Chl} \cdot Chl) + K_{bg} \qquad (2)$$

where k_{Chl} is the specific light attenuation coefficient for phytoplankton ($m^2\ mg^{-1}$) determined by the slope of linear regression of K_{PAR} (m^{-1}) on chlorophyll a concentration in the euphotic zone (Chl, in $mg\ m^{-3}$). K_{bg} is the background attenuation (m^{-1}), determined as the intercept with the K_{PAR} axis of the same linear regression. To analyse the relationship between chlorophyll concentrations and K_{PAR}, we performed regression analyses of K_{PAR} on Chl (with or without $\log_e$ transformation, depending on the normality of the residuals). The residuals from these regression analyses indicate background attenuation, as the influence of chlorophyll a is excluded. These residuals were used to determine the influence of suspended detritus on K_{PAR}, by correlating them with suspended detritus concentrations ($C_{detritus}$). As these residuals were not normally distributed, a nonparametric Spearman's rank correlation was used. Similarly, K_{PAR} and PIM were also correlated with a Spearman's rank correlation. Next, to test whether the relationship between K_{PAR} and chlorophyll a concentrations differed between areas, we also performed an analysis of covariance of K_{PAR}, with area as factor and Chl as covariate.

Solar irradiance was integrated over the mixed depth to determine the total integrated irradiance in the mixed layer by the following equation (Loiselle *et al.*, 2007):

$$Q_t = I_0/(k_{Chl} \cdot Chl + K_{bg}) \cdot (1 - e^{-(k_{Chl} \cdot Chl + K_{bg})Z_{mix}}) \qquad (3)$$

where Q_t is the total integrated irradiance in the mixed layer ($mol\ photon\ m^{-2}\ day^{-1}\ m$) and I_0 is the incident irradiance just below the water surface.

Estimating maximum phytoplankton biomass under light limitation

We used a light limitation approach based on the carrying capacity of phytoplankton biomass developed by Loiselle *et al.* (2007, 2008). This approach uses the calculated available irradiance (Q_t) and the chlorophyll a biomass per unit area ($mg\ m^{-2}$) to determine where light limitation occurs. Chlorophyll a biomass per unit area can be calculated when Chl concentration in $mg\ m^{-3}$ is multiplied with Z_{mix}. When Q_t is plotted against chlorophyll a biomass per unit area, a linear regression of 10 data points with highest chlorophyll a over the Q_t range
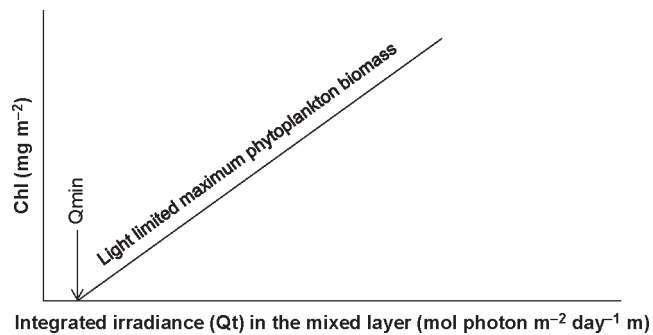
Fig. 2 The relationship between daily depth integrated light irradiance and phytoplankton biomass per unit area (mg Chl *a* m^{-2}) under light-limited conditions over the mixed layer. The line represents the maximum potential chlorophyll *a* concentrations when light is limited (upper limit), determined by regression of 10 sites with highest chlorophyll *a* concentrations. The intercept represents minimum light requirement (Q_{min}) for phytoplankton growth and the slope is the expected maximum phytoplankton biomass under light limitation.

defines the carrying capacity for phytoplankton biomass under light limitation in a steady state (Fig. 2). The minimum irradiance to allow phytoplankton biomass is the intercept with the Q_t axis, and the critical light requirement is the slope of the same linear regression. From this, we calculated the expected chlorophyll a biomass per unit area under light limitation:

$$W = Q_t - Q_{min}/\psi \qquad (4)$$

where W is the expected depth integrated chlorophyll a biomass per unit area ($mg\ m^{-2}$), Q_{min} is the minimal light requirement for allowing phytoplankton biomass ($mol\ photon\ m^{-2}\ day^{-1}\ m$) and ψ is the critical light requirement [$mol\ photon\ m^{-1}\ day^{-1}$ ($mg\ m^{-2}$ chlorophyll $a)^{-1}$].

By comparing the measured chlorophyll a ($mg\ m^{-2}$) with the expected light-limited maximum chlorophyll a (W), the relative degree of limitation by light and/or other factors was determined. Measured chlorophyll a located further from the expected W is probably limited by factors such as nutrients, so we calculated the distance between measured chlorophyll a and W. The latter (W) is calculated by using a combination of eqns 2, 3 and 4 for each measured chlorophyll a concentration. Note that the distance between measured chlorophyll a and W increases exponentially by using eqn 3, because phytoplankton biomass cannot increase linearly with light, as phytoplankton itself will have a negative feedback on irradiance when increasing in biomass (Loiselle *et al.*, 2007, 2008). The distance is then plotted against P, N and detritus concentrations, and correlations are tested with Pearson's or Spearman's rank, according to

normality of the data, to investigate the potential role of nutrients and detritus dynamics in determining phytoplankton biomass. With increasing distance, chlorophyll is less likely to be limited by light and must be limited by another factor. A negative correlation between distance and nutrients or detritus suggests that nutrients or detritus might become limited when light conditions are good. A positive or no correlation might indicate a limitation by other factors not measured in this study.

Results

Spatial and seasonal dynamics

Variables associated with stratification and water column stability, such as T_{water} and N^2, differed between seasons but not between areas (Table 1). Highest temperatures and stability occurred during the short rains (September–December; Table 1). Water column mixing was deepest during the dry season (June–August) and shallow during the short and long rains. This seasonal trend in mixing and temperature was observed in both shallow as well as deeper parts of the Gulf (Fig. 3).

Spatial and seasonal effects differed among water quality variables (Table 1). Total phosphorus concentration varied seasonally with a slightly higher concentration during the short rains (September–December) than the long rains (January–May). Total nitrogen concentration and TN : TP molar ratio showed a strong spatial pattern with decreasing values from shallow to deep water. TN also varied seasonally, with highest concentrations during the dry season and short rains and lowest during the long rains. From the particulate fractions, POC varied spatially with highest concentrations in shallow water and lowest concentrations in deep water and seasonally with highest concentrations

Table 1 Summary table of means with *post hoc* pairwise comparisons and results of the Kruskal–Wallis tests of effects of area (shallow, intermediate and deep water) and season (dry period, short and long rains) on physical conditions, light-associated parameters, nutrients and phytoplankton

	Area			Season			Area		Season	
	Shallow (<5 m)	Intermediate (5–10 m)	Deep (15–25 m)	Dry	Long rains	Short rains	H	P	H	P
Stratification										
T_{water} (°C)	24.75	24.98	24.94	23.92[a]	24.98[b]	25.74[b]	2.19	NS	131.10	<0.001
N^2 (10^{-3})	0.49	0.36	0.39	0.25[a]	0.42[ab]	0.56[b]	2.29	NS	18.92	<0.001
Z_{max} (m)	4.56[a]	8.54[b]	22.15[c]	12.01	11.70	11.53	188.99	<0.001	0.71	NS
Z_{mix} (m)	2.35[a]	3.93[b]	11.25[c]	6.85[b]	5.50[a]	5.18[a]	56.03	<0.001	19.76	<0.001
Water quality parameters (mg L^{-1})										
TN	1.42[c]	0.89[b]	0.48[a]	1.06[b]	0.80[a]	0.92[b]	105.32	<0.001	8.65	0.013
TP	0.08	0.08	0.07	–	0.07[a]	0.09[b]	2.23	NS	24.88	<0.001
TN : TP molar	45.92[c]	25.96[b]	11.81[a]	–	31.66	20.77	56.07	<0.001	1.21	NS
PIM	17.66	30.71	86.22	13.81[a]	79.95[b]	43.56[a]	4.44	NS	14.48	<0.001
POC	11.76[c]	8.03[b]	5.64[a]	7.17[a]	10.94[b]	7.32[a]	40.96	<0.001	12.78	0.002
DOC	1.03[b]	1.24[b]	0.32[a]	–	0.86	–	11.97	0.003	–	–
CDOM	1.91[b]	1.21[ab]	1.00[a]	–	1.37	–	9.22	0.010	–	–
HA	0.0023	0.0011	0.0012	–	0.0015	–	8.13	NS	–	–
Light-associated parameters										
Z_{euph} (m)	2.77[a]	3.52[b]	5.57[c]	4.83[c]	3.38[a]	3.62[b]	91.02	<0.001	28.62	<0.001
Secchi depth (m)	0.63[a]	1.08[b]	1.91[c]	1.42[c]	1.10[b]	1.07[a]	142.20	<0.001	17.17	<0.001
K_{PAR} (m^{-1})	2.52[a]	1.87[b]	1.04[c]	1.37[a]	2.05[c]	2.01[b]	82.70	<0.001	17.73	<0.001
Phytoplankton (µg L^{-1})										
Chlorophyll *a*	17.06[c]	15.32[b]	9.25[a]	13.24	14.96	13.45	85.46	<0.001	0.472	NS
Cyanobacteria	3.55[c]	3.21[b]	0.96[a]	1.48[a]	2.01[a]	4.18[b]	53.42	<0.001	31.81	<0.001
Chlorophytes	0.09	0.00	0.00	0.03	0.02	0.04	6.02	NS	0.004	NS
Diatoms	1.02[b]	1.17[b]	0.67[a]	0.76[a]	0.80[a]	1.29[b]	30.19	<0.001	39.66	<0.001

Significance levels were corrected according to Bonferroni with df = 2 except for seasonal effect on TP and TN : TP in which significance level was at $P < 0.05$ with df = 1. Mean values with different superscripts differ significantly.
H, test statistic Kruskal–Wallis; NS, not significant; P, significance level; T_{water}, water column temperature; N^2, buoyancy frequency; Z_{max}, maximum depth; Z_{mix}, mixed depth; Z_{euph}, euphotic depth; K_{PAR}, light attenuation coefficient; TN, total nitrogen; TP, total phosphorus; POC, particulate organic carbon; PIM, particulate inorganic matter; DOC, dissolved organic carbon; CDOM, chromophoric dissolved organic matter; HA, humic acid; DOC, CDOM and HA were sampled in May 2012.
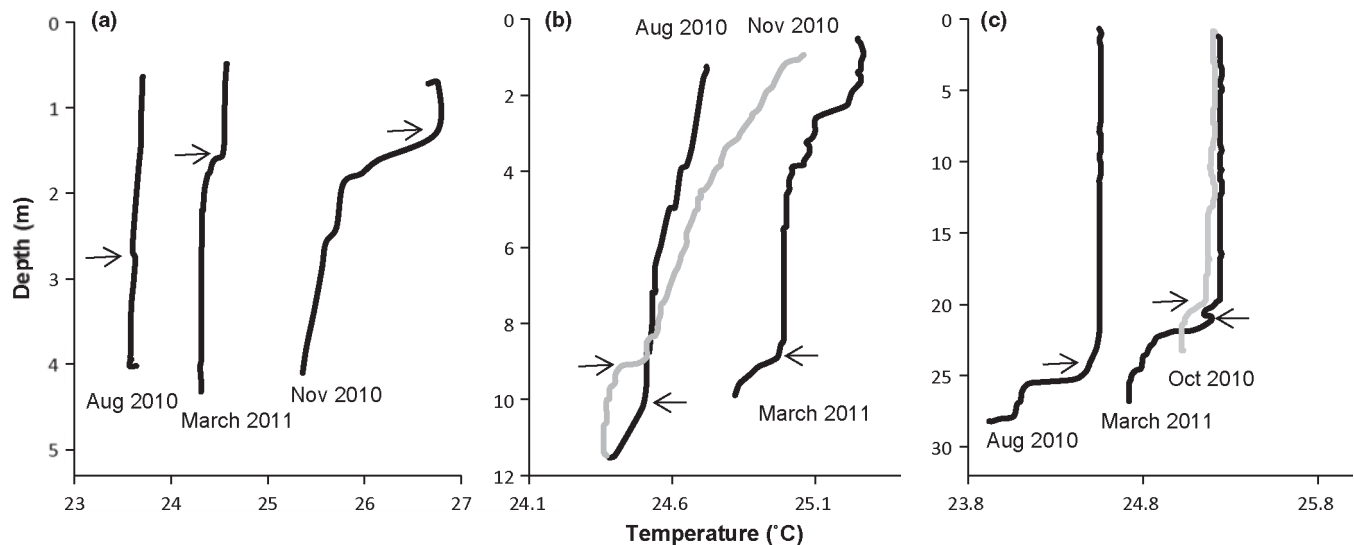
Fig. 3 Temperature-depth profiles at three sampling stations of contrasting depths on one occasion each season in the Mwanza Gulf. (a) At the most southern and shallow sampling station of 4–5 m depth, measurements were taken at 11:21, 10:15 and 11:58 h, respectively, (b) at an sampling station of intermediate depth (10–12 m depth), measurements were taken at 11:31, 10:42 and 13:37 h, respectively, and (c) at the most northern and deep station of 25–30 m depth, measurements were taken at 9:13, 10:46 and 10:44 h, respectively. Arrows indicate the mixing depths.

during the long rains. Particulate inorganic matter was seasonally affected and showed the highest concentration during the long rains. From the dissolved organic matter fractions, both DOC and CDOM varied spatially. Dissolved organic carbon concentration was lowest in deep water, whereas CDOM was highest in shallow water and lowest in deep water. Humic acid (HA) concentrations were very low and did not vary between areas.

Chlorophyll *a* concentrations varied from shallow to deep water and to a lesser extent between seasons (Table 1). Total chlorophyll *a* concentration, as well as chlorophyll concentrations of the main taxonomic phytoplankton groups, all decreased with depth. Cyanobacteria and diatoms also varied seasonally, with highest concentrations during the short rains, whereas chlorophytes occurred only at very low concentrations in all areas and seasons. Phytoplankton density in September 2010 and April 2011 (stations 1, 3 and 6) showed very low abundances of N-fixing phytoplankton species (<4.5% of total abundance). N-fixing species found in September 2010 were *Anabaena spp.* and *Cylindrospermopsis africana*; in April 2011 *Anabaena spp.*, *Cylindrospermopsis africana, C. cuspus, C. philippinensis, C. raciborskii* and *C. helicoida.* On both occasions close to the date of phytoplankton sampling, N : P ratio was highest in shallow water (36.4 on 26 August 2010 and 71.1 on 1 April 2011) and lowest in deep water (24.5 on 27 August 2010 and 19.1 on 31 March 2011).

Light-associated parameters were all affected spatially and seasonally (Table 1). The light attenuation coefficient (K_{PAR}) decreased from shallow to deep water, following the chlorophyll *a* trend. Highest K_{PAR} values occurred during the long rains, although seasonal differences were less conspicuous than spatial differences. Euphotic zone depth and Secchi depth showed similar spatial trends with greatest values in deep water and during the dry season.

Light conditions in Mwanza Gulf

A power regression model best described the relationship between K_{PAR} and chlorophyll *a* concentration ($K_{PAR} = 0.27 \cdot Chl^{0.71}$, $R^2 = 0.47$, $F = 67.94$, $P < 0.0001$, $n = 80$: Fig. 4a). However, the high values of K_{PAR} and extent of the variation around the relationship suggested that background light attenuation (K_{bg}) was high and varied between areas (Fig. 4a). When using ANCOVA, with area as factor and chlorophyll *a* concentration as covariate, we indeed found a strong influence of both chlorophyll and area on K_{PAR} ($R^2 = 0.69$, $F = 55.03$, $P < 0.0001$, $n = 80$: Fig. 4b). There was no interaction between chlorophyll and area ($F = 0.78, P = 0.46, n = 80$), and the decreasing intercept from shallow to deep water indicates a decreasing influence of background light attenuation (K_{bg}) from shallow to deep water on K_{PAR} (Fig. 4b). The specific attenuation coefficient for chlorophyll *a* (k_{chl}) was 0.0357 ($\mu g\ L^{-1}$) m^{-1} (95% CL = 0.016–0.055).
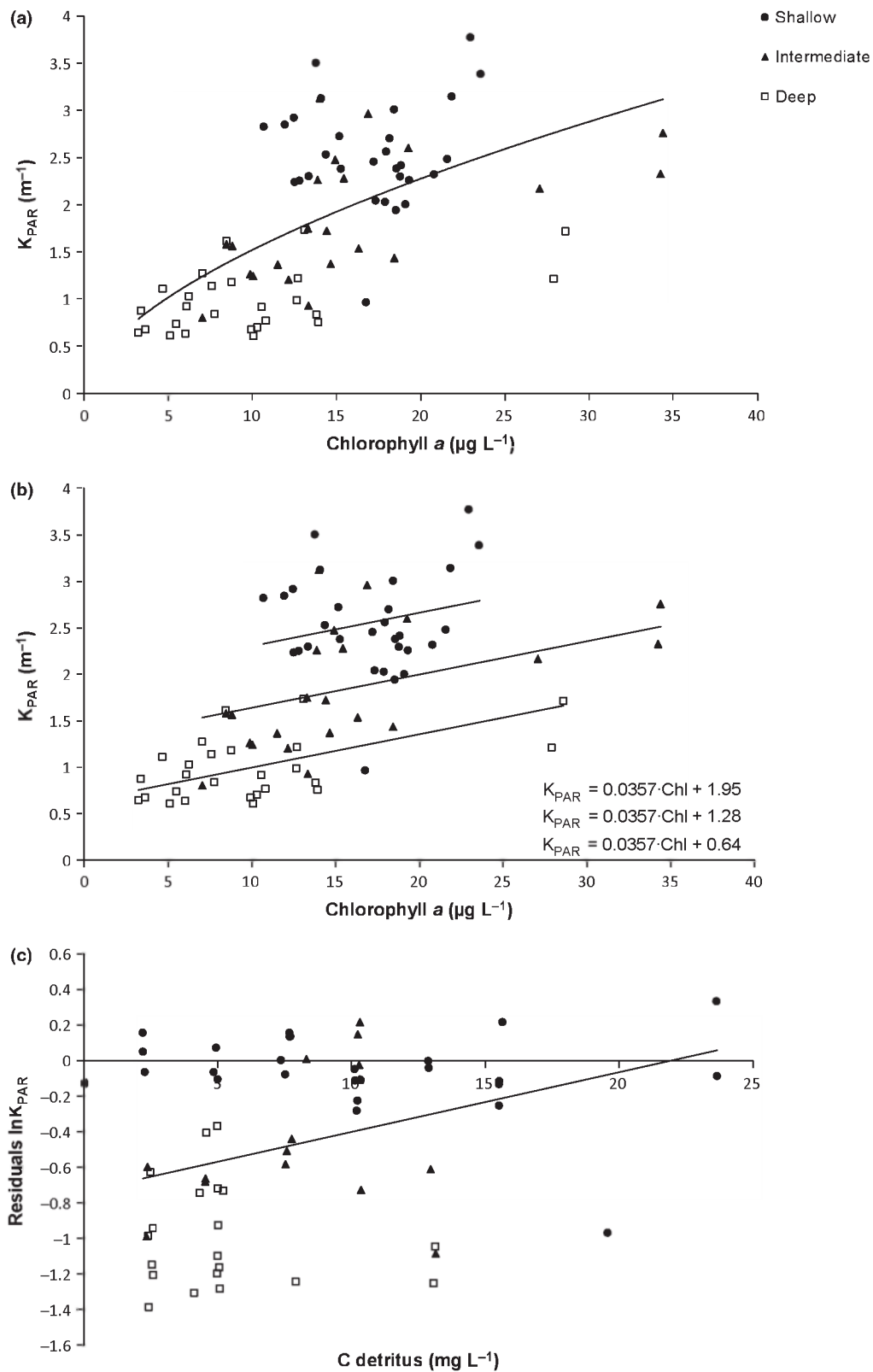
Fig. 4 The relationship between chlorophyll *a* concentration and the light attenuation coefficient (K_{PAR}) in the Mwanza Gulf: (a) power regression of chlorophyll *a* concentrations versus K_{PAR} in Mwanza Gulf ($R^2 = 0.47$, $n = 80$, $P < 0.0001$), (b) linear regression of chlorophyll *a* versus K_{PAR} in Mwanza Gulf and (c) regression of detritus concentrations (mg C L^{-1}) versus residuals of $\ln K_{PAR}$ ($R^2 = 0.12$, $n = 61$, $P = 0.007$).

A high K_{bg} in shallow water can be caused, among other factors, by suspended detritus. There was a significant positive correlation between the suspended detritus concentration ($C_{detritus}$) with the residuals of K_{PAR} from the power regression ($r_s = 0.27$, $P = 0.03$), suggesting that detritus played a significant role in explaining the differences in light attenuation in Mwanza Gulf. However, in the regression, only 12% of the variance of residuals was explained (Fig. 4c), indicating that, in addition to chlorophyll and detritus, other light absorbers like PIM or CDOM could have contributed to light attenuation in the Mwanza Gulf. Particulate inorganic matter was not significantly correlated with K_{PAR} ($P = 0.33$) and, because of the limited data on the dissolved fractions, we could not directly test the influence of CDOM or DOC on K_{PAR}.

Limitation on phytoplankton biomass

Shallow and intermediate water was more light-limited than deep water, and data points were in general located closer to the upper limit of chlorophyll *a* concentrations per unit area under light limitation (Fig. 5). The minimum light requirement to allow phytoplankton biomass was 9.01 mol photon m^{-2} day^{-1} m. The critical light requirement was 0.064 mol photon m^{-1} day^{-1} (mg m^{-2} chlorophyll *a*)$^{-1}$.

The calculated distance to the upper limit of chlorophyll *a* was plotted against nutrients and detritus (Fig. 6). A Spearman's rank test showed a significant negative correlation of TN concentrations with distance from the upper limit ($r_s = -0.24$, $P = 0.04$). A negative correlation of detritus with distance was found ($r_s = -0.21$, $P = 0.04$). Correlation between TP concentrations and distance was very weak and not significant ($r_s = -0.08$, $P = 0.61$).

Discussion

Spatial and seasonal dynamics

Stratification in the Mwanza Gulf varied among seasons, but the differences in mean mixed depth were not more than 2 m between seasons. This relatively weak effect of season suggests that stratification was not persistent throughout the rainy seasons. Lake Victoria has distinct diurnal rainfall and air convection patterns (Nicholson & Yin, 2002), which can build up and breakdown stratification on a daily basis. In the Mwanza Gulf, the water was mostly calm in the morning, but winds picked up in the afternoons (I. Cornelissen, pers. observ.), probably causing a breakdown of the stratification built up the previous night. This diurnal break-up of the stratification was also observed in inshore waters of 15 m in Uganda (Macintyre, Romero & Kling, 2002).

The TN and phosphorus concentrations observed here were within the range reported by other authors for Lake Victoria at similar depths (TP: 0.03–0.15 and TN: 0.5–1.5 mg L^{-1}; Mugidde, 2001; Gikuma-Njuru, 2008; Haande *et al.*, 2011; Ngupula, Mbonde & Ezekiel, 2011). Total phosphorus did not show a spatial trend, which also corresponds to other studies (Hecky, 1993; Mugidde, 1993). More than half of the P loading into the lake originates from atmospheric wet and dry deposition. Run-off is only of local importance (Tamatamah *et al.*, 2005). Total nitrogen concentrations were about threefold higher in shallow than in deep water, resulting in higher TN : TP ratios in shallow water, corresponding to other studies in Lake Victoria (Mugidde, 2001; Gikuma-Njuru & Hecky, 2005).

In deep water, PIM probably originated from wastewater from Mwanza City and from river discharges and
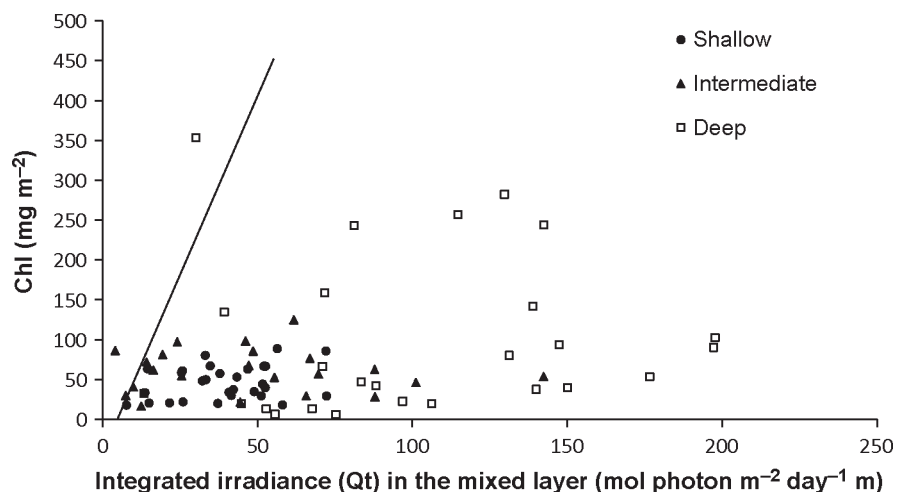
Fig. 5 Chlorophyll *a* concentration per unit area and integrated light irradiance over the mixed layer in the Mwanza Gulf. The line represents the maximum potential chlorophyll *a* concentrations when light is limited (upper limit), determined by regression of 10 sites with highest chlorophyll *a* concentrations per unit area and lowest integrated irradiance ($R^2 = 0.57$, $n = 10$, $P = 0.01$). Sites close to upper limit are more light-limited than points far from the upper limit: $n = 80$.

from resuspension of sediment through turbulence in shallow water (Lung'ayia *et al.*, 2000; Machiwa, 2010). The high PIM concentrations observed during the long rainy season were probably caused by high land run-off into the lake and resuspension of sediment (Lung'ayia *et al.*, 2000). Particulate organic carbon concentration in our study was twofold higher inshore than offshore, which corresponds with spatial trends of particulate carbon in other studies in the Mwanza Gulf and in Ugandan water (Mugidde, 2001; Hecky *et al.*, 2010; Machiwa, 2010).
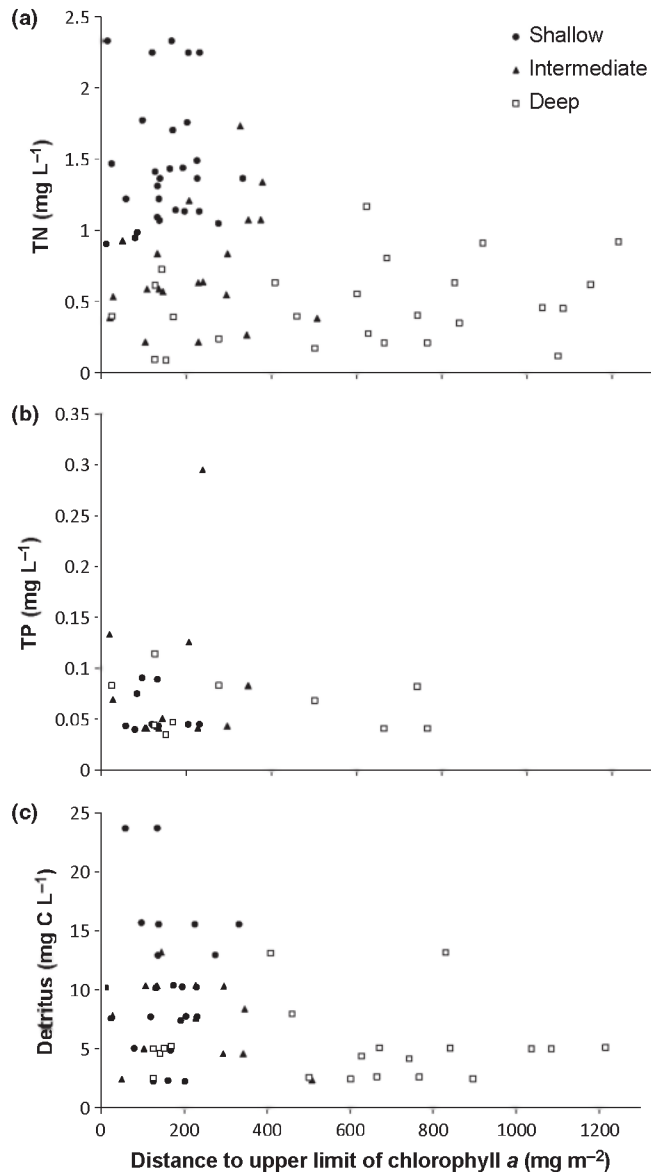
Fig. 6 Distances between measured chlorophyll *a* concentrations and the calculated maximum concentrations under light limitation in relation to varying nutrient and detritus concentrations: (a) total nitrogen concentrations (TN; *n* = 76), (b) total phosphorus concentrations (TP; *n* = 34) and (c) detritus concentrations (*n* = 57).

Chlorophyll *a* concentrations observed in the Mwanza Gulf fell in the same range as those measured by Shayo *et al.* (2011) in Mwanza Gulf and by Ngupula *et al.* (2012) in Tanzanian waters, but were in general two- to threefold lower than in highly eutrophic gulfs in Uganda, such as Napoleon and Murchison Gulf (Lehman & Branstrator, 1994; Mugidde, 2001; Yasindi & Taylor, 2003; Silsbe *et al.*, 2006; Cózar *et al.*, 2007; North *et al.*, 2008; Okello *et al.*, 2010; Haande *et al.*, 2011). The decrease in chlorophyll concentration from shallow to deep water suggests that nutrients in shallow water were in excess, enabling a high chlorophyll concentration until light became limited. Deeper mixing than the euphotic depth and possible N limitation resulted in lower chlorophyll concentrations in deeper water. Similar to other studies on the Ugandan side of Lake Victoria, cyanobacteria were found to be the dominant phytoplankton group in all locations and throughout the study period (Okello *et al.*, 2010; Haande *et al.*, 2011). The very low concentration of chlorophytes also corresponds with other studies in Mwanza Gulf and Lake Victoria (Akiyama *et al.*, 1977; Lung'ayia *et al.*, 2000; Kling *et al.*, 2001; Gikuma-Njuru, 2008; Ngupula *et al.*, 2011).

Light conditions in Mwanza Gulf

Secchi depth was less strongly related to K_{PAR} in Mwanza Gulf (R^2 = 0.75, *n* = 99: Fig. 7), than in Ugandan waters (R^2 = 0.90, *n* = 112: Fig. 7; Silsbe, 2004). The relationship obtained paralleled that found for Ugandan waters, but our Secchi depths were consistently 20 cm greater than in Uganda at identical K_{PAR} values. As
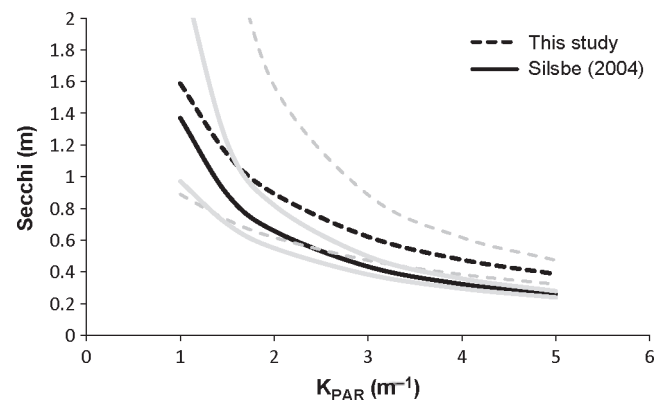

Fig. 7 Regression of K_{PAR} and Secchi depth of this study in Mwanza Gulf and Silsbe (2004) in Ugandan waters. Grey dashed lines represent 95% prediction intervals of this study, and grey lines represent 95% prediction intervals of the study of Silsbe (2004).

K_{PAR} and Secchi depth measure different optical properties, that is, K_{PAR} measures attenuation of light in the visible wavelength range and Secchi measures clarity (Preisendorfer, 1986), K_{PAR}–Secchi depth relationships differ between types of water. Koenings & Edmundson (1991) found a tenfold range of K_{PAR}–Secchi depth relationship between different types of lakes with either stained (high in CDOM concentrations), turbid (high in concentrations of suspended particles) or clear waters. Our K_{PAR}–Secchi depth relationship can be classified in between clear and turbid waters. The wider 95% prediction intervals of our relationship compared with that for Uganda (Fig. 7) suggest that there is additional spatial variation in the sources of light absorption within the Mwanza Gulf.

Morel & Prieur (1977) classified oceanic waters as 'case I' water, in which phytoplankton and detritus derived from phytoplankton contribute predominantly to the light attenuation in water, while in 'case II' water sediments and CDOM play a dominant role in light attenuation. In our study, K_{PAR} values were much higher in relation to the chlorophyll a range than in Ugandan and Kenyan waters (Silsbe, 2004; Loiselle *et al.*, 2008) and in oceanic case I waters (Morel, 1988), suggesting that light absorbers other than phytoplankton contributed to the light attenuation (background attenuation K_{bg}) and that the Mwanza Gulf might be considered as a case II water (Fig. 8). Loiselle *et al.*, (2008), who found a similar relationship between chlorophyll and K_{PAR} as Silsbe *et al.*, (2006), identified their study sites as case II waters. Our study showed high variation ($R^2 = 0.47$) between K_{PAR} and chlorophyll a, suggesting
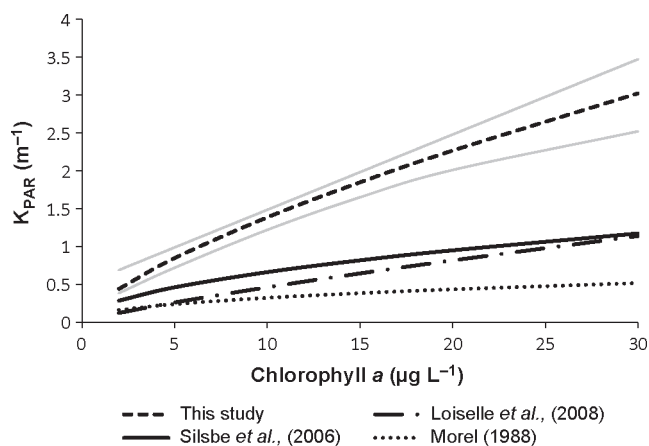
that the relative contribution of chlorophyll to light absorption varied spatially.

It becomes even more evident how strong the light attenuation by non-algal absorption in our study sites was, when we compare the integrated irradiance (Q_t) of Morel's type I waters (which have negligible non-algal absorption), with the Q_t in Mwanza Gulf at similar chlorophyll concentrations and surface irradiance. Our study shows that non-algal absorption removed 83, 78 and 67% of the integrated irradiance in shallow, intermediate and deep water, respectively. This indicates that light limitation was caused by non-phytoplankton light absorbing properties rather than by self-shading of phytoplankton in the Mwanza Gulf.

In the Mwanza Gulf, besides phytoplankton, suspended detritus played an increasing role in PAR attenuation from deep to shallow water. In addition, shallow water had higher CDOM and DOC concentrations than deep water (Table 1), which suggests that CDOM and DOC were probably of terrestrial origin (Loiselle *et al.*, 2007). Chromophoric dissolved organic matter concentrations were of similar magnitude as those in the Nyanza Gulf (Loiselle *et al.*, 2007). However, as chlorophyll a concentrations were much higher in the Nyanza Gulf, the relative contribution of CDOM to light attenuation could be of more importance in the Mwanza Gulf than in the Nyanza Gulf.

Limitations of phytoplankton biomass

The specific attenuation coefficient for chlorophyll a ($k_{Chl} = 0.036$ µg L^{-1} m, 95% CL = 0.016–0.055) was considerably higher and varied more than in Ugandan and Kenyan Gulfs (0.019 ± 0.002 (SD) µg L^{-1} m; Loiselle *et al.*, 2008). The specific attenuation coefficient for chlorophyll a (K_{Chl}) of 414 data sets of temperate freshwater and marine waters ranged from 0.004 to 0.029 µg L^{-1} m (Krause-Jensen & Sand-Jensen, 1998). The coefficient depends on physiological state, photo-adaptation and historical light exposure of phytoplankton and can vary considerably within and between aquatic ecosystems with different taxonomic phytoplankton communities (Dubinsky & Berman, 1981). The high k_{Chl} coefficient in our study suggests that light attenuation was relatively fast at a relatively low chlorophyll a biomass and that light became limited at a low chlorophyll a biomass. Furthermore, we found that the minimal and critical light requirements for phytoplankton were similar and 7.5-fold higher than in Ugandan and Kenyan gulfs, respectively (Loiselle *et al.*, 2007). We also found that shallow and intermediate water was more light-limited

Fig. 8 Regression of chlorophyll a concentrations and K_{PAR} of studies in southern Lake Victoria (this study), northern Lake Victoria (Silsbe *et al.*, 2006; Loiselle *et al.*, 2008) and oceanic waters (Morel, 1988). Grey lines represent 95% CL (this study).

(closer to upper limit for phytoplankton biomass) than deep water, because of higher background attenuation (K_{bg}) due to detritus and possibly CDOM. Although other studies confirm that, in general, phytoplankton growth in Lake Victoria is light-limited, they suggest that this is due to self-shading when phytoplankton biomass is high, especially in shallow water and during periods of stratification (Guildford *et al.*, 2003; Gikuma-Njuru & Hecky, 2005). In the Mwanza Gulf, where biomass was much lower than in northern Lake Victoria Gulfs, self-shading is expected to play a smaller role.

Our results suggest that factors other than light might be limiting under specific local conditions. Nitrogen was probably limited in deep water when light was not limited. This is confirmed by the TN : TP ratio of 11.8, which is lower than the ratio of 20 : 1 at which N generally becomes limiting for phytoplankton growth (Guildford & Hecky, 2000). A possible cause for low N concentration might have been deoxygenation in deep water, enhancing denitrification (Hecky, 1993). The high TN : TP ratio of 46 in shallow water found in the present study indicates a tendency for P limitation besides light limitation (Guildford & Hecky, 2000). Through N-fixation, N could accumulate in the water column. Unfortunately, direct measurements of N-fixation were not available. However, based on the very low abundances of N-fixing phytoplankton species in September 2010 and April 2011, we infer that the concurrently measured high N : P ratios in shallow water were not caused by N-fixation. The high nitrogen content observed in this study in the Mwanza Gulf may be better explained by inputs from run-off from cultivated and urbanised land, river discharges and internal N loading through low denitrification rates in well-oxygenated sediment and resuspension of sediments (Hecky, 1993; Lung'ayia, Sitoki & Kenyanya, 2001; Présing *et al.*, 2001). Furthermore, the slow flushing character and lack of extensive wetlands in connection with the Mwanza Gulf enable accumulation of N. The apparent lack of N-fixation is in contrast to other studies in Lake Victoria, in the Ugandan region, where N-fixation was high and considered an important N source (Hecky, 1993). N-fixation was especially high under optimal light conditions in shallow water with shallow mixed depths (Mugidde *et al.*, 2003; Guildford *et al.*, 2003). Possibly the low abundances of N-fixers we found might be an indication that light conditions in Mwanza Gulf were less optimal for N-fixers compared to other parts of Lake Victoria.

The degree of light limitation in our study was probably biased, as we estimated mixed depths from temperature profiles measured in the mornings when diurnal stratification was strongest. Complete mixing of the water column would probably occur once a day in the late afternoon, resulting in deeper mixed depths over much of the day. To demonstrate how much distances are affected by deeper mixing, we ran the light limitation analysis again with the original data, but assuming a 50% deeper mixed depths and using two alternative scenarios: (i) keeping the chlorophyll concentration per unit area over the mixed layer equal to the observed concen-
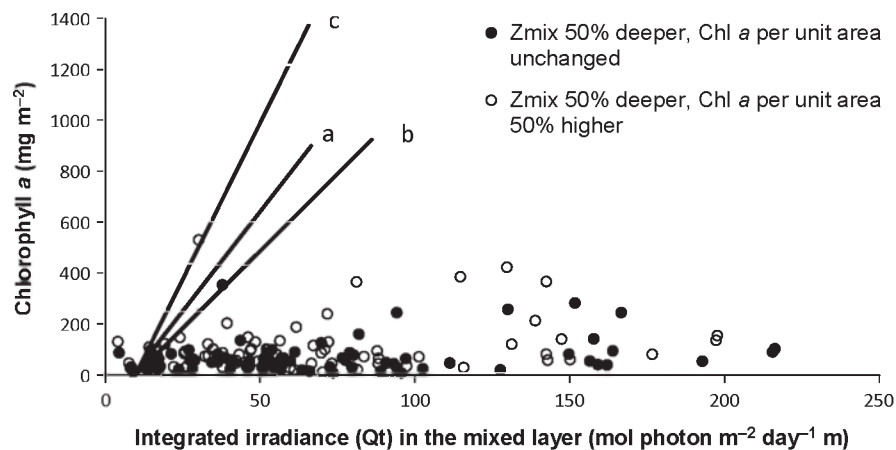

Fig. 9 Chlorophyll *a* concentration per unit area and integrated light irradiance over mixed layer in Mwanza Gulf. The lines represent the maximum potential chlorophyll *a* concentrations when light is limited (upper limit). Three lines were calculated: (a) based on the original data (for data points see Fig. 5), (b) based on simulated data (black dots), assuming a Z_{mix} of 50% deeper than observed but with chlorophyll *a* concentrations per unit area equal to the observed values and (c) based on simulated data (open circles), assuming a Z_{mix} of 50% deeper than observed, and with chlorophyll *a* concentrations per unit area 50% higher than observed Z_{mix} (i.e. assuming that the concentration chlorophyll per volume in the mixed depth remained equal).

tration per unit area, assuming that the concentration per unit volume below the observed mixed depth is zero and thus resulting in lower concentrations per unit volume over the simulated mixed depths and (ii) keeping the chlorophyll concentration per unit volume over the mixed layer equal to the observed concentration per unit volume, which resulted in higher concentrations per unit area with the simulated deeper mixed depths (Fig. 9).

According to scenario (i), distances increased with 5% on average (line b, black dots in Fig. 9), whereas in scenario (ii) distances increased with 46% on average (line c, open circles). This means that if we assume a greater mixed depth than in our measurements, in both scenarios, distances increase and therefore light limitation is less likely to occur than in our original calculations. Therefore, on a time scale of 24 h, we most probably overestimated the importance of light limitation and thus underestimated the effect of other factors limiting phytoplankton biomass. Thus, our conclusions that other factors besides light might be limiting in the Mwanza Gulf are strengthened rather than diminished.

Several studies suggest that primary production in Lake Victoria might not increase further with eutrophication, because nutrients are in excess and light limits further phytoplankton biomass production (Silsbe *et al.*, 2006; Sitoki *et al.*, 2010). This may account for the highly eutrophic gulfs in the north with very high phytoplankton biomass, but our study shows that besides light, nutrients can be limiting in the Mwanza Gulf and phytoplankton production is likely to depend on specific local environmental conditions. A further increase in eutrophication could lead locally to higher chlorophyll *a* concentrations under optimal light and mixing conditions. However, this does not mean that primary production and lake productivity will continue to increase at a similar rate, because photosynthetic efficiency decreases with chlorophyll *a*. (Silsbe *et al.*, 2006). Eutrophication affects the whole of Lake Victoria, but its heterogeneous environment should be considered when assessing water quality and implementing measures to reduce eutrophication.

Acknowledgments

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