Phytoplankton primary productivity characteristics in response to photosynthetically active radiation in three Kenyan Rift Valley saline–alkaline lakes

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Phytoplankton photosynthetic characteristics in the Kenyan Rift Valley lakes Bogoria, Nakuru and Elmentaita were studied between November 2003 and February 2005. In these world-famous saline–alkaline lake systems, long-term continuous monitoring and photoautotrophic primary productivity modelling have been done for the first time. High light attenuation coefficients were observed with lakes means around $13\ m^{-1}$ reflecting the huge phytoplankton biomass. No photo-inhibition was observed in the primary productivity field measurements. High values of the photosynthesis–irradiance curve initial slope (α) up to 0.85 (mg O_2 mg Chl $a^{-1}\ h^{-1}$)(μmol photons $m^{-2}\ s^{-1}$)$^{-1}$ and a low onset of productivity saturation (E_k) down to 11.4 μmol photons $m^{-2}\ s^{-1}$ as an acclimation to poor light supply were found. For the trophogenic zone, high mean net primary production (NPP) rates of 6.8, 10.7 and 8.5 g $O_2\ m^{-2}\ day^{-1}$ were recorded for Bogoria, Nakuru and Elmentaita. For the whole water column, NPP decreased to -1.4, 1.6 and 7.2 g $O_2\ m^{-2}\ day^{-1}$ because of high community respiration. Modelling of the gross primary production (GPP, Chlorophyll a, light supply, initial slope α, maximum production rates considered) gave annual values of 4.9, 6.8 and 4.2 kg $O_2\ m^{-2}\ year^{-1}$, respectively, for Bogoria, Nakuru and Elmentaita, annual NPP values down to the compensation depth were 70, 65 and 55% of the GPP.

INTRODUCTION

Inland saline lakes are characterized by salinities of more than $3\ g\ L^{-1}$ and lacking connection to the marine environment. Their development is favoured by closed drainage (endorheic) conditions and they are common in the arid (25–200 mm annual precipitation) and semi-arid (200–500 mm annual precipitation) basins of the world (Hammer, 1986). Shiklomanov (1990) estimates that globally the volume of inland saline water systems (85 000 km^3) is just slightly less than that of freshwater systems (105 000 km^3). Williams (2002) describes these lakes as very important natural assets with considerable aesthetic, cultural, economic, recreational, scientific, conservation and ecological values for mankind.

Tropical saline alkaline lakes have been associated with high photoautotrophic primary productivity, being recognized as among the world's most productive ecosystems mainly through the studies of Talling *et al.*

(1973) and Melack and Kilham (1974). Phytoplankton productivity in lakes, estuaries and oceans plays an essential role in element cycling and food supply to heterotrophs (Cloern, 1996). For the saline alkaline endorheic lakes in arid and semi arid regions, the dependence on phytoplankton productivity is even greater since they tend to have minimal macrophyte growth and low allochthonous organic carbon input due to limited rainfall and inflows. The high phytoplankton biomass in most of these lakes further makes the contribution of microphytobenthic community to the productivity to be very low due to the resulting poor light climate in most of the water column other than the immediate surface zone.

Saline alkaline lakes offer restrictive biotopes with little faunal and floral diversity exploiting them but with very high biomass (Vareschi and Jacobs, 1985). Though poor in floral diversity, primary productivity in these lakes, especially the tropical ones, is very high most of the time due to high temperatures, intense irradiance and a constant photoperiod (Talling, 1965; Talling and Lemoalle, 1998). These attributes are also reflected in the three Kenyan Rift Valley saline–alkaline lakes of Bogoria, Nakuru and Elmentaita (Melack and Kilham, 1974; Vareschi, 1982; Melack, 1988). Their high phytoplankton productivity is mainly contributed by the enormous biomass of the cyanobacterium *Arthrospira fusiformis* (Vorochinin) Komarek (syn. *Spirulina fusiformis* Vorochinin) especially in L. Bogoria and Nakuru where it dominates the species-poor phytoplankton community most of the time (Ballot *et al.*, 2004). A large consumer population, which include birds, zooplankton and fish among others, are supported by this phytoplankton biomass directly and indirectly. The bird population is dominated by the lesser flamingo *Phoeniconaias minor* Geoffroy, the greater flamingo *Phoenicopterus ruber ruseus* Pallas and the pelicans *Pelecanus onocrotalus* L. (Vareschi, 1978). The zooplankton community is composed of the rotifers *Brachionus dimidiatus* Bryce and *B. plicatilis* Muller,

the copepod *Lovenula africana* Daday and a few insects species (Vareschi and Vareschi, 1984; Yasindi *et al.*, 2002; Harper *et al.*, 2003). The introduced tilapine fish (*Oreochromis alcalicus grahami* Boulenger) is mainly found in L. Nakuru with a small biomass also present in L. Elmentaita.

While some primary production experiments have been done in these lakes, few of them have involved long-term continuous monitoring and none has used models for the estimation of temporal productivity. Modelling under consideration of continuously recorded irradiance data makes the exercise more accurate in the long run and we therefore included such calculations in this study. Another goal of this investigation was to study temporal dynamics of primary productivity and the fluctuations of the photosynthesis–irradiance (P–E) parameters. Most of the works on primary productivity studies in these lakes were done in the 1970s with minimal temporal follow up of the P–E dynamics (Melack and Kilham, 1974) and for the last 25 years no study on P–E parameters on these lakes has been published. This study aimed to estimate productivity and compare these data with those obtained from previous studies so as to establish the trend of these lakes primary productivity. In addition, we compared photosynthetic parameters and primary production of the phytoplankton community of the Lakes Nakuru, Elmentaita and Bogoria.

METHOD

Study area and sites description

This study was done in three Kenyan Rift Valley saline–alkaline lakes of Bogoria, Nakuru and Elmentaita. Location and morphometric characteristics of these lakes are given in Table I. Throughout the sampling period, high incident radiation was recorded

Table I: *Geographical locations of the study lakes and the sampling sites for primary productivity and morphometric characteristics of the Lakes Bogoria, Nakuru and Elmentaita (McCall, 1967; Vareschi, 1982; Melack, 1988; Mwaura and Moore, 1991; Harper et al., 2003)*

	Lake Bogoria	Lake Nakuru	Lake Elmentaita
Geographical position	N 00° 15′ E 36° 05′	S 00° 20′E 36° 05′	S 00° 27′E 36° 15′
Sampling site	00° 15′43″N, 036° 05′32″E	00° 21′12″S, 036° 05 00″E	00° 26′ 06″S, 036° 14′44″E
Altitude (m a. s. l)	990	1759	1782
Surface area (km^2)	34	40	20
$Z_{(mean)}$ (cm)	575 ± 16	110 ± 3	46 ± 3
$Z_{(max)}$ (cm)	1020	450	300
Catchment area (km^2)	1500	1800	500
Rainfall (mm year^{-1})	700	800	600–1200

other than during the cloudy days with mean light values during the day ranging between 800 and 1850 µmol photons $m^{-2} s^{-1}$. Day temperatures ranged between 25 and 35°C with minimal fluctuations throughout the year. Daily breezes from the late afternoon into the evening are characteristic of this region. This causes polymictic conditions resulting in diel cycles of thermal stratification around midday and an isothermal state at night. The lakes are located in a semi-arid area with a highly variable rainfall. The long rainy season is normally observed between April and June, whereas short rains are typical around late October to November. High water loss experienced through evaporation coupled with the seasonal rainfall pattern results into temporal fluctuations of lake water levels. For a detailed description of physico-chemical characteristics, see Oduor and Schagerl (2006).

Lake Bogoria is located in the north-western part of Kenya, ~270 km from Nairobi. It is a Ramsar site surrounded by the L. Bogoria Game Reserve and fed by a few impermanent springs from the escarpment on the east and west that includes the Emsoss and the Wasagess rivers flowing from the north. No macrophytes grow along its shores except near hot freshwater springs where low growing salt tolerant grasses such as *Sporobolus spicata* (Vahl) Kunth. and sedges such as *Cyperus rubicundus* Vahl. and *C. laevigatus* L. may be found (Harper *et al.*, 2003).

Lake Nakuru is a shallow pan lying next to the Nakuru town and is surrounded by the Lake Nakuru National park. It is recharged mainly by rainfall which is low with peaks during April/June and October (Fig. 1). It receives inflows from three seasonal surface streams, namely the Njoro, Makalia and Nderit draining from the Mau Forest and a small spring, the

Fig. 1. Lake Nakuru monthly rainfall data (L. Nakuru weather station) and the water level fluctuations observed during this study period from November 2003 to February 2005.

Baharini springs at the northern end. The effluent from the town's sewage system is also discharged into the lake.

Lake Elmentaita is a very shallow pan floored by coarser salt-impregnated sedimentary material. It is fed by three highly seasonal small streams, the Mbaruk, Kariandus and Memeroni. Some hot springs along the southern end of the lake supply water but the quantity is very low to influence the lake's water volume. Due to the dry spells and its endorheic nature, heavy evaporation takes place making the lake dry up at times.

Monthly samplings were carried out between November 2003 and February 2005. Rainfall data for L. Nakuru were provided by the L. Nakuru National park weather station and solar radiation data received in this area were provided by the Kenya Meteorological Services (Nakuru Weather Station). The daily radiation given in MJ $m^{-2} day^{-1}$ data was converted into mol photons $m^{-2} day^{-1}$ by a conversion factor of 4.6 and assuming that PhAR was 45% of total solar radiation (Kohl and Niklisch, 1988; Wetzel and Likens, 1991). Underwater radiation further considered a loss of 5% of irradiance impinging on the water surface to reflection (Wetzel and Likens, 1991). For production models (see below), daily radiation was divided into 5 min intervals by combining the daily radiation obtained from the weather station with real 24 h PhAR measurements recorded on sampling days at the water surface (datahog l, Skye instruments, recording interval was 5 min).

Three offshore sampling sites, at least 500 m from the nearest shoreline were selected in each of the three lakes. The geographical locations for each of these sites are given in Table I (Magellan Sportrak GPS Thales Navigation). Light levels were measured at the surface, 10, 20, 30, 50, 60, 80 and 100 cm depths with the light metre (SKP 200, Skye Instruments) and the mean light attenuation coefficient K_d (m^{-1}) was calculated from these measurements (Kirk, 1994). Water samples were collected from an integrated depth of 40 cm from the surface using an Schindler sampler. After vigorous shaking, transparent and dark bottles were filled immediately with the sample for the estimation of primary productivity. The filled duplicate transparent and dark bottles were suspended vertically at specific depths. Oxygen content was determined after incubation experiments lasting between 45 and 60 min carried out around midday by means of an oxygen probe (WTW 340i with a battery stirrer). Volume to area conversion of photosynthesis was done by the trapezoidal integration of the depth-productivity curve area. The daily areal productivity of the sampling days was determined from the hourly values by multiplying
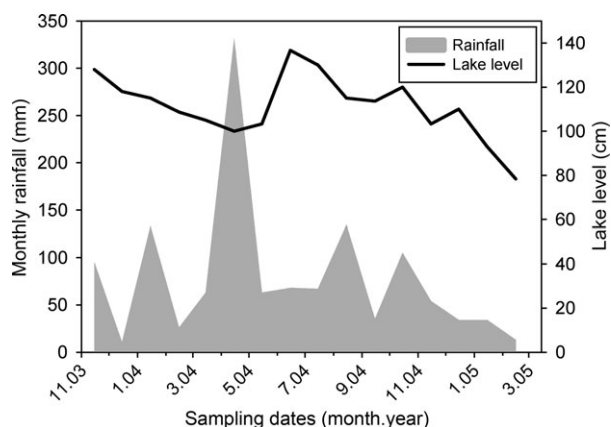
the hourly productivity values by the number of hours of sunlight and a factor of 0.9 according to Talling (1965) and Talling et al. (1973).

Chlorophyll a (Chl a) was extracted using 90% acetone after gentle vacuum filtration under dim light through Ederol BM/C filters. The filters were stored at $-20°C$ for a minimum of 8 h to aid in the bursting of the cells, then homogenized in a tissue grinder covered with the extraction solvent. After 12 h extraction time at $+4°C$ in the dark, the extract was centrifuged and the absorbance of the supernatant measured spectrophotometrically at 663 nm (Pharmacia Biotech Novaspec II). Chl a concentrations were calculated according to Talling and Driver (1961).

Samples for phytoplankton biovolume estimation were fixed using 3% Lugoĺs iodine and stored in brown bottles. Using an inverted microscope (Nikon Diaphot), quantitative analysis of these samples was done through cells counting and measurements at $400×$ magnification according to Utermöhl (1958). Biovolumes of the various taxa were estimated using geometric formulae of the shapes of the respective cells according to Sun and Liu (2003), Hillebrand et al. (1999) and Tümpling et al. (1999). At least 20 cells for each taxon identified were measured and the mean of the measurements used to work out the biovolumes. The cell biovolume was converted to biomass by using the conversion factor 1 (Wetzel and Likens, 1991).

P–E dependence was determined using Chl a normalized values by fitting the maximum gross photosynthetic rate P_{max}^B, the initial slope (α^B) and photoinhibition (β^B) according to the empiric equation of Platt et al., (1980) to the measured values (least squares method using Excel Solver): actual Production P [mg O_2 (mg Chl a)$^{-1}$ h^{-1}] at a given irradiance E (μmol photons m^{-2} s^{-1}) is $P = P_s^B (1-e^{-a}) e^{-b}$. Expression a corresponds to; $a = \alpha^B E/P_s^B$ and $b = \beta^B E/P_s^B$. P_s^B is a scaling factor for the specific productivity termed as the maximum potential photosynthetic rate and β^B characterizes the photoinhibition process [mg O_2 (mg Chl a)$^{-1}$ h^{-1} (μmol m^{-2} s^{-1})$^{-1}$]. Its value relates to maximum specific productivity P_{max}^B in that when $\beta^B > 0$, then $P_s^B > P_{max}^B$. If $\beta^B = 0$, then $P_s^B = P_{max}^B$.

The equation after Jassby and Platt (Jassby and Platt, 1976) was used to generate the estimated daily and annual productivity in the lakes after establishing that there was no photoinhibition noticeable. According to this model, the actual gross production P [mg O_2 (mg Chl a)$^{-1}$ h^{-1}] at a given irradiance E (μmol photons m^{-2} s^{-1}) is $P = P_{max}^B$ tanhyp $[(\alpha^B E)/P_{max}^B)]$, where P_{max}^B is the maximum photosynthetic rate [mg O_2 (mg Chl a)$^{-1}$ h^{-1}] and α^B is the initial slope [mg O_2 (mg Chl a)$^{-1}$ h^{-1}(μmol photons m^{-2} s^{-1})$^{-1}$]. For

computation of the daily aerial photosynthesis, the model equation and irradiances, E_z in 5 min interval at the given depths were used. The depths (z) were calculated as follows: the water column was partitioned into layers with an upper limit and a lower limit of $l_i = (n_i+n_i^2)/2$, where n_i is the thickness of the layer (cm units). The depth z in the middle of the layer was used for the mean light supply E_z in this layer and was calculated by aid of the attenuation coefficient K_d: $E_z = \exp$ (ln $E_0 - K_d$ Z), where E_0 is the given surface radiation. Annual production was estimated through summation of daily production values generated from the model. To compare our annual primary productivity estimates to the productivity of other biomes, the biomes net primary production (NPP) (g organic matter m^{-2} year^{-1}) from the literature were converted to NPP (g O_2 m^{-2} year^{-1}) using the factor 0.465 (organic matter to C), the carbon–oxygen mole ratio and the productivity quotient 1.2 (APHA, 1995). The variable data were analysed for correlation and regression using the SPSS 12.0 statistical package.

RESULTS

An overview of physical and chemical variables of these lakes observed during this study is listed in Table II.

Table II: Physico-chemical variables, nutrients and Chlorophyll a values in the three saline– alkaline lakes during the study period

Variable	Bogoria	Nakuru	Elmentaita
Total phosphorus (μM L^{-1})	202 ± 2	78 ± 2	40 ± 3
SRP (μM L^{-1})	137 ± 4	19 ± 1	3 ± 0
Dissolved organic P (μM L^{-1})	36 ± 4	44 ± 3	28 ± 4
Total nitrogen (μM L^{-1})	291 ± 16	846 ± 44	869 ± 46
Nitrate (μM L^{-1})	5 ± 0	23 ± 1	5 ± 1
Ammonium (μM L^{-1})	3 ± 0	11 ± 2	25 ± 0
Dissolved organic N (μM L^{-1})	166 ± 10	666 ± 42	601 ± 34
Silica (μM L^{-1})	997 ± 36	1709 ± 178	1816 ± 178
Chlorophyll a (μg L^{-1})	388 ± 26	646 ± 34	267 ± 29
Phytoplankton biomass (mg L^{-1})	31.9 ± 4.2	60.4 ± 2.6	28.6 ± 4.3
pH	9.93 ± 0.04	10.35 ± 0.02	9.90 ± 0.07
Conductivity (mS cm^{-1})	70.4 ± 0.0	28.5 ± 0.6	37.9 ± 4.0
Salinity (‰)	49 ± 0	18 ± 0	26 ± 0
Oxygen conc. (mg L^{-1})	13.1 ± 1.3	17.1 ± 0.9	9.2 ± 0.8
Water temperature °C	27.9 ± 1.7	24.1 ± 1.6	23.1 ± 2.3
Alkalinity (meq L^{-1})	1132 ± 14	327 ± 10	376 ± 37
Cl$^-$ (meq L^{-1})	176.0 ± 59.9	67.3 ± 15.0	215.0 ± 136.9
SO$_4^{2-}$ (meq L^{-1})	8.2 ± 0.3	5.0 ± 1.4	14.1 ± 9.5
F$^-$ (meq L^{-1})	72.3 ± 16.5	17.4 ± 5.3	70.5 ± 49.1
Na$^+$ (meq L^{-1})	1348.7 ± 50.6	413.1 ± 98.4	718.8 ± 537.4
K$^+$ (meq L^{-1})	19.2 ± 2.3	8.5 ± 2.6	15.9 ± 12.7

Values given as means ± SE.

Table III: Curve fitted mean specific P–E parameters values according to Platt et al. (1980) in the three Rift Valley saline–alkaline lakes during the study period

Parameter	Bogoria	Nakuru	Elmentaita
P_s^B	11.8 ± 1.0	8.6 ± 0.7	20.9 ± 3.1
P_{max}^B	12.1 ± 1.1	8.1 ± 0.6	18.6 ± 2.0
α^B	0.34 ± 0.1	0.19 ± 0.04	0.25 ± 0.07
β^B	<0.001	<0.001	<0.001
E_k	40.7 ± 7.1	37.8 ± 5.7	128.1 ± 32.4
K_d	12.7 ± 0.2	13.8 ± 0.3	12.5 ± 0.3
E_0	1107 ± 75	1105 ± 34	1044 ± 51

Values given as mean $\pm$ SE. P_s^B and P_{max}^B [mg O_2 (mg Chl a)$^{-1}$ h^{-1}], α^B and β^B [mg O_2 (mg Chl a)$^{-1}$ h^{-1} (μmol photons m^{-2} s^{-1})$^{-1}$], E_k and E_0 (μmol photons m^{-2} s^{-1}), K_d (m^{-1}).

More discussions on these variables may also be found in various papers (Millbrink, 1977; Melack, 1988; Harper *et al.*, 2003; Ballot *et al.*, 2004; Oduor and Schagerl, 2006).

Underwater light climate

Poor underwater light climate characterized these lakes with high light attenuation coefficients observed during this study (Table III). Correspondingly, low Secchi
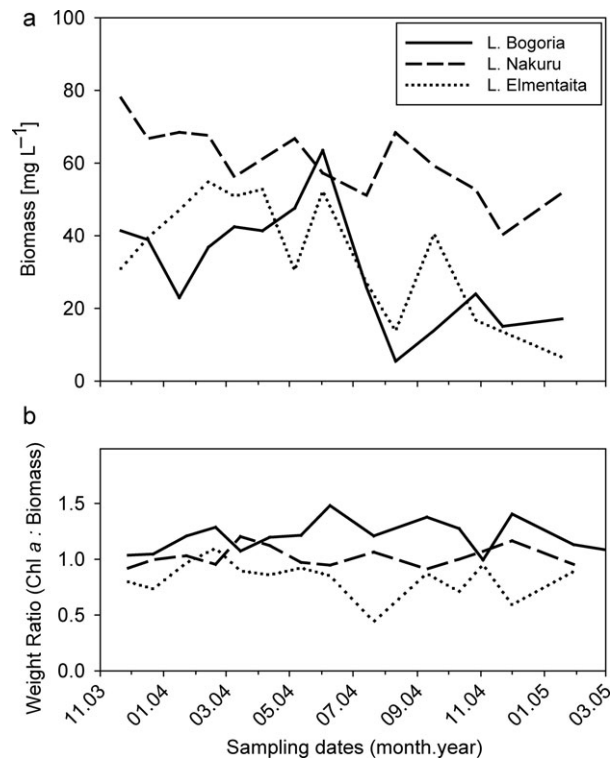

Fig. 2. Temporal trend of phytoplankton biomass (top) and the chlorophyll *a* concentration to phytoplankton biomass ratio (bottom) in the three lakes during this study.

depth readings were recorded with a mean of 25.7 ± 0.8 (SE) cm, 27.6 ± 0.6 (SE) cm and 19.9 ± 0.1 (SE) cm, respectively, for the lakes Bogoria, Nakuru and Elmentaita.

Phytoplankton biomass and Chl *a*

High phytoplankton biomass characterized these lakes during most of the time but with large temporal fluctuations especially for L. Bogoria and Elmentaita (Fig. 2a). The biomass ranged from 6.5 to 54.8 mg L^{-1} for L. Elmentaita, 40.3 to 77.9 mg L^{-1} for L. Nakuru and from 5.8 to 51.4 mg L^{-1} for L. Bogoria (Table II, Fig. 2a). Though the contribution of *A. fusiformis* to the total biomass was high in all the three lakes most of the time, diatoms and the green alga *Monoraphidium minutum* were recorded in higher abundances especially for L. Elmentaita. High Chl *a* concentrations were observed with L. Bogoria having monthly mean values ranging from 74 to 831 μg L^{-1}, for L. Nakuru it ranged between 295 and 1336 μg L^{-1}, and for L. Elmentaita from 42 to 871 μg L^{-1} (Table II). The mean percentage ratio of Chl *a*: biomass was high with a mean of 1.12% (range 0.90 to 1.41%) for L. Bogoria, 1.05% (range 0.91 to 1.32%) for L. Nakuru and 0.80% (range 0.51 to 1.10%) for L. Elmentaita. Temporal trends of this ratio showed minimal fluctuations most of the time except between July and November 2004 in L. Elmentaita and L. Bogoria (Fig. 2b).

Field measurements of pelagic primary productivity

High daily rates of primary production characteristic of hypertrophic tropical lakes were observed (Table IV). Mean hourly gross primary production rates were 1.45 ± 0.11 (SE), 1.75 ± 0.16 (SE) and 0.94 ± 0.10 (SE) g O_2 m^{-2} h^{-1} respectively for L. Bogoria, L. Nakuru and L. Elmentaita. Corresponding net rates were 1.05 ± 0.10 (SE), 1.33 ± 0.13 (SE) and 0.64 ± 0.08 (SE) g O_2 m^{-2} h^{-1}. Higher primary productivity values were measured between April and May during the rainy period while low values typically were found between September and October. Photosynthesis was confined within a narrow zone near the surface of $\sim$50 cm for L. Bogoria and Nakuru while L. Elmentaita had $<$30 cm euphotic depth.

Photosynthesis–irradiance relationship

Compared to other lake ecosystems, high values of the photosynthetic–irradiance (P–E) parameters (P_{max}^B and α^B) and low onsets of the photosynthetic saturation

Table IV: *Ranges and mean (parenthesis) measured primary productivity values of this study and the previously published work (Bracketed values with superscript ()^a are productivity values determined through the diel changes in oxygen concentration in free water)*

Lake	GPP (g O_2 m^{-2} day^{-1})	NPP (g O_2 m^{-2} 12 h^{-1})	NPP (g O_2 m^{-2} day^{-1})	Reference
Aranguadi	(47–57)[a]			Talling et al., 1973
Bogoria	4.0 to 22.2 (16.9 ± 1.4)	7.9 to 19.9 (11.4 ± 1.1)	−13.1 to 8.7 (−1.4 ± 0.2)	This study
Elmentaita	2.0 to 23.2 (10.1 ± 1.5)	1.0 to 17.0 (6.9 ± 1.2)	−2.4 to 25 (7.2 ± 0.2)	This study
Elmentaita	0.5 to 1.2			Livingstone and Melack, 1984
Naivasha	12	9.8		Millbrink, 1977
Nakuru	10.0 to 30.0 (20.0 ± 6.7)	7.5 to 22.8 (14.4 ± 1.4)	−7.6 to 11.5 (1.6 ± 0.2)	This study
Nakuru	12.5 to 25.2	6.4 to 21.1	0.1 to 11 (1.0 to 3.5)	Vareschi, 1982
Nakuru	5.4 to 8.6 (22 to 38)[a]			Melack and Kilham, 1974
Nakuru	8.8			Millbrink, 1977
Sonachi	−0.7 to 18.7 (4.5 to 22.3)[a]	1.4 to 6.8	−3 to 12.0	Melack, 1988

(E_k) were observed (Table III). Specific initial slopes (α^B) and specific maximum photosynthetic rates (P^B_{max}) varied significantly between L. Elmentaita and the other two lakes (Kruskal–Wallis ranked test, $P < 0.05$, $n = 35$). While L. Bogoria and Nakuru had very low E_k, values with the averages of 40.7 ± 7.5 (SE) and 13.8 ± 0.3 (SE) µmol photons m^{-2} s^{-1} respectively, L. Elmentaita had significantly higher values with a mean of 128.1 ± 32.4 (SE) µmol photons m^{-2} s^{-1} (Table III). Compared to the other values of P–E parameters from other ecosystems, the values generated from this study are much higher and are expected of the tropical regions (Table V).

Modelling of primary productivity

A significant correlation and a good fit were observed between the field measured gross primary productivity and values generated with the model (Wilcoxon ranked test; L. Bogoria, $P = 0.463$, L. Nakuru, $P = 0.245$ and L. Elmentaita, $P = 0.346$) (Fig. 3). Though L. Nakuru gave high GPP rates with a maximum of 31.4 g O_2 m^{-2} day^{-1}, its NPP values down to the lake bottom (mean depth 1.1 m) were very low with a mean of only

1.6 ± 0.2 (SE) g O_2 m^{-2} day^{-1}. However, its NPP down to the compensation depth is relatively high [10.7 ± 0.2 (SE) g O_2 m^{-2} day^{-1}]. The model shows that in all the lakes, over 90% of primary productivity was confined within 0.4 m depth from the surface with only insignificant productivity below 1 m depth in both L. Bogoria and L. Nakuru (Table VI). On an annual basis, GPP values generated were very high but due to the high community oxygen demand in L. Nakuru and L. Bogoria, the annual NPP values were drastically reduced with L. Bogoria generating a mean negative value below 1 m (Table VII). However, its annual NPP within the trophogenic zone compares well with some of the highest producing biomes in the world (Table VII). The model shows reduction in primary productivity in all the lakes from July up to November 2004, followed by an increase in GPP in L. Bogoria and Nakuru (Fig. 4).

DISCUSSION

Pelagic primary productivity is the key source for higher trophic levels in lakes with minimal macrophyte growth

Table V: *Comparison of the ranges of P–E parameters from this study with others published from different locations (P^B_{max} (mg O_2 mg Chl a^{-1} h^{-1}), α^B ((mg O_2 mg Chl a^{-1} h^{-1})(µmol photons m^{-2} s^{-1})$^{-1}$)and E_k (µmol photons m^{-2} s^{-1}), E_k (µmol photons m^{-2} s^{-1}))*

| Reference	Location	P^B_{max}	α^B	E_k
This study	Bogoria, Kenya	6.0 to 17.6	0.15 to 0.70	15.6 to 88.8
This study	Nakuru, Kenya	5.0 to 10.8	0.06 to 0.57	19.3 to 168.3
This study	Elmentaita, Kenya	11.2 to 43.9	0.05 to 0.85	11.4 to 428.3
Talling, 1965	Victoria, E. Africa	20.0 to 30.0		46.0 to138.0
Talling et al., 1973	Kilotes, Ethiopia	16.3 to 27.6		
Talling et al., 1973	Aranguadi, Ethiopia	11.0 to 18.0		
Melack, 1988	Sonachi, Kenya	6 to 13		
Gervais and Behrendt, 2003	Müggelsee, Germany	4.5 to 15.8	0.02 to 0.06	255 to 280
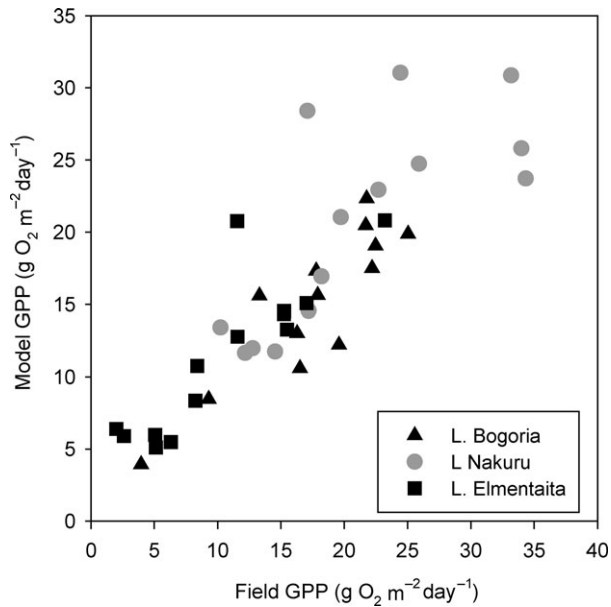
Fig. 3. Comparison of field and model GPP relationship for the Rift Valley saline−alkaline lakes during this study.

as in the saline alkaline lakes. With high consumer biomass as observed in the Kenyan Rift Valley saline alkaline lakes, the demand on primary producers is even higher. Vareschi (1978) estimated for L. Nakuru that a single adult flamingo takes up ∼70 g dry mass of *Arthrospira* daily. He further stated that this rate may vary from one lake to the other due to the variations on the size of *Arthrospira* in the different lakes as well as on the phytoplankton biomass present at the given time. Based

Table VI: Daily (24 h) primary production rates generated by the Jassby and Platt (1976) model for the studied Rift Valley saline−alkaline lakes down to the specified depths (mean) from the surface

Lake	GPP (g O_2 m^{-2} day^{-1})	NPP (g O_2 m^{-2} day^{-1})
Bogoria (compensation depth−0.36 m)	3.5 to 21.8 (12.1 ± 0.2)	−0.4 to 14.2 (6.8 ± 0.2)
Bogoria (chemocline - 1.00 m)	3.9 to 23.6 (13.3 ± 0.2)	−13.3 to 8.7 (−1.4 ± 0.3)
Nakuru (compensation depth−0.38 m)	7.8 to 27.0 (16.6 ± 0.2)	4.1 to 19.7 (10.7 ± 0.2)
Nakuru (whole lake depth - 1.10 m)	8.0 to 31.4 (17.6 ± 0.2)	−7.6 to 11.5 (1.6 ± 0.2)
Elmentaita (compensation depth - 0.37 m)	4.3 to 28.4 (11.7 ± 0.2)	0.8 to 25.3 (8.5 ± 0.2)
Elmentaita (whole lake depth - 0.43 m)	4.3 to 29.0 (11.7 ± 0.3)	−5.8 to 20.4 (7.2 ± 0.2)

Values given as range and mean with standard error in parenthesis (mean ± SE).

on this estimate and the fact that flamingo numbers in a single lake may sometimes be over one million birds, the uptake from the lake may go up to over 70 g dry mass of *Arthrospira* being removed per day. If we estimate a conversion factor of 1.37 from *Arthrospira* dry mass to oxygen productivity (1 g $O_2 \equiv 14.6$ kJ; (Brylinsky, 1980; 1 g *A. fusiformis* dry mass $\equiv 20$ kJ; Vareschi and Jacobs, 1985), a daily net productivity demand of around 2.4 g O_2 m^{-2} day^{-1} for 1 million birds is needed, which is exceeded with ease in our models (Table VII). However, one has to consider the demand from other consumers like fish and zooplankton, which complete the picture of a very high requirement on primary productivity in these lakes. Though our measured primary productivity values were high with the maximum GPP being 29.7 g O_2 m^{-2} (12 h)$^{-1}$ measured on 21 April 2004 at L. Nakuru, higher values have been reported from other lakes in this region (Table IV). Using the diurnal changes in oxygen concentration in free water, Melack and Kilham (1974) obtained gross primary productivity values from 31 to 36 g O_2 m^{-2} (12 h)$^{-1}$ for L. Nakuru. Highest GPP rates of 57 g O_2 m^{-2} day^{-1} were recorded for L. Aranguadi (Ethiopia) by Talling *et al.* (1973). Beside differences in the consideration of respiration (12 or 24 h), reasons such as oxygen losing as a result of super-saturation in the bottles in experiments taking long times, lack of mixing within the bottles that results into lack of fluctuations in the irradiance received by the cells have been suggested to be major causes of the lower values got with the bottles when compared with the free water method (Melack and Kilham, 1974; Orlando and Zucchi, 2001). We tried to overcome those problems by vigorous shaking of the canister (for lowering the initial oxygen content) and short exposure times (maximum was 1 h).

From the Jassby and Platt (1976) model, high annual GPP values were generated confirming the high photosynthetic capacity of phytoplankton in these lakes. However, NPP rates integrated over the lake's depth and 24 h were quite low (Fig. 4). The decreased NPP rates inspite of the high GPP rates in these lakes was commented already by Vareschi (1987) who stated that these rates were comparable to those of eutrophic lakes in the temperate regions. Poor light climate in the water column below 0.5 m in L. Nakuru and L. Bogoria makes a large part of the water column dark and dependent on the energy generated within the narrow trophogenic zone.

The NPP values are more important ecologically as they represent the energy available to other trophic levels. However, the cardinal problem in determining net primary productivity is the issue of respiration since respiration measured is always whole community

Table VII: *Comparison of model generated annual GPP and NPP values estimates down to various depths from this study with published values from other biomes and ecosystems*

Ecosystem type	GPP (g O_2 m^{-2} year^{-1})	NPP (g O_2 m^{-2} year^{-1})	Reference
Tropical rainforest		1488–5208 (2381)	Whittaker and Likens, 1975
Savannah		298–2976 (1339)	Whittaker and Likens, 1975
Lake and stream		149–2232 (595)	Whittaker and Likens, 1975
Swamp and marsh		1190–5208 (4464)	Whittaker and Likens, 1975
L. Elmentaita (whole depth–0.43 m)	4207	2649	This study
L. Elmentaita (down to compensation depth - 0.37 m)	4281	3106	This study
L. Nakuru (whole depth–1.10 m)	6854	615	This study
L. Nakuru (down to compensation depth–0.38 m)	6440	4164	This study
L. Bogoria (down to chemocline depth–1.00 m)	4875	−496	This study
L. Bogoria (down to compensation depth–0.36 m)	4436	2486	This study
Lake Sonachi, Kenya		1580	Melack, 1988

respiration. Due to this, model estimates of NPP taken as a difference between GPP and respiration tend to show negative values on some days due to high community respiration, especially when 24 h are considered. This explains the huge difference between GPP and NPP in the lakes Bogoria and Nakuru from our models (Fig. 4) when compared with L. Elmentaita. The high
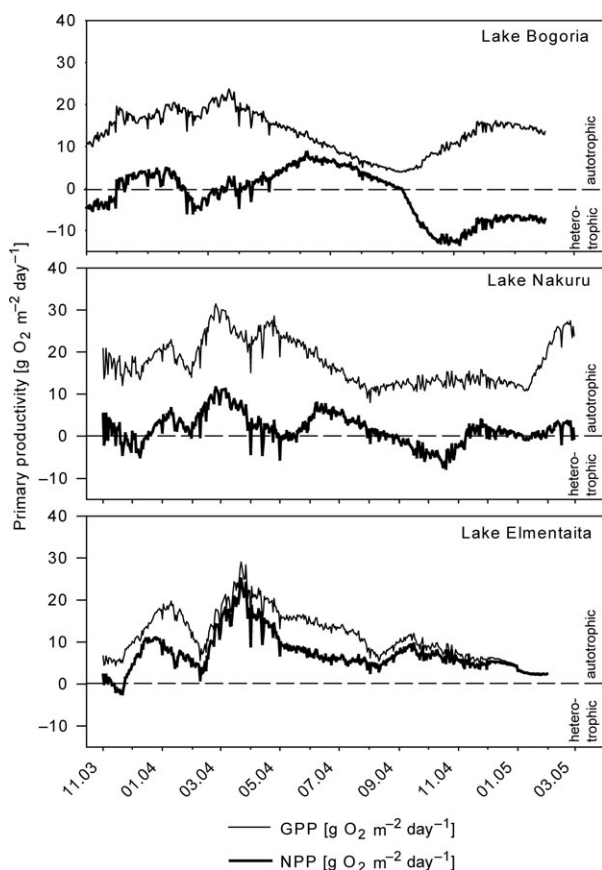

Fig. 4. GPP and NPP generated by the Jassby and Platt (1976) model for the chemocline in L. Bogoria and the whole water column in Nakuru and Elmentaita.

oxygen demand may be attributed to the high community respiration especially from the huge microbial biomass as suggested by Kilham (1981) and Yasindi *et al*. (2002). Oxygen demand in L. Bogoria was even enhanced by an algal crash that occurred between July and September 2004. We assume that microbes decomposing dead algae required some oxygen thereby lowering the community NPP values below zero between September 2004 and February 2005 (Fig. 4, Table VI).

While the values generated by the model compare well with the field data published by other authors, these values may still be underestimates of primary productivity in these lakes. Gervais and Behrendt (2003) state that estimating daily productivity from midday incubation by assuming that primary productivity is proportional to the global radiation as we did, has some considerable error of about $\pm 30\%$. This could be due to the dynamic diurnal pattern in the relationship between productivity and irradiance that can be related to chlorophyll content, photoinhibition, nutrition or feedback inhibition by accumulated photosynthates (Prezelin *et al*., 1991; Henley, 1993; Schubert and Forster, 1997).

In spite of the high continuous incident irradiance at the surface, light limitation within the water body is still a major factor lowering productivity in some tropical lakes (Talling, 2001). The high phytoplankton biomass and the resulting self-shading makes the underwater light climate poor due to strong light attenuation. This limits light availability within a narrow zone near the water surface (Vareschi and Jacobs, 1985; this study). Various adaptations to this poor light climate include presence of aerotopes as in *A. fusiformis* for appropriate positioning for light harvesting, and physiological acclimation of reaching P_{max} at low irradiance (E_k) as shown by the low E_k values and steep initial slopes (α) in these lakes (Table IV; Harris, 1978).

Variations in P_{max}^B observed in this study could be attributed to the temporal changes in the phytoplankton

composition. This type of fluctuation is a common feature in natural populations of phytoplankton (Cote and Platt, 1983; Kyewalyanga *et al.*, 1998; Raven and Geider, 2003). This might explain the greater fluctuations in $P–E$ parameters observed in L. Elmentaita when compared with the other two lakes, since it had more diverse phytoplankton taxa showing big variations in species composition during this study (Schagerl and Oduor, subm.). Cote and Platt (1983) and Harding *et al.* (1982) observed that the onset of saturation (E_k) expresses the phytoplankton photoacclimational state. Even though a correlation was observed between P_{max} and irradiance, P_{max} is not dependent on the incident irradiance (Harris, 1978). Compared to other previous studies in this region, the P_{max} values from our study fall within the ranges reported by these authors, confirming the high photosynthetic capacity of the phytoplankton in these lakes (Table V).

In conclusion, it can be appreciated that though the conditions prevailing in the Rift Valley saline–alkaline lakes tend to inhibit the growth of diverse phytoplankton community, it is conducive for exploitation by the well-adapted organisms. The relatively abundant nutrients supply, high water temperature, daily constant photoperiodicity and the rapid growth of the well adapted *A. fusiformis* and other phytoplankton allow for provision of adequate organic matter. This then provides nutrition to the large number of consumers inhabiting these lakes whose livelihood is dependent mainly on the pelagic primary productivity of the phytoplankton.

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