

Effects of environmental factors on cyanobacteria dynamics in Lake Baringo, Kenya

Casianes O. Olilo,^{1*} William A. Shivoga,² John J. Kitetu³ and Simon Agembe²

¹Kenya Marine & Fisheries Research Institute, Kisumu Centre, Kisumu, Kenya, ²Department of Biological Sciences, Masinde Muliro University of Science & Technology, Kakamega, Kenya and ³Department of Environmental & Life Sciences, School of Science, Engineering & Technology, Kabarak University, Kabarak, Kenya

Abstract

The dominance of cyanobacterial algae in light-limited, shallow freshwater Lake Baringo is a major environmental concern in regard to Kenyan water quality and public health protection agencies. Accordingly, this study focused on determining the effect of different environmental factors on cyanobacteria dynamics in different sediment disturbance zones of the lake and in different seasons. This study also sought to bridge the knowledge gap regarding the influence of water clarity on cyanobacteria dynamics in the lake. Samples were collected from the field, stored in ice and transported to the laboratory for nutrient analyses. Cyanobacteria cultures isolated from the lake were grown under a 12:12 light/dark cycle. The frequency of dividing cells (FDC) technique, and a fluorescence microscopy technique, was used to count growing cyanobacteria cells. Specific cyanobacteria organic carbon synthesis was significantly negatively correlated with turbidity for the southern ($r = -0.6573$; $P < 0.05$) and central sediment disturbance zones ($r = -0.6847$; $P < 0.05$). This study indicated that water clarity is an environmental phenomenon that facilitates the movement of cyanobacteria into the turbid areas of the lake, where their production levels are significantly high, in contrast to the clear water along the edges of the water–land interface during the wet season (April to August) and dry season (September to March). Water clarity potentially enhances cell division inhibition and multiplication, thereby positively influencing cyanobacteria dynamics in Lake Baringo. Thus, it is concluded that the cyanobacteria growth rate resulting from use of the FDC technique suggests a link with inflowing water clarity that can be used to monitor in-lake water quality, to better manage cyanobacteria blooms in Lake Baringo and in lakes and reservoirs elsewhere.

Key words

cyanobacteria dynamics, environmental factors, growth rates, Lake Baringo, organic carbon synthesis.

INTRODUCTION

Cyanobacteria blooms are a major environmental threat to water quality and public health protection agencies globally. The existence of cyanobacteria in lakes and oceans is an old subject, dating back to the mid-1950s (Rhode 1955). Cyanobacteria were first studied by marine ecologists, who identified this small-sized planktonic fraction (0.2 to 2 μm) in marine ecosystems (Johnson & Sieburth 1979; Fahnenstiel *et al.* 1986; Waterbury *et al.* 1986). Currently, studies on the population dynamics of cyanobacteria through auto fluorescence photosynthetic pigments are now possible because of the development of fluorescence microscopy (Hagström *et al.* 1979). The

frequency of dividing cells (FDC) technique was first proposed by Hagström *et al.* (1979), helping us to better understand algal blooms. The seasonal and zonation aspects of cyanobacterial algal blooms in shallow freshwater lakes are linked to different environmental factors that influence their dynamics (Havens *et al.* 1998), with cyanobacteria dominating many eutrophic lakes worldwide (Dokulil & Teubner 2000; Oliver & Ganf 2000). There are differing opinions on how to best study cyanobacteria, with some arguing that more environmental factors (i.e. nutrients, temperature and light availability) and biological processes (i.e. predation by herbivores) need to be measured to better determine their influence on cyanobacteria population structures and functions in their habitats (Kagami & Urabe 2001; O'Farrell *et al.* 2007). In spite of these differing views on the metrics to be mea-

*Corresponding author. Email: olilocasianes@yahoo.com

Accepted for publication 3 November 2014.

sured, however, they hardly explain the interactions between environmental factors, inflowing water behaviour and the dynamics of cyanobacteria. Furthermore, Reynolds (1997) reported that cyanobacteria and other phytoplankton taxa have adopted diverse ecological strategies linked to their structural variability. At the same time, however, all these findings have been based on laboratory experiments, in contrast to open lake conditions. Those laboratory-based findings include variable irradiance (Wu *et al.* 2005; Helbling *et al.* 2006), temperature (Gao *et al.* 2008) and salinity (Kebede 1997) and although they are acceptable at an experimental scale, field experiments are nevertheless required to support their validity in nature.

Cyanobacteria bloom formation mechanisms have nevertheless been the basis for various studies (Kong & Gao 2005), which have identified different types of bloom formations in lakes, including sedimentation of cyanobacteria blooms (Visser *et al.* 1995), subsequent cyanobacterial persistence in lake surface sediments (Brunberg & Blomqvist 2002), cyanobacteria migrations (Verspagen *et al.* 2005), increases in cyanobacterial biomass (Cao *et al.* 2005) and benthic cyanobacteria mobility to the surface (Jacoby *et al.* 2000). These cyanobacteria pose serious health threats to humans and animals through contamination of water resources for drinking, recreation and industrial use (Pizzolon *et al.* 1999). Naselli-Flores *et al.* (2007) reported, however, that cyanobacteria structures have traits facilitating their adaptation to prevailing environmental conditions. Some studies have only considered cyanobacteria as a source of food for fish, ignoring their links to inflowing waters (Tokus Ogulu & Unal 2003; Muhling *et al.* 2005; Zielinska & Chojnacka 2009). Other studies have only looked at adaptations of some cyanobacteria groups in saline and alkaline environments (Dadhech *et al.* 2010), where morphological variability was exhibited (Muhling *et al.* 2003; Ballot *et al.* 2004; Wang & Zhao 2005). Although these studies are important in helping us better understand cyanobacteria dynamics, they do not link water clarity to these important taxa.

The first report on the geology and limnology of Lake Baringo Basin dates back to the early 1920s (Gregory 1921), with these surveys being followed by the 1929–1931 Cambridge Expedition to the East African lakes regarding water quality and fish stocks (Beadle 1932; Jenkin 1932; Worthington & Ricardo 1936). These studies revealed that algae were the primary sources of nutrient cycling and energy flow in the Lake Baringo ecosystem (Talling & Talling 1965; Richardson & Richardson 1972; Hecky & Kilham 1973). Although some information was provided on the relationship between environmental

factors and algal communities in Lake Baringo (Melack 1976; Beadle 1981; Kallqvist 1987; Gasse *et al.* 1993), none of them linked water clarity to cyanobacteria dynamics. Although numerous studies have since been conducted on the Lake Baringo ecosystem (Vareschi 1978; Vareschi & Vareschi 1984; Graeme & Kiplagat 1995; Vonshak 1997; Talling & Lemoalle 1998; Ballot *et al.* 2002; Harper *et al.* 2003; Oduor *et al.* 2003; Shargel & Oduor, 2003; Oduor & Schagerl 2007a; Schagerl & Oduor 2008; Krienitz & Kotut 2010; Kaggwa *et al.* 2013; Krienitz *et al.* 2013), the frequency of dividing cells method described by Hagström *et al.* (1979) has not been utilized to investigate the dynamics of cyanobacteria and other algal populations. These previous studies (Oduor & Schagerl 2007a; Schagerl & Oduor 2008; Krienitz & Kotut 2010) have not demonstrated the relationships between water clarity and the large temporal cyanobacteria biomass fluctuations in the lake. Thus, the presented study focused on determining the effects of environmental factors on cyanobacteria dynamics, as well as bridging the knowledge gap on the influence of water clarity on cyanobacteria dynamics in different sediment disturbance zones and seasons for Lake Baringo.

MATERIALS AND METHODS

Study site

Lake Baringo is situated between latitudes $0^{\circ} 36' N$ and $0^{\circ} 45' N$ and longitudes $36^{\circ} 04' E$ and $36^{\circ} 10' E$ (Ssentongo 1979), at an altitude of 975 m above sea level in the Rift Valley Basin of Africa (Fig. 1). The main morphometric and hydrological characteristics of Lake Baringo are summarized in Table 1. The lake discharges its water through an underground drainage system in the northern zone. The lake water is yellow-brown in colour (Kallqvist 1987), due to iron–silt complex which circulates during the daily afternoon mixing of the water column from north-easterly wind turbulence.

The lake basin was characterized in this study by a hot and dry weather condition, characteristic of a semi-arid climate. It received <50 mm of rainfall per month for a total of seven months in a year. The basin was conclusively a dry area for most months of the year, with air temperatures ranging from a minimum of $22^{\circ} C$ (July) to a maximum of $39^{\circ} C$ (March), and a lake surface evaporation rate of 1500 mm yr^{-1} .

Study design

For the purposes of this study, the lake was divided into three disturbance zones: (i) southern sediment disturbance zone; (ii) central sediments disturbance zone; and

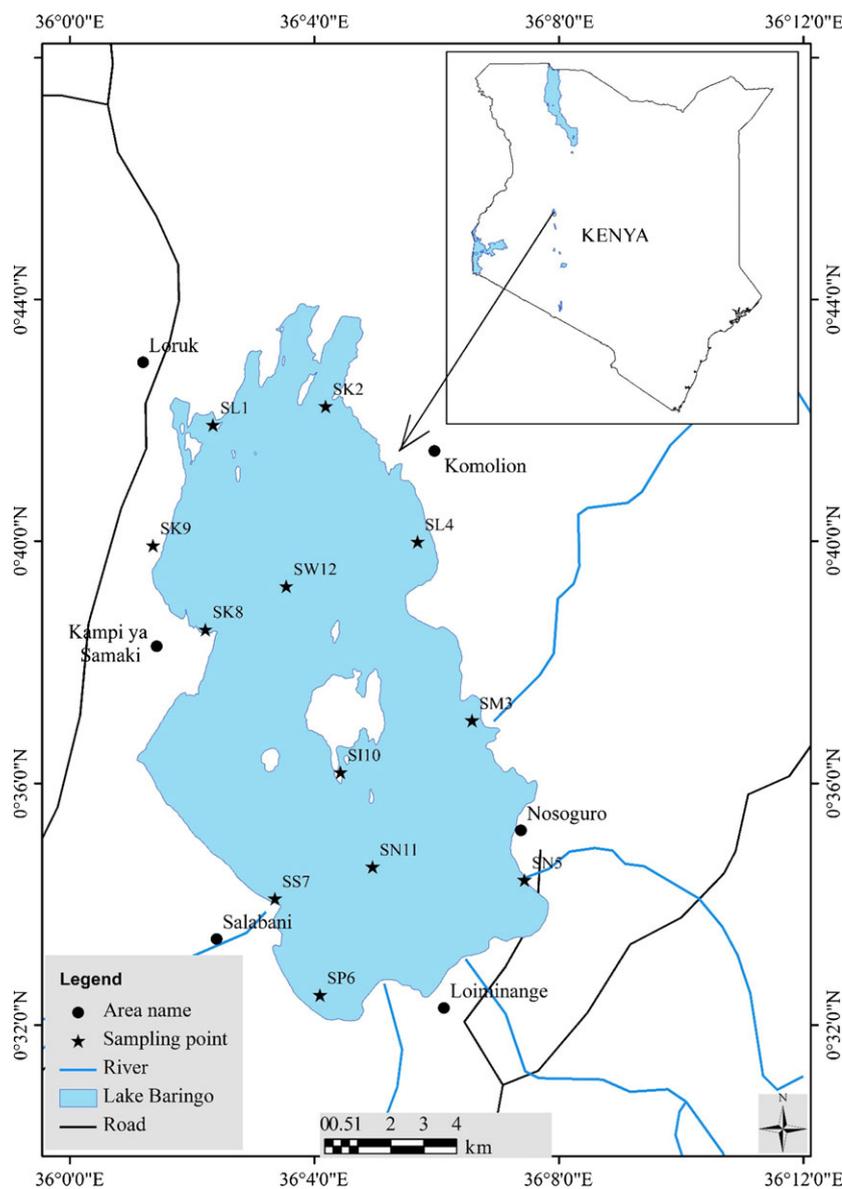


Fig. 1. Map of Lake Baringo, drainage rivers and sampling sites. Notes for Lake Baringo Fig. 1 map: Southern Zone: (SM3 = Mukutan River mouth; sampling site number 3; SN5 = Ngelesha River mouth; sampling site number 5; SP6 = Perkera River mouth sampling site number 6; SS7 = Endao River mouth sampling site number 7; SN11 = Molo and Ol Arabel River mouths); Central Zone: SI10 = Kokwa Island; sampling site number 10; SK8 = Kampi Ya Samaki; sampling site number 8; SW12 = William Island; sampling site number 12; KMFRI = Kenya Marine and Fisheries Offices; sampling site number 9; Northern Zone: SL1 = Loruk; sampling site number 1; SK2 = Komolion; sampling site number 2; SL4 = Longicharo, sampling site number 4).

(iii) northern sediments disturbance zone. The study was conducted over a period of twelve months (June 2007 to May 2008). The southern disturbance zone was characterized by a silt muddy benthic area of a 2 to 3.45 m depth, with a transparency of 0.045 m. This zone receives water from the Kapthurin, Ngelesha, Endao, Perkerra, Molo, Ol Arabel and Ngasotok rivers. It exhibits a high sediment disturbance, including a swampy area bordering

the lake with aquatic macrophyte vegetation. These sites were influenced by the main rivers draining to the lake, with macrophytes and wetlands along the shoreline.

The central sediment disturbance zone had mixed sandy and rocky shoreline. It receives inflowing water from the Mukutan River and contains a sandy gravel and silt benthic area of a 2 to 3.5 m depth, with a transparency of 0.06 m. This zone receives waste water from the

Table 1. Mean morphometric characteristics of Lake Baringo, June 2007 to May 2008

Feature	Units	Level
Area	km ²	132
Mean depth	m	3.5
Precipitation	mm yr ⁻¹	600
Drainage basin area	km ²	6 820
Water volume	m ³	726 × 10 ⁶
Water residence time	years	12.7
Water level	m	1.5 to 1.7
Lake length (L) and width (W)	km	22 (L) × 12 (W)
Mean annual temperature	°C	26
Hydrological parameters	Inflow	—
	Rainfall	400–1000
	Basin discharge	180–250
	Outflow	m ³ s ⁻¹
	Evaporation	1500–2000
	Underground seepage	50–150

Kampi ya Samaki Centre and Island Camp Hotel, both being important sources of phosphate and nitrates to the lake. It is a moderate sediment disturbance zone, being bordered by aquatic macrophytes, with hot springs from Kokwa Island draining into the lake. North-easterly winds dominate in this zone, stirring and re-suspending the bottom sediments in this zone every afternoon more than in the two other zones. The northern sediment disturbance zone had a rocky shoreline and a rocky cliff with a maximum depth of 5.5 m. The benthic area contains sand mixed with mud, with a transparency of 0.083 m. It is a low sediment disturbance zone, being sparsely surrounded by aquatic macrophytes.

The southern sediment disturbance zone comprised five sampling sites (SM3, SN5, SP6, SS7 and SN11), the central sediment disturbance zone had three sampling sites (SI 10, SK8 and SW12), and the northern sediments disturbance zone had three sampling sites (SL1, SK2 and SL4).

Field experiments

Field experiments were performed following the procedure described by Rippka *et al.* (1979). Photosynthetically active radiation (PAR) and transmittance were measured with a multi-sensor instrument at the beginning and end of each incubation. The total incident radiation at a meteorological station on the shores of Lake Baringo was measured with a solar metre. Cyanobacterial samples

were collected at 0600 Hr with a Van Dorn water sampler at depths selected on the basis of per cent incident light attenuation within the euphotic zone (100, 50, 25 and 1%). They were fixed with a 5% acid iodine solution and kept in a cool box at 4 °C for later analysis at the Nakuru Municipality laboratory. Primary production was measured in situ using light and dark bottles incubated by means of a multiple holder for 4 hours. The initial water samples were immediately fixed with Winkler reagents. Triplicate 150 mL light and dark bottles were filled simultaneously with a sample splitter to ensure a uniform initial oxygen concentration. The filters were prepared and enumerated for both total and dividing *M. aeruginosa* cells. The rate of cyanobacterial production (CP) of the natural population of *M. aeruginosa* was computed using the specific growth rates data, following the equation described by Carpenter and Campbell (1988), and modified by Callieri *et al.* (1996) as follows:

$$CP(\text{mgCm}^{-3}\text{d}^{-1}) = \mu\text{FDC} \cdot N_0 \cdot C_{\text{cell}}^{-1} \quad (1)$$

where: μFDC = cyanobacteria-specific growth rates; N_0 = cyanobacteria population size at the start of the exponential phase; and C_{cell}^{-1} = an average carbon content. A carbon content of 126 = 8 fg C cell⁻¹ was used for this calculation, being a value determined analytically from 20 replicates analyses of the laboratory cultures. For each sampling site on each sampling date, vertical profiles of temperature, turbidity, pH, dissolved oxygen concentration and electrical conductivity were measured using a multi-parameter water quality metre (MODEL WQC 24. Yellow Spring Instruments OH, USA and MODEL YSI 85, Yellow Spring Instruments Ohio, USA). Water transparency was measured with a 20 cm Secchi disc.

Laboratory analyses

Chlorophyll a was measured spectrophotometrically after extraction with 90% acetone and mechanically ruptured GFC filters, following the procedures described by Talling (1969). Cyanobacteria taxon were identified with identification keys of Kocielek and Spaulding (2003), Komarek (2003), Komarek *et al.* (2003) and Shubert (2003). The cells of each taxon were enumerated, and dimensions measured using an inverted microscope (Leica, Model DMIL 520804, Leica Microsystems, Wetzlar GmbH, Germany), with a 100X and 200X magnification, as described by Utermohl (1958). To count cyanobacteria, 2–3 mL of the samples was sedimented for at least 6 hours, and individuals of the most abundant species were counted on 100 randomly selected fields under the inverted microscope, using a 400X magnification. The

biovolume of the cyanobacteria taxon was estimated, using geometric formulae of the shapes similar to the respective phytoplankton cells described by Hillebrand *et al.* (1999). At least 40 cells were measured to provide the average size and biovolume for each identified cyanobacteria taxon. A factor described by Wetzel and Likens (1991) was used to convert cell volume (mm^{-3}) into biomass (mg). Cyanobacteria biomass was estimated from density and mean cell volume, following the procedure described by Smayda (1990).

Microcystis aeruginosa from Lake Baringo was extracted and used to explore zones and seasonal variations under controlled conditions and to compute cell division times. Several cultures of this isolate were grown in modified McIlvaine medium with a 12:12 light/dark cycle light period, beginning at 0600 Hr at $70 \mu \text{Em}^{-2} \text{s}^{-1}$ and 25°C . A few days (5) prior to the start of a diel experiment, a 10 mL aliquot of an exponentially growing culture was diluted with 1500 mL of McIlvaine medium. Each time the culture resumed log phase growth, as determined by *in vivo* fluorescence, the cultures were poured into replicate experimental flasks of 500 mL volume, and the diel experiment begun. Time-course experiments began at 0600 Hr on the basis of a 24 hour cycle. Samples were preserved with 1% formaldehyde, buffered with 0.1 M sodium phosphate and kept at 4°C . Unstained $0.2 \mu \text{m}$ filters were used for all cell counts. A Zeiss Axio-plan fluorescence microscope, equipped with a blue excitation filter set, was used to determine cell number and FDC (Hagström *et al.* 1979). From the time the cell wall exhibited invagination, a cell was considered to be in division phase until two distinct cells could be identified (Hagström *et al.* 1979). For each sample, a minimum number of 400 total cells and 100 dividing cells were enumerated at a magnification of 1250X, following the procedure of Callieri *et al.* (1996) and American Public Health Association (APHA) (1992). The appropriate 0.95 confidence limit, which was computed using the procedure of Cassel (1965) as a percentage of count, was around 10% for total count and 20% for dividing cells. Total phosphate, reactive phosphorus and organic phosphorus were analysed following the procedure of Strickland and Parsons (1968). Nitrate nitrogen ($\text{NO}_3\text{-N}$), nitrite nitrogen ($\text{NO}_2\text{-N}$), organic nitrogen and ammonium nitrogen ($\text{NH}_4\text{-N}$) were analysed following the procedure described in American Public Health Association (APHA) (1992).

Data analyses

The data were smooth-transformed prior to computing the instantaneous and specific growth rates of cyanobac-

teria. The cell numbers and FDC data were smoothed by the use of a 3 elements moving average (Callieri *et al.* 1996) to obtain a better estimate of growth rates. The transformations were performed for both laboratory and field FDC results to reduce errors in the data set. The net growth rate (μ) was calculated using the equation described by Callieri *et al.* (1996), as follows:

$$\mu = \frac{1}{t} \ln \frac{N_t}{N_0} \quad (2)$$

where: N_0 = population size at initial point of exponential phase; N_t = population size at final point of exponential phase; and t = time required for this growth. The division time (t_d) of the extracted *M. aeruginosa* population was computed on the basis of the equation described by McDuff and Chisholm (1982) and modified by Callieri *et al.* (1996) as follows:

$$\mu \text{FDC} = \frac{1}{n(t_d)} \sum_{i=1}^{i=n} \ln(1 + f_i) \quad (3)$$

where: n = number of sampling intervals; f_i = fraction of dividing cells for each sampling interval; and μFDC = specific growth rate. Statistical analyses were performed to determine the correlation coefficient between cyanobacteria organic carbon synthesis, growth rates and environmental factors, using Statistical Analysis Software (SAS Institute Inc. 2003). The coefficient of variation (CV %) for replicate estimations was <2%.

RESULTS

Environmental factors

Lake Baringo reached its thermal peak in dry season (Fig. 2). The standard error of mean (SEM, $\sigma_{\bar{x}}$) of all environmental variables are summarized in Table 2. The temperature that triggered cyanobacteria algal blooms ranged from 22 to 24°C , while the temperature that triggered cyanobacterial germination ranged from 15 to 30°C reaching its maximum of 18 – to 21°C during the wet season. There was a significant seasonal variation ($P < 0.05$, $df = 35$) in water temperatures only in the southern zone. The turbidity was significantly different among the zones ($P < 0.05$, $df = 35$) and sampling sites ($P < 0.05$, $df = 35$), but not among the depths in all the sampled zones. The SEM turbidity was 751.71 ± 0.08 NTU for the entire lake. These variations were not significantly different.

The transparency values were low, ranging from a minimum of 0.02 m at the Island camp in the central zone, to a maximum of 0.14 m at the Molo river mouth in the southern zone. The zones did not exhibit any sig-

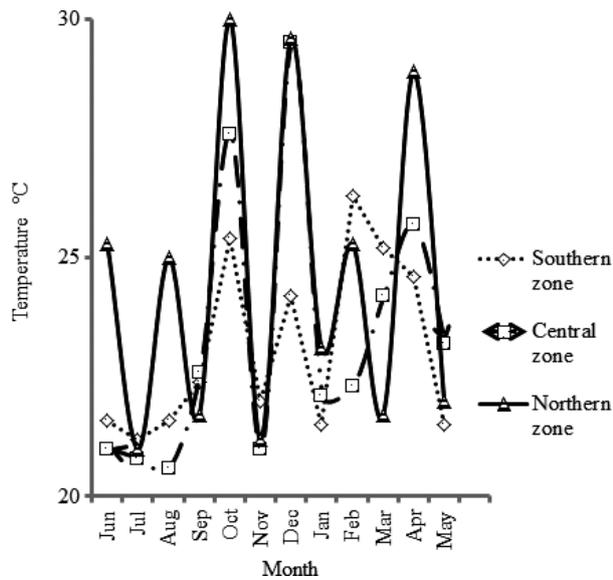


Fig. 2. Monthly mean water temperature ($^{\circ}\text{C}$) in different Lake Baringo sediment disturbance zones, June 2007 to May 2008.

nificant difference in mean transparency. The SEM transparency in the wet season in 2007 was 0.05 ± 0.01 m, which fell to a minimum SEM transparency of 0.03 ± 0.001 m in the same season. The lake transparency increased to a maximum SEM transparency of 0.06 ± 0.01 m in the dry season, exhibiting a seasonal fluctuation. The transparency was strongly correlated with the total dissolved solids (TDS) concentration ($r = 0.99$; $P \leq 0.05$, $df = 35$).

In the southern zone, 80% of incident photosynthetically active radiation (PAR) was absorbed within the first 2.4 m, 1% reaching the 3.5 m depth (Fig. 3). The transmittance was highest from 3 m to the bottom of the lake, according to the cyanobacteria density distribution. The incident PAR in the northern zone was reduced to <10% within the first 1 m. The transmittance was very low, exhibiting one strong maximum and one minimum between the 1.5 m and 3.5 m depth, corresponding to high cyanobacteria densities. The 1% incident light level was located between 2 and 3.5 m in the central zone, with a decreased transmittance at the 2.5 m depth, indicative of high cyanobacteria densities.

There were no seasonal variations in the dissolved oxygen concentration in the lake. Although no zone was significantly different from the others, each sampling site within the three zones were significantly different from the other sites ($P < 0.05$, $df = 35$). There was a significant difference in the means of the percentage of dissolved oxygen saturation during both the wet and short rainy seasons ($P < 0.05$, $df = 35$).

The lake had a SEM conductivity of $1740 \pm 0.29 \mu\text{S cm}^{-1}$ during the wet and short rainy seasons, with no seasonal variations observed throughout the study period as the mean values for most sampling sites ranged between 1 500 to 2 000 $\mu\text{S cm}^{-1}$. The wet and short rainy seasons had a SEM pH of 8.66 ± 0.15 . The pH values for the sampling sites within the central zone of the lake were significantly different from each other ($P < 0.05$, $df = 2$). The mean pH also was significantly different seasonally ($P < 0.05$, $df = 3$). The pH values were low in all the zones in the wet season (April to August), but subsequently increased during the short rainy season (September to March). The seasonal SEM total alkalinity was $8.42 \pm 0.43 \text{ mg L}^{-1}$, with the mean total alkalinity in the central zone sampling sites exhibiting significant differences ($P < 0.05$, $df = 11$). There was a significant difference in the total alkalinity during the two seasons ($P < 0.05$, $df = 11$). An SEM total alkalinity of $8.42 \pm 0.43 \text{ mg L}^{-1}$ was observed during the wet rainy and short rainy seasons. The nutrient analyses indicated neither total phosphorus nor reactive phosphorus limited algal growth in Lake Baringo during the dry and wet seasons, with no significant differences noted in all three study zones. The total phosphorus concentration ranged from a minimum of $27.0 \mu\text{g L}^{-1}$ at the Island Camp sampling site in the southern zone, to a maximum of $59.70 \mu\text{g L}^{-1}$ in the central lake zone. The zones exhibited a SEM total phosphorus concentration of $46.27 \pm 2.25 \mu\text{g L}^{-1}$, with a significant difference in concentrations in the study zones ($P < 0.01$, $df = 2$) and sampling sites ($P < 0.01$, $df = 11$), although not for vertical depths. No significant differences in total phosphorus concentrations were observed seasonally in the lake. There was a significant relationship between the total nitrogen:total phosphorus ratios (TN:TP; $P \leq 0.01$; $r = 0.89$; $P \leq 0.05$). Each of these parameters can be predicted with the following relationship:

$$\ln(\text{TN} : \text{TP}) = -6.78 + 12.41\ln(\text{TP}) - 5.59\ln(\text{TP}^2) \quad (4)$$

The SEM total nitrogen for the lake was $193.98 \pm 18.46 \mu\text{g mL}^{-1}$. The TN:TP ratio exhibited distinct variations, with the southern zone exhibiting the highest ratio, followed by the northern and central zones, respectively. Seasonally, the SEM total nitrogen was $193.93 \pm 9.35 \mu\text{g L}^{-1}$ during the wet season. There was a significant difference in total nitrogen ($P < 0.01$, $df = 3$) in the lake during the short and long rainy seasons. The mean total nitrogen concentration in the lake was significantly different in the three zones ($P < 0.01$, $df = 2$) and

Table 2. Mean and standard error spatial variation of environmental factors and cyanobacteria variables in different sediment disturbance zones in Lake Baringo, June 2007 to May 2008

Variable	Unit	Standard error of mean (SEM; $\sigma_{\bar{x}}$)			Degrees of freedom (Df)	F	P-value
		Northern	Central	Northern			
Area	km ²	59 ± 0.03	43 ± 0.01	30 ± 0.02			
Mean depth	m	2.5 ± 0.06	3.5 ± 0.03	4.5 ± 0.1	(2, 35)	4.23	<0.01
Temperature	°C	25.34 ± 1.30	23.94 ± 1.30	25.42 ± 1.8	(2, 35)	4.2	<0.01
Turbidity	NTU	751.71 ± 87.87	566 ± 13.58	832 ± 18.1	(2, 35)	4.71	<0.01
Total dissolved solids	µg L ⁻¹	967.5 ± 92.28	750.4 ± 60.79	370.20 ± 30.75	(2, 35)	28.2	<0.01
Water transparency	m	0.03 ± 0.01	0.04 ± 0.01	0.044 ± 0.014	(2, 35)	2.01	<0.05
Dissolved oxygen concentration	Mg L ⁻¹	5.33 ± 0.23	6.33 ± 0.24	5.34 ± 0.2	(2, 35)	11.3	<0.05
Oxygen saturation	%	89.98 ± 3.64	90.05 ± 7.25	90.05 ± 7.25	(2, 35)	2.19	<0.05
Conductivity	µS cm ⁻¹	1 740 ± 120.29	1 150 ± 110.56	1 738.18 ± 170	(2, 35)	7.25	<0.05
pH	pH units	8.06 ± 0.15	8.66 ± 0.28	7.62 ± 0.29	(2, 35)	0.72	<0.05
Total alkalinity	µg L ⁻¹	8.42 ± 0.34	7.42 ± 0.43	7.4 ± 1.2	(2, 35)	0.13	<0.05
Total phosphorus concentration	µg L ⁻¹	46.46 ± 1.98	43.46 ± 1.98	594.89 ± 1	(2, 35)	59.9	<0.01
Total nitrogen concentration	µg L ⁻¹	123.93 ± 9.35	193.93 ± 9.35	184.61 ± 14	(2, 35)	7.74	<0.01
Cell abundance	cells × 10 ³ mL ⁻¹	52.22 ± 3.03	139.82 ± 3.33	95 ± 1.8	(2, 35)	9.41	<0.05
Specific growth rate	mg cm ⁻³ d ⁻¹	2.6 ± 0.03	2.83 ± 0.04	2.6 ± 0.03	(2, 35)	3.67	<0.05
Net growth rate	mg cm ⁻³ d ⁻¹	1.22 ± 0.25	1.2 ± 0.31	1.2 ± 0.01	(2, 35)	4.62	<0.05
Specific organic carbon synthesis	mg cm ⁻³ d ⁻¹	15.39 ± 0.04	14.52 ± 0.04	15.39 ± 0.22	(2, 35)	9.65	<0.05
Net organic carbon synthesis	mg cm ⁻³ d ⁻¹	7.35 ± 0.04	5.8 ± 0.04	7.35 ± 0.1	(2, 35)	4.43	<0.05
Cyanobacteria loss	cells × 10 ³ mL ⁻¹	9.41 ± 0.04	8.72 ± 0.04	8.11 ± 0.13	(2, 35)	3.25	<0.05

sampling sites ($P < 0.01$, $df = 11$), as well as in the vertical depths ($P < 0.05$, $df = 3$).

Cyanobacteria abundance, growth rates and organic carbon synthesis

The main cyanobacteria parameters measured in different zones of the lake are summarized in Table 2. The bloom increased at the onset of the wet season, and crashed at the midpoint of the dry season. There were minimal stratifications in the dry season, with afternoon winds mixing the lake. The bloom started to become evident in the middle of the wet season, progressing to the beginning of the dry season. Cyanobacteria abundance (Fig. 4) in the lake ranged from a minimum of 22×10^3 cells mL⁻¹ to a maximum of 60×10^3 cells mL⁻¹ in Loruk (northern zone) and the Molo River mouth (southern zone), respec-

tively. The zones had an SEM cell abundance of $139.82 \pm 0.33 \times 10^3$ cells mL⁻¹. The lake zones were significantly different ($P < 0.05$, $df = 2$), as well as the sampling sites ($P < 0.05$, $df = 11$) within the zones. The lake had a SEM seasonal cell abundance of $52.22 \pm 3.03 \times 10^3$ cells mL⁻¹, with a seasonal significant difference in the mean cell abundance ($P < 0.05$, $df = 3$). However, the cyanobacteria abundance was correlated with the water temperature ($r = 0.54$, $P \leq 0.05$). The cyanobacteria abundance also was correlated with the TN:TP ratios in all three lake zones ($r = 0.56$; $P \leq 0.05$). The total phosphorus and total nitrogen concentrations were each correlated with the cyanobacteria abundance in the lake ($r = 0.87$, $P \leq 0.05$) and ($r = 0.56$; $P \leq 0.05$), respectively. The cyanobacteria abundance was significantly correlated with turbidity ($r = 0.96$; $P \leq 0.05$) in the lake zones. It also

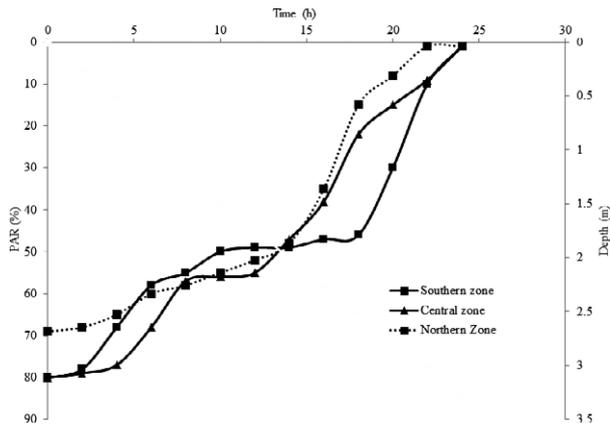


Fig. 3. Per cent photosynthetically active radiation in Lake Baringo southern, central and northern sediment disturbance zones during diel field experiments, June 2007 to May 2008.

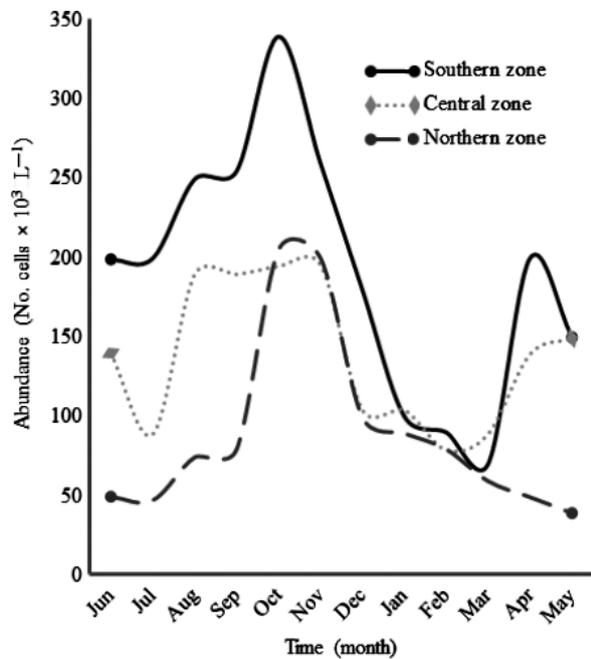


Fig. 4. Mean spatial distribution and abundance of cyanobacteria cells (10³ cells L⁻¹) in Lake Baringo, June 2007 to May 2008.

was significantly correlated with the dissolved oxygen concentration in the lake ($r = 0.86, P \leq 0.05$).

The *Microcystis aeruginosa* growth rates (μ_{FDC}) and net growth rates (μ_X) were computed from cyanobacterial cultures incubated in the laboratory. The initial steps involved obtaining a cell division time (t_d) of a *Microcystis aeruginosa* strain isolated from Lake Baringo, to calculate specific growth rate and production from in situ experiments. The sample-specific growth rate (μ_{FDC}) ranged from a minimum of 1.19 to a maximum of 4.5 mg cm⁻³

d⁻¹. The SEM-specific growth rate of cyanobacteria was 2.7 ± 0.46 mg cm⁻³ d⁻¹. The levels rose significantly high during the dry months, compared to the rest of the months ($P < 0.05, df = 11$). The specific cyanobacteria growth rate was correlated with the frequency of dividing cells ($r = 0.41; P \leq 0.05$). The specific cyanobacteria growth rate was related to the TP:TN ratio ($r = 0.37; P \leq 0.05$), with the rate being correlated with the turbidity in the southern zone ($r = 0.52; P \leq 0.05$). The SEM cyanobacteria net growth rate in the lake zones was 1.39 ± 0.21 mg cm⁻³ d⁻¹, and there was a significant difference in the mean cyanobacteria net growth rate in the zones ($P < 0.05, df = 2$). The sample SEM net growth rate ranged from 0.67 to 2.08 mg cm⁻³ d⁻¹, with the seasonal SEM net cyanobacteria growth rate being 1.18 ± 0.24 mg cm⁻³ d⁻¹. There also was a significant difference in the mean cyanobacteria net growth rate ($P < 0.05, df = 3$) during the long and short rainy season.

The seasonal cyanobacteria SEM-specific growth rate was 2.7 ± 0.46 , with a correlation between specific growth rate and water turbidity ($r = 0.54; P \leq 0.05$) in the central zone. There also was a correlation between net-specific growth rate and turbidity in the northern zone ($r = 0.23; P \leq 0.33$). The chlorophyll-a levels reached a maximum in the southern zone during the wet season, in contrast to the central and northern zones, which exhibited maximum values during the short rains (Fig. 5). The cyanobacteria-specific organic carbon synthesis was correlated with the lake water temperatures ($r = 0.49; P \leq 0.05$). The specific cyanobacteria organic carbon synthesis in the southern zone was correlated with water turbidity ($r = 0.49; P \leq 0.05$), with the specific organic

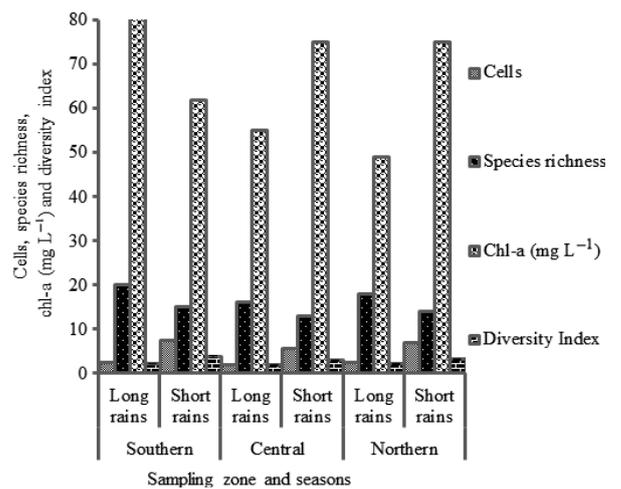


Fig. 5. Cyanobacteria total cell isolates, species richness, chlorophyll-a (mg L⁻¹) and Shannon–Wiener diversity index for different seasons and zones in Lake Baringo, June 2007 to May 2008.

carbon synthesis being significantly correlated with lake water turbidity ($r = 0.39$; $P \leq 0.05$). The specific organic carbon synthesis was correlated with cell abundance ($r = 0.56$, $P \leq 0.05$), with the overall specific cyanobacteria organic carbon synthesis exhibiting a correlation with turbidity ($r = 0.47$; $P \leq 0.05$). The southern zone exhibited the highest cyanobacteria production rates, followed by the central and northern zones, respectively. The absolute SEM net cyanobacteria organic carbon synthesis was $7.14 \pm 0.77 \text{ mg cm}^{-3}\text{d}^{-1}$, with the mean monthly sample cyanobacteria net organic carbon synthesis values ranging from 2.99 to $13.28 \text{ mg cm}^{-3}\text{d}^{-1}$. Seasonally, the net cyanobacteria organic carbon synthesis was observed with peaks only in the wet seasons and low levels in the dry season. The SEM cyanobacteria loss estimates was $9.41 \pm 2.78 \text{ mg cm}^{-3}\text{d}^{-1}$, with the loss being significantly different during the wet season ($P < 0.05$, $df = 3$). The laboratory culture experiments with the isolated *Microcystis aeruginosa* cyanobacteria cells from the lake revealed a diel cell division pattern, with a maximum frequency of dividing cells at 15 hours, while the minimum division time was about 3 hours. The cells divided continuously throughout the 24 hour cycle, although a decreased cell division was observed during darkness. The cells divided slowly, with the daily cell rate division being obtained after multiplying for a constant number of hours (12), assuming exponential growth. This assumption was later confirmed in subsequent experiments. The majority of the autotrophic cells were phycoerythrin-rich cyanobacteria of the *Microcystis* type, with eukaryotic algae representing <12% of the autotrophic cyanobacteria.

DISCUSSION

Effects of environmental factors on cyanobacteria dynamics

The largest portion of cyanobacteria recruitment occurred at a temperature of 18 to 20°C , with no recruitment observed below 14°C . *Microcystis* recruitment starting at 15°C required an optimum temperature of 20°C to reach its peak. The photosystem II (PS II) of *Microcystis* inoculated under low temperature (4°C) provided a high fluorescence intensity because it was intact at low temperature, but was reactivated at high temperature. When the water temperature was above 20°C , dissolved inorganic nitrogen and free carbon dioxide were depleted from the water, resulting into cyanobacterial dominance. The variation in seasonal temperature peaks observed in the southern zone was attributed to the fluctuating pattern of inflow waters from the catchment rivers during the wet (April to August) and dry (September to March)

months. The highest temperatures experienced in the northern zone occurred because the zone does not have an outlet, but does have an underground drainage. Warmer temperature in Lake Baringo coincided with the development of anoxia conditions, thereby stimulating the formation of new cyanobacteria colonies, attributable to higher temperatures influencing a gradual physiological increase in esterase activity that supports the viability of *M. aeruginosa* on surface sediments, as suggested by Latour *et al.* (2004). The short rains sedimentation occurred as a consequence of increased carbohydrates and reduced buoyancy at reduced temperatures for *Microcystis* (Sitoki *et al.* 2012).

The observed low light extinction in the southern zone can be explained in terms of suspended particles in the ecotone zone (i.e. land–water interface). The clarity decreases from the shallow to deep areas, being attributable to slow flushing and high inputs of water from the rivers and streams in the southern zone. This zone favoured cyanobacteria, which could possibly use bicarbonate as a carbon source (Dokulil & Teubner 2000). Water clarity resulting from the low turbidity and high transparency promoted changes in cyanobacteria density and biomass in the southern zone. Furthermore, the observed water clarity in this zone is a new behaviour that promotes the concept of plasticity genes in Lake Baringo cyanobacteria populations. This concept refers to the regulatory loci that directly respond to specific environmental stimuli within the clear water by triggering a specific series of structural changes in the cyanobacteria (Pigliucci 1996). Information on this concept within Lake Baringo and elsewhere, however, is relatively sparse. The water clarity in the southern zone attributable to clear inflowing rivers is a phenomenon representing a new dimension in Lake Baringo characteristics. The drainage waters in rivers draining to lakes usually contain suspended sediments and are more turbid than the water in the recipient lake. The findings of the present study, however, contrast with this known phenomenon and fundamental lake behaviour, with this emerging idea being explainable in terms of Tilman's resource-ratio theory (Taylor & Williams 1975; Tilman 1977, 1982, 1985), Hysteresis Theory (Scheffer 1998) and Resilience Theory (Holling 1973). According to Tilman's resource-ratio theory, the coexistence of cyanobacteria and other algal taxa is unstable because the former consumes relatively more of the available light, as well as being tolerable of lower light conditions. Cyanobacteria can result in a higher turbidity at the same nutrient level as for other algae, which imply they use relatively more light than other algal taxa at lower light levels (Scheffer *et al.* 1997), consistent with

the higher level of clear water entering Lake Baringo. This clear water creates a temporary water zone that remains stable at the ecotone before overlapping into a normal resilient turbid water condition at a distance of 50 m into the open water, characteristic of a condition known as hysteresis (Holling 1973; Scheffer 1998; Gunderson 2000). For the purposes of the present study, resilience refers to the capacity of the stable turbid water state of the Lake Baringo ecosystem, and the cyanobacteria dominance in the lake, to withstand perturbations from such events as increased clear water shocks that may rebuild and renew themselves without shifting into a qualitatively alternative stable state. In other words, resilience represents the magnitude of the perturbations which the stable turbid water state of Lake Baringo ecosystem can absorb without shifting into a qualitatively different stable state, a unique phenomenon of tropical Lake Baringo. This behaviour may produce major effects on the cyanobacteria population dynamics in this shallow turbid tropical lake. Coupled with the toxic nature of cyanobacteria, water clarity seems to influence the dynamics of these algal taxa, thereby posing a major environmental concern to water users and animals living in Lake Baringo. Furthermore, the southern sediment disturbance zone exhibits water clarity, compared to the central and northern sediment disturbance zones, likely due to the proximity of the adjacent Kichirtit Swamp. This observation contrasts significantly with the known behaviour of most lakes, for which the water in the river mouths entering them are more turbid than the water in the main body of the lake (Scheffer *et al.* 1993). When a critical turbidity was reached whereby the net plant growth was negative, the plants were replaced by cyanobacteria (Scheffer *et al.* 1993), which is a critical concept for managing cyanobacteria blooms and water quality in shallow eutrophic lakes. This alternative state also occurred in Lake Baringo, with a shift between *Microcystis* and *Oscillatoria* dominance, and by other algae (i.e. the phenomenon was not restricted to plant–algae switches; Scheffer *et al.* 1997). The rivers draining into Lake Baringo pass through swampy wetlands that filter the incoming water, which reduces turbidity through settling of the suspended sediment particles in the river water. There is a possibility that the cyanobacteria and other algal taxa in the inflow waters also could be filtered by the adjacent wetland, inducing the growth and multiplication of cyanobacteria in the central and northern sediment disturbance zones of Lake Baringo, in contrast to the clear water in the southern zone. The turbidity in the central and northern sediment disturbance zones is influenced by the afternoon north-easterly winds. This pro-

cess of gradual increasing turbidity from southern sediment disturbance zone towards the central and northern sediment disturbance zones, respectively, explains the resilient nature of Lake Baringo throughout the year. Sediment mixing was the most important factor in initiating and enhancing the recruitment of cyanobacteria, particularly *Microcystis* and *Anabaena*.

Relationship between nutrients and cyanobacteria dynamics

The high cyanobacteria diversity and changes in taxonomic structure coincided with increases in total phosphorus concentrations from 30 to 100 $\mu\text{g L}^{-1}$, which implied higher soluble reactive phosphorus concentrations than those of nitrite nitrogen, nitrate nitrogen and ammonium nitrogen. There was corresponding higher chlorophyll-a concentrations observed in the lake. Thus, the results point to the fact that the availability of nutrients can have an effect on cyanobacteria nutrient stoichiometry, which probably explains the small differences in chlorophyll-a levels between the high and low measured nutrient levels. Nitrogen was probably the most algal growth-limiting nutrient because the chlorophyll-a concentrations in all three sediment disturbance zones indicated it was the single most important nutrient for cyanobacteria growth in the inshore areas. Nutrients were a critical cause of cyanobacteria blooms and their seasonal intersystem variations in the central and northern sediment disturbance zones. Ammonium nitrogen and nitrates nitrogen were both limiting nutrients, while total phosphorus was not absolutely limiting, supporting the eutrophic nature of the lake, with the high total and reactive phosphorus levels supporting this observation (Manca *et al.* 1992).

Relationship between TN:TP ratio and cyanobacteria dynamics

As noted above, nitrogen was probably the most important factor for cyanobacteria growth in Lake Baringo. The lake remains a nitrogen-deficient system compared to other freshwater lakes, however, as evidenced in the low TN:TP ratio in the offshore areas and a higher TN:TP ratio in the southern sediment disturbance zone. The present study indicates that obvious N-limited growth of cyanobacteria appears to start with a low TN:TP ratio, with the average ratio being low in the shallow depths of the inshore waters of Lake Baringo. Cyanobacteria were primarily limited by nitrogen under conditions of sufficient light for algal growth, an observation consistent with that of Smith and Bennet (1999), who reported that light, rather than nitrogen, is always the most important

enhancing factor for cyanobacteria growth in both the inshore and offshore areas.

Relationship between cell abundance, organic carbon synthesis and cyanobacteria growth rates

The observed cyanobacteria numbers were more directly linked to cell abundance. The biological process of cell growth in the southern lake zone, for example, was linked to cyanobacterial abundance. There was an indication that cyanobacteria exhibited a very high, but discontinuous, growth potential, with the cell abundance decreasing from the southern to the central and northern zones, respectively. This changed abundance could be attributable to the turbidity levels, which also increased in the southern, central and northern zone sequence, respectively. The cyanobacteria abundance had direct linkages to net and specific organic carbon synthesis and growth rates in Lake Baringo. As the FDC method was utilized to count tropical cyanobacteria species in this shallow lake, this method also could be applied to predict the cyanobacteria population organic carbon synthesis and growth rates, consistent with the results of studies on growth rate and sedimentation of cyanobacteria cells by Callieri *et al.* (1996). *Microcystis aeruginosa* cells from Lake Baringo exhibited a diel cell division pattern, being made possible by the FDC technique for evaluating the organic carbon synthesis and growth rates in the lake. This observation indicates a constancy during the dark period as a result of the second light-dependent gap in DNA synthesis at the end of the cell cycle. A large proportion of cyanobacteria in the southern zone was decomposed and deformed during sedimentation in the short rainy season. A resting cyanobacteria stage on the sediments were never encountered in the present study, although the cyanobacteria were supposed to exhibit renewed growth and return to the pelagic phase, where they could remain buoyant because of their density, which approaches that of fresh water at 1.1 g cm^{-3} . No *Anabaena* species developed non-growth stages, in contrast to other studies showing that *Anabaena* had developed akinetes (Paerl 1988).

It was found that cyanobacteria migration from benthic sediments to the water surface provided a benthic source for initiating new pelagic growth in the southern zone of the lake. New pelagic cyanobacteria biomass created additional proportional values to those already existing in water, thereby completing their life cycle and increasing bloom formations. This finding also agrees with the hypothesis that benthic stocks provided pelagic cyanobacteria in lakes mainly via migration or move-

ment in the surface water (Zhang *et al.* 2005). These study results indicated that maximum production processes occurred in October and November each year. The synthesis losses (estimated as the difference between specific organic carbon and net organic carbon synthesis) indicated that from 30 to 77% of the potential cyanobacterial production forms the organic biomass that comprised about 8 to 142% of the net production in the Lake Baringo ecosystem. This could be achieved by factoring in the effects of environmental factors on cyanobacteria dynamics. Our data on freshwater *Microcystis aeruginosa* strains isolated from Lake Baringo exhibited very different division times when cultured at different temperatures and light levels, a finding that is contrary to that observed for *Synechococcus* spp, which exhibited division time of 3 hours (Campbell & Carpenter 1986).

As noted above, cyanobacteria migration from benthic sediments to the water surface in the southern zone provided a benthic source for initiating new pelagic growth. Furthermore, new pelagic cyanobacteria biomass created additional proportional values to the already-existing ones, completing their life cycle and increasing bloom formations, in agreement with the hypothesis that benthic stocks provide pelagic cyanobacteria in lakes mainly via migration or movement at the water surface (Zhang *et al.* 2005). Results of the present study on freshwater strains of *Microcystis aeruginosa* isolated from Lake Baringo exhibited very different division times when cultured at different temperatures and light levels, contrary to the finding that *Synechococcus* spp had division time of 3 hours (Campbell & Carpenter 1986; Fahnenstiel *et al.* 1986; Waterbury *et al.* 1986; Callieri *et al.* 1996).

CONCLUSION

The results of the present study indicate that different environmental factors triggered the spatio-temporal variation of organic carbon synthesis, growth rates, recruitment and blooms of cyanobacteria in Lake Baringo. Freshwater strains of *Microcystis aeruginosa* isolated from the lake exhibited different division times when cultured at different temperatures and light levels. The seasonal aspect of cyanobacteria blooms in Lake Baringo depended on such factors as temperature, light availability, water transparency and turbidity and nutrients (nitrite-, nitrate- and ammonium-nitrogen nitrogen). Photosynthetically active radiation, nitrogen and phosphorus concentrations, and water turbidity were the most important factors for cyanobacteria organic carbon synthesis, growth rates and recruitment in Lake Bar-

ingo. Most of the rivers draining to the lake through swamps facilitate the removal of suspended solids and sediment particles, thereby increasing inflowing water clarity. Perennial diurnal mixing and upwelling of lake water contributed partly to the turbidity observed in the central and northern sediment disturbance zones in the lake. The lake has soft bottom sediments easily scoured by winds and brought to the water surface. The higher water temperatures preceded cyanobacteria cell division and multiplication, and seasonal changes in cyanobacteria algal blooms in the lake indicated linkages between temperature and the emergence of the recruited cells from benthic algae to the pelagic zone. The present study showed that the increased temperature for cyanobacteria recruitment into the pelagic zone supported increased organic carbon synthesis and growth rates. Reduced Secchi depth was due partly to cyanobacteria algal scums, increasing lake water turbidity. The present study also determined that the frequency of dividing cells technique is a robust method for detecting cyanobacteria growth and abundance in a turbid water ecosystem. Integrated nutrient and cyanobacteria management are expected to be one of the essential best management practices for Lake Baringo. The present study also indicated that water clarity is an environmental phenomenon that helps explain the clear water inflows to the lake in the southern sediment disturbance zone. These various study results are useful for detecting changes and stress signs in the Lake Baringo ecosystem. The turbidity levels, however, increased significantly in the southern sediment disturbance zone, and this current trend could reverse when the Lake Baringo water volume increases twofold from increased rainfall during the long rains (April to August).

Although determining the effects of protozoan grazing pressure on cyanobacteria population dynamics was beyond the scope of the present study, it is recommended that further investigations regarding these links under different environmental conditions in this shallow, stable and resilient turbid freshwater lake be undertaken. Furthermore, the potential of the probable spatial and temporal bio-fence mechanism to create a separating barrier to keep cyanobacteria from fresh drinking water also needs investigations. Thus, it is concluded that determination of the cyanobacteria growth rate resulting from the FDC technique, combined with inflow water clarity, is a preferable guide for improving water quality and designing best management practices for cyanobacteria blooms in Lake Baringo, and in lakes and reservoirs elsewhere.

ACKNOWLEDGEMENTS

Grateful thanks are given to the Baringo technical staff of the Kenya Marine and Fisheries Research Institute (KMFRI) for their able assistance in field sample collection. The present study was conducted within the Faculty of Environmental Science and Resources Development in the Department of Environmental Science, Egerton University. Laboratory experiments and analyses were carried out at the Nakuru Municipal Laboratory. Thanks also are due Dr. Isaiah Tabu of Egerton University for his assistance in data analyses and statistical work. Zack Ogari of KMFRI is thanked for his useful contributions to the manuscript. The KMFRI staff at the Lake Baringo station assisted in field data collection. We also are grateful to the Tonolli Memorial Fund, administered by the Society of International Limnology (SIL) for funding this research work. All those who contributed directly or indirectly in this research effort are gratefully appreciated.

REFERENCES

- American Public Health Association (APHA) (1992) Standard Methods for the Examination of Water and Wastewater, 18th edn. American Public Health Association, Washington D.C., U.S.A.
- Ballot A., Pflugmacher A., Niegand C., Kiplagat K. & Krienitz L. (2002) Cyanobacterial toxins in Lake Baringo, Kenya. *Limnologia* **33**, 2–9.
- Ballot A., Dadheech P. & Krienitz L. (2004) Phylogenetic relationship of *Arthrospira*, *Phormidium* and *Spirulina* strains from Kenyan and Indian water bodies. *Algol. Stud.* **113**, 37–56.
- Beadle L. C. (1932) Scientific Results of the Cambridge Expedition to the East African lakes, 1930–1. 4. The waters of some East African lakes in relation to their fauna and flora. *J. Linn. Soc. Zool.* **38**, 157–211.
- Beadle L. C. (1981) The Inland waters of Tropical Africa p. 475. Longman, London.
- Brunberg A. K. & Blomqvist P. (2002) Benthic overwintering of *Microcystis* colonies under different environmental conditions. *J. Plankton Res.* **24**, 1247–52.
- Callieri C., Berton R., Amicucci E. A., Pinolini M. L. & Jasser I. (1996) Growth rates of freshwater Picocyanobacteria measured by FDC: problems and potentials for the estimation of cyanobacteria organic carbon synthesis. *Arch. Hydrobiol. Spec. Issues Advac. Limnol.* **48**, 93–103.
- Campbell L. & Carpenter E. J. (1986) Diel pattern of cell division in marine *Synechococcus* spp. (Cyanobacteria): use of frequency of dividing cell technique to measure growth rate. *Mar. Ecol. Prog. Ser.* **32**, 139–48.

- Cao H. S., Kong F. X., Tan J. K., Zhang X. F., Tao Y. & Yang Z. (2005) Recruitment of total phytoplankton, chlorophytes and Cyanobacteria from lake sediments recorded by photosynthetic pigments in a large, shallow lake (Lake Taihu, China). *Int. Rev. Hydrobiol.* **90**, 345–55.
- Carpenter E. J. & Campbell L. (1988) Diel pattern of cell division and growth and growth rate of *Synechococcus* spp. in Long Island Sound. *Mar. Ecol. Prog. Ser.* **47**, 179–83.
- Cassel E. A. (1965) Rapid graphical method for estimating the precision of direct microscopic counting data. *Appl. Microbiol.* **13**, 293–6.
- Dadheech K. P., Ballot A., Casper P., Kotut K., Novelo E. & Lemma B. (2010) Phylogenetic relationship and divergence among planktonic strains of *Arthrospira* (Oscillatoriales, Cyanobacteria) of African, Asian and American origin deduced by 16S-23S ITS and Phycocyanin operon sequences. *Phycologia* **49**, 361–72.
- Dokulil M. & Teubner K. (2000) Cyanobacterial dominance in lakes. *Hydrobiologia* **438**, 1–12.
- Fahnenstiel G. L., Sicko-Goad L., Scavia D. & Stoermer E. F. (1986) Importance of cyanobacteria in Lake Superior. *Can. J. Fish Aquat. Sci.* **43**, 235–40.
- Gao K., Li P., Watanabe T. & Hebling W. E. (2008) Combined effects of ultraviolet radiation and temperature on morphology, photosynthesis and DNA of *Arthrospira* (*Spirulina*) *platensis* (Cyanophyta). *J. Phycol.* **44**, 777–86.
- Gasse F., Talling J. F. & Kilham P. (1993) Diatom assemblages in East Africa: Classification, distribution and ecology. *Rev. Hydrobiol. Trop.* **16**, 3–34.
- Graeme P. & Kiplagat K. W. (1995) The influence of the diel climatic cycle on the depth-time distribution of phytoplankton and photosynthesis in a shallow equatorial lake (Lake Baringo, Kenya). *Hydrobiologia* **304**, 1–8.
- Gregory J. W. (1921) Rift Valley and Geology of east Africa. London.
- Gunderson L. H. (2000) Ecological resilience - in theory and application. *Ann. Rev. Ecol. Syst.* **31**, 425–39.
- Hagström A., Larsson U., Horstedt P. & Normark S. (1979) Frequency of dividing cells a new approach to the determination of bacterial growth rates in aquatic environment. *Appl. Environ. Microbiol.* **37**, 805–12.
- Harper D. M., Childress B. R., Harper M. M., Boar R. R., Hickey P. & Mills S. C. (2003) Aquatic biodiversity and saline lakes: Lake Bogoria National Reserve, Kenya. *Hydrobiologia* **500**, 259–76.
- Havens K. E., Philips E. J., Cichra M. F. & Li B. L. (1998) Light availability as a possible regulator of cyanobacteria species composition in a shallow subtropical lake. *Freshw. Biol.* **39**, 547–56.
- Hecky R. E. & Kilham P. (1973) Diatoms in alkaline saline lakes. Ecology and geochemical implications. *Limnol. Oceanogr.* **18**, 53–91.
- Hebling W. E., Gao K., Ai H., Zengling M. & Villafane E. V. (2006) Differential responses of *Nostoc sphaeroides* and *Arthrospira platensis* to solar ultraviolet radiation exposure. *J. Appl. Phycol.* **18**, 57–66.
- Hillebrand H., Durselen D. C., Kirschtel D., Pollinger U. & Zohary T. (1999) Biovolume calculation for pelagic and benthic microalgae. *J. Phycol.* **35**, 403–24.
- Holling C. S. (1973) Resilience and stability of ecological systems. *Ann. Rev. Ecol. Syst.* **4**, 1–23.
- Jacoby J. M., Collier D. C., Welch E. B., Hardy F. J. & Crayton M. (2000) Environmental factors associated with a toxic bloom of *Microcystis aeruginosa*. *Can. J. Fish Aquat. Sci.* **57**, 231–40.
- Jenkin P. M. (1932) Reports on the Percy Sladen Expedition to some Rift Valley lakes in Kenya in 1929. VII. Summary of the ecological results, with special reference to the alkaline lakes. *Annals & Mag. Nat. Hist.* **9**, 133–81.
- Johnson P. W. & Sieburth J. M. (1979) Chroococoid cyanobacteria in the sea: A ubiquitous and diverse phototrophic biomass. *Limnol. Oceanogr.* **24**, 928–35.
- Kagami M. & Urabe J. (2001) Phytoplankton growth rate as a function of cell size: an experimental test in Lake Biwa. *Limnology* **2**, 111–7.
- Kaggwa M. N., Burian A., Oduor S. O. & Schagerl M. (2013) Ecomorphological variability of *Arthrospira fusiformis* (Cyanoprokaryota) in African soda lakes. *MicrobiologyOpen* **2**, 881–91.
- Kallqvist T. (1987) Primary Production and Phytoplankton in Lake Baringo and Lake Naivasha, Kenya. Report No. E8041905. Norwegian Institute for Water Research, Blindern, Oslo, 59 pp.
- Kebede E. (1997) Response of *Spirulina platensis* (= *Arthrospira fusiformis*) from Lake Chitu, Ethiopia, to salinity stress from sodium salts. *J. Appl. Phycol.* **9**, 551–8.
- Kociolek P. J. & Spaulding S. A. (2003) Symmetrical naviculoid diatoms. In: *Freshwater algae of North America: Ecology and Classification* (eds Wehr D. J. & Sheath G. R.) pp. 637–9. Academic Press, San Diego.
- Komarek J. (2003) Coccolid and colonial Cyanobacteria. In: *Freshwater Algae of North America: Ecology and Classification* (eds Wehr D. G. & Sheath G. R.) pp. 39–110. Academic Press, San Diego.
- Komarek J., Kling H. & Komarkova J. (2003) Filamentous cyanobacteria. In: *Freshwater Algae of North America:*

- Ecology and Classification (eds J. D. Wehr & R. G. Sheath) pp. 117–96. Academic Press, San Diego.
- Kong F. X. & Gao G. (2005) Hypothesis on cyanobacteria bloom-forming mechanism in large shallow lakes, allelopathy. *Acta Ecol. Sin.* **25**, 589–59.
- Krienitz L. & Kotut K. (2010) Fluctuating algal food populations and the occurrence of Lesser Flamingos (*Phoeniconaias minor*) in three Kenyan Rift Valley lakes. *J. Phycol.* **46**, 1088–96.
- Krienitz L., Dadheech K. P. & Kotut K. (2013) Mass developments of the cyanobacteria *Anabaenopsis* and *Cyanospira* (Nostocales) in the soda lakes of Kenya: ecological and systematic implications. *Hydrobiologia* **703**, 79–93.
- Latour D., Sabido O., Salencon M. J. & Girauet H. (2004) Dynamics and metabolic activity of the benthic cyanobacterium *Microcystis aeruginosa* in the Grangent reservoir (France). *J. Plankton Res.* **26**, 719–26.
- Manca M., Calderon A. & Mosselo R. (1992) Limnological research in Largo Maggiore: studies on hydrochemistry and plankton. In: Guilizzoni, P., tartari, G. & Guisaani, G. (eds.): Limnology in Italy. *Mem. Ist. Ital. Idrobiol.* **50**, 171–200.
- McDuff R. E. & Chisholm S. W. (1982) The calculation of in situ growth rate of phytoplankton population from fractions of cells undergoing mitosis: a clarification. *Limnol. Oceanogr.* **27**, 783–8.
- Melack J. M. (1976) Primary productivity and fish yields in tropical lakes. *Trans. Am. Fish. Soc.* **105**, 575–80.
- Muhling M., Harris N., Belay A. & Whitton A. B. (2003) Reversal of helix orientation in the cyanobacterium *Arthrospira*. *J. Phycol.* **39**, 360–7.
- Muhling M., Belay A. & Whitton A. B. (2005) Variation in fatty acid composition of *Arthrospira* (Spirulina) strains. *J. Appl. Phycol.* **17**, 137–46.
- Naselli-Flores L., Padis A. K. J. & Albay M. (2007) Shape and size in phytoplankton ecology: do they matter? *Hydrobiologia* **578**, 157–61.
- Oduor O. S. & Schagerl M. (2007a) Temporal trends of ion contents and nutrients in three Kenyan Rift Valley saline-alkaline lakes and their influence on phytoplankton biomass. *Hydrobiologia* **584**, 59–68.
- Oduor S. O., Schagerl M. & Mathooko J. M. (2003) On the limnology of Lake Baringo (Kenya): I. Temporal physico-chemical dynamics. *Hydrobiologia* **506–509**, 121–7.
- O'Farrell I., Pinto P. T. & Izaguirre I. (2007) Phytoplankton morphological response to the underwater light conditions in a vegetated wetland. *Hydrobiologia* **578**, 65–77.
- Oliver R. L. & Ganf G. G. (2000) Freshwater blooms. 2000. In: *The Ecology of Cyanobacteria: Their Diversity in Time and Space* (eds B. A. Whitton & M. Potts) pp. 149–94. Kluwer Academic Publishers, Dordrecht, the Netherlands.
- Paerl H. W. (1988) Nuisance phytoplankton blooms in coastal, estuaries, and inland waters. *Limnol. Oceanogr.* **33**, 823–47.
- Pigliucci M. (1996) How organisms respond to environmental changes: from phenotypes to molecules (and vice versa). *Tree* **11**, 168–73.
- Pizzolon L., Tracanna B., Prósperi C. & Guerrero J. M. (1999) Cyanobacterial blooms in Argentinean inland waters. *Lakes Reserv. Res. Manage.* **4**, 101–5.
- Reynolds C. S. (1997) Vegetation Processes in the Pelagic: A Model for Ecosystem Theory. Pp. 371 in O. Kinne, ed, Excellence in ecology. Ecology Institute, Oldendorf Luke, Germany.
- Rhode W. (1955) Productivity: Can plankton proceed during winter darkness in subarctic lakes? *Verh. Int. Ver. Limnol.* **12**, 117–22.
- Richardson J. L. & Richardson J. (1972) History of an African lake and its climatic implications. *Ecol. Monogr.* **42**, 499–534.
- Rippka R., Deruelles J., Waterbury J. B., Herman M. & Stainer R. Y. (1979) Generic assignments, Strain histories and properties of pure culture of cyanobacteria. *J. Gen. Microbiol.* **111**, 1–61.
- SAS Institute Inc. (2003) JMP® for Windows. Version 5.1 [computer program]. SAS Institute Inc., Cary, N.C.
- Schargel M. & Oduor S. O. (2003) On the limnology of Lake Baringo (Kenya): II Pelagic primary production of algal composition of Lake Baringo, Kenya. *Hydrobiologia* **121**, 506–509.
- Schagerl M. & Oduor O. S. (2008) Phytoplankton community relationship to environmental variables in three Kenyan Rift Valley saline-alkaline lakes. *Mar. Freshwater Res.* **59**, 129–36.
- Scheffer M. (1998) Ecology of Shallow Lakes p. 357. Chapman & Hall, London.
- Scheffer M., Hosper S. H., Meijer M. L., Moss B. & Jeppesen E. (1993) Alternative equilibria in shallow lakes. *Trends Ecol. Evol.* **8**, 275–9.
- Scheffer M., Rinaldi S., Gragnani A., Mur L. & Van Nes Scheffer E. H. (1997) On the dominance of filamentous cyanobacteria in shallow, turbid lakes. *Ecology* **78**, 272–82.
- Shubert E. (2003) Nonmotile coccoid and colonial green algae. In: *Freshwater Algae of North America: Ecology and Classification* (eds Wehr D. J. & Sheath G. R.) pp. 253–308. Academic Press, San Diego.
- Sitoki L., Kurmayer R. & Rott E. (2012) Spatial variation of phytoplankton composition, biovolume, and resulting

- microcystin concentrations in the Nyanza Gulf (Lake Victoria, Kenya). *Hydrobiologia* **691**, 109–22.
- Smayda J. T. (1990) Novel and Nuisance Phytoplankton Blooms in the Sea: Evidence for a Global Epidemic, Proceedings of the Fourth International Conference on Toxic Marine Phytoplankton: in E. Graveland and L. Elder, eds. (Elsevier Science Publishing Co., New York, 1990), Preprint 1-3.
- Smith V. H. & Bennet S. J. (1999) Nitrogen:phosphorus supply ratios and phytoplankton community structure in lakes. *Arch. Hydrobiol.* **146**, 37–53.
- Ssentongo G. W. (1979) On the fishes and fisheries of Lake Baringo. *Afr. J. Trop. Hydrobiol. Fish.* **3**, 95–106.
- Strickland J. D. H. & Parsons T. R. (1968) A practical handbook of Seawater analysis. Bull. Fisj. Res. Bd. Can. 167. 311 pp.
- Talling J. F. (1969) General Outline of Spectrophotometric methods. In R. A. Vollenweider, A Manual for measuring primary production in Aquatic Environments (Ed). R. A. IBP Handbook. 12, 22-24.
- Talling J. F. & Lemoalle J. (1998) Ecological dynamics of tropical inland waters. Cambridge University Press. (U. K.). 441p
- Talling J. F. & Talling L. (1965) The chemical composition of African lake waters. *Int. Rev. ges. Hydrobiol.* **50**, 421–63.
- Taylor P. A. & Williams P. J. L. (1975) Theoretical studies on the coexistence of competing species under continuous flow conditions. *Can. J. Microbiol.* **21**, 90–8.
- Tilman D. (1977) Resource competition between planktonic algae: an experimental and theoretical approach. *Ecology* **58**, 338–48.
- Tilman D. (1982) Resource Competition and Community Structure. Princeton University Press, Princeton, New Jersey, USA.
- Tilman D. (1985) The resource-ratio hypothesis of plant succession. *Am. Nat.* **125**, 827–52.
- Tokus Ogulu O. & Unal K. M. (2003) Biomass nutrient profiles of microalgae: *Spirulina platensis*, *Chlorella vulgaris* and *Isochrysis galbana*. *Food Chem. Toxicol.* **68**, 4.
- Utermohl H. (1958) Zur Vervollkommnung der quantitativen Phytoplankton-Methodik. *Mitt. Int. Ver. Theor. Ang. Limnol.* **9**, 1–38.
- Vareschi E. (1978) Ecology of Lake Nakuru (Kenya). I. Abundance and feeding of Lesser Flamingo. *Oecologia* **32**, 11–35.
- Vareschi E. & Vareschi A. (1984) Ecology of Lake Nakuru (Kenya). IV. Biomass and distribution of consumer organisms. *Oecologia* **61**, 70–82.
- Verspagen J. M. H., Snelder E. O. F. M., Visser P. M. *et al.* (2005) Benthic–pelagic coupling in the population dynamics of the harmful cyanobacterium *Microcystis*. *Freshwater Biol.* **50**, 854–67.
- Visser P. M., Ibelings B. W. & Mur L. R. (1995) Autumnal sedimentation of *Microcystis* spp. as a result of an increase in carbonate ballast at reduced temperature. *J. Plankton Res.* **17**, 919–33.
- Vonshak A. (1997) Spirulina: Growth, Physiology and Biochemistry. In: Spirulina platensis (Arthrospira): Physiology, Cell-Biology And Biotechnology (ed. Vonshak A.) pp. 43–65. Taylor and Francis Ltd., London.
- Wang P. Z. & Zhao Y. (2005) Morphological reversion of *Spirulina* (Arthrospira) platensis (Cyanophyta): from linear to helical. *J. Phycol.* **41**, 622–8.
- Waterbury J. B., Watson S. W., Guillard R. R. I. & Brand L. E. (1986) Widespread occurrence of a unicellular, marine, planktonic cyanobacterium. *Nature* **277**, 293–4.
- Wetzel R. G. & Likens G. E. (1991) Limnological analyses p. 391. Springer Verlag, New York, Inc.
- Worthington E. B. & Ricardo C. K. (1936) Scientific results of the Cambridge Expedition to the East African lakes 1930-31:15 – The Fish of Lake Rudolf and Lake Baringo. *J. Linn. Soc. Zool.* **39**, 353–89.
- Wu H., Gao K., Villafane E. V., Watanabe T. & Helbling W. E. (2005) Effects of solar uv radiation on morphology and photosynthesis of filamentous cyanobacterium arthrospira platensis. *Appl. Environ. Microbiol.* **71**, 5004–13.
- Zhang X. F., Kong F. X., Cao H. S., Tan J. K., Tao Y. & Wang M. L. (2005) Research on recruitment dynamics of blooms - forming cyanobacteria in Meiliang Bay, Taihu Lake. *Chin. J. Appl. Ecol.* **16**, 1346–50.
- Zielinska A. & Chojnacka K. (2009) The comparison of biosorption of nutritionally significant minerals in single and multi-mineral systems by the edible microalga *Spirulina* sp. *J. Sci. Food Agric.* **89**, 2292–301.