

Seasonality of Primary productivity of phytoplankton of Lake Bosomtwe, Ghana -West Africa

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Abstract

The primary productivity and seasonality of phytoplankton and its seasonality in Lake Bosomtwe (Ghana), West Africa were studied from September 2005 to August 2006 using the dissolved oxygen method. The wet weight biomass ($0.41 \pm 0.37 \text{ gCm}^{-2}\text{d}^{-1}$, $n=25$), Chlorophyll *a* ($52.11 \pm 19.51 \text{ mg m}^{-2}$, $n=17$), mixed layer depth ($9.28 \pm 3.47 \text{ m}$, $n=25$), euphotic depth ($4.43 \pm 1.76 \text{ m}$, $n=25$), ratio of mixed layer to euphotic depth (2.17 ± 0.74 , $n=25$), secchi disc depth ($1.52 \pm 0.34 \text{ m}$, $n=25$), irradiance ($1180 \pm 341.28 \text{ } \mu\text{E m}^{-2}\text{s}^{-1}$, $n=25$), extinction coefficient (0.97 ± 0.46 , $n=25$), and total phosphorus concentrations ($1.84 \pm 0.49 \text{ } \mu\text{mol L}^{-1}$, $n=20$) were measured to assess their influence on the productivity of the phytoplankton. Our assessment revealed high areal gross productivity of the phytoplankton ($4.72 \pm 1.56 \text{ gC m}^{-2} \text{ d}^{-1}$, $n = 25$) which is within the range for tropical African lakes, but concurrent high areal community respiration rates ($4.34 \pm 2.78 \text{ gC m}^{-2} \text{ d}^{-1}$, $n = 25$) contributed to a low net productivity ($0.37 \pm 2.32 \text{ gC m}^{-2} \text{ d}^{-1}$, $n = 25$) and growth rates ($0.14 \pm 0.33 \text{ d}^{-1}$, $n = 21$). Variabilities in the gross productivity of the phytoplankton were high (CV = 33.10 %) and driven by similarly high variabilities in the physicochemical and biological parameters. Productivity also exhibited clear seasonality associated with the mixing and stratification of the lake. The physicochemical and biological parameters (mixed layer depth, euphotic depth, secchi disc depth, irradiance, chlorophyll *a*, and the community respiration) all had a positive relationship with the primary production) whiles ratio of mixed layer to euphotic depth, total phosphorus, wet weigh biomass had a negative relationship with the gross productivity. Of all the measured parameters, only areal community respiration ($r^2 = 30.6 \%$) had a significant predictive value ($r^2 < 0.05$).

Introduction

Biological differences in aquatic systems may be expressed both qualitatively and quantitatively as the abundance of composite biomass, diversity, or rate of new organic matter production. However, the rate of primary productivity is known to provide a more dynamic view of an aquatic system's evolution representing the immediate results of the interaction between physicochemical and biological variables, and a quicker response to trophic changes than biomass. It provides a more valuable record of changes in the trophic state of an aquatic system, whilst a

measure of the standing crop provides only a static picture of the system (Goldman, 1968). Hence, the factor of greatest importance in aquatic systems is often the assessment of the rate at which organic matter is formed from inorganic matter and accumulated. The basic process involved is photosynthesis, which in lacustrine environments of lakes, is largely performed by the phytoplankton (Melack, 1976).

Primary productivity of a water body provides an index of potential energy support at the base of the foodweb and therefore the system's capacity to support the ecosystem.

It is considered a sensitive and relatively accurate indicator of eutrophication and its measure is often mandatory in the monitoring and assessment of ecological status of aquatic ecosystems (Smith, 2007). Phytoplankton productivity in aquatic systems also plays an essential role in element cycling and food supply to heterotrophs (Cloern, 1977). Consequently, information on the extent, variability and regulation of photosynthetic productivity of phytoplankton has been and still are some of the main objectives in phytoplankton ecology (Felip and Catalan, 2007).

The phytoplanktons are the major primary producers in the pelagic zone of aquatic systems. In closed-basin lakes like Lake Bosomtwe which are relatively deep compared to their surface area, with steep bathymetry, the dependence of phytoplankton primary production is even greater. This is because such lakes tend to have minimal macrophyte growth and low allochthonous organic carbon input due to limited littoral areas and inflows from the catchment (Puchniak *et al.*, 2009).

Like other organisms, phytoplanktons are regulated by the nature of their physico-chemical and biological environment which affect resource availability as well as foodweb interactions (Lewis, 1978; Huisman *et al.*, 2004). Previous work suggests little nutrient stress for the phytoplankton of Lake Bosomtwe. For instance, nitrogen and phosphorus concentrations were observed to be above the levels of famine for phytoplankton (Karikari and Bosque-Hamilton, 2004; Awortwi *et al.*, 2015). In environments where phytoplankton productivity is not limited by nutrients, there is often increased control of physical factors on the photosynthetic activities of the phytoplankton (Morabito and

Pugnetti, 2000). Thus, these major nutrients may not limit the growth of phytoplankton of the lake while meteorology and its associated physicochemical factors are the primary drivers of the phytoplankton dynamics of the lake (Awortwi *et al.*, 2015).

Rates of phytoplankton primary productivity in tropical African lakes range from 0.8 in Lake Tanganyika to 30.90 gCm⁻²d⁻¹ in Haartbeespoort Dam (Awortwi, 2009). The most productive systems are shallow, extremely nutrient-rich lakes where the combination of year-round high irradiances and shallow water column yields a high effective light climate (Beadle, 1981). This combined with high water transparency per unit of production, high sustained biomass per unit area, and high temperatures, which allow high rates of microbial decomposition and nutrient recycling, results in high areal production rates (Lewis, 1974).

Knowledge about the phytoplankton of Lake Bosomtwe is limited, with mentions by Whyte (1975) of phytoplankton as food organisms for the zooplankton and fish of the lake and Post *et al.* (2008) of phytoplankton in relation to mercury biomagnification in a phytoplanktivorous cichlid, *Sarotherodon multifasciatus*, and other fishes in Lake Bosomtwe. Awortwi *et al.* (2015) is the major study that focused entirely on the phytoplankton although mainly on the dynamics of the phytoplankton biomass of the lake.

Our objective of this study is therefore to provide foundational information about the primary productivity of the phytoplankton of Lake Bosomtwe. We report an assessment of primary productivity and its seasonal variability for the phytoplankton in relation to relevant physicochemical and biological factors over a one year period (September, 2005 – August, 2006).

Materials and methods

Study area

Lake Bosomtwe is located at an altitude of 99 m amsl in the Ashanti region, the south-central part of Ghana (06°30'N; 01°25'W, Fig. 1). The lake is 8 km in diameter and 78 m in depth, with a surface area of 48.6 km² and has a drainage basin measuring 103.2 km² (Turner *et al.* 1996). It lies in a one-million-year old meteorite impact crater, a circular depression 11 km diameter within the semi-deciduous forest/savanna potential zone of West Africa (Hall & Swaine, 1981). The catchment is semi-forested and semi-cultivated and the average monthly temperature is about 26 °C while annual precipitation measures about 1136 mm (Puchniak *et al.*, 2009). Lake Bosomtwe is the only naturally occurring lake in West Africa. The steep-sided closed basin of the lake makes inflowing streams dilute compared to the concentrated soda lake (Whyte, 1975). Because the crater impact breccia tends to hinder groundwater inflow, Lake Bosomtwe obtains over 80 % of its water input from direct precipitation and it loses water principally

through evaporation (Turner *et al.*, 1996). The chief mineral constituents are the bicarbonates and sulphates of sodium and potassium and the essential nutrients, phosphates and nitrates appear to be adequate for phytoplankton growth (Karikari & Bosque-Hamilton, 2004). The lake's water conductivity ranges from 1182 to 1283 μScm^{-1} while the pH averages around 8.9 with an alkalinity of 10320 $\mu\text{mol L}^{-1}$ and a salinity of 0.32 g L⁻¹ (Puchniak *et al.*, 2009). At the base of the lacustrine foodweb, the chlorophytes dominate the species richness but the biomass is dominated by the cyanobacteria (Awortwi *et al.*, 2015). The extant fish species in the lake are all cichlids known to be relatively tolerant of the hypoxic conditions which the lake experiences annually during mixing periods (Post *et al.*, 2008).

Sampling for phytoplankton productivity and wet weight biomass determination

The *in-situ* light and dark bottle oxygen method was employed to quantify phytoplankton photosynthesis and community respiration at 7 depths that covered adequately the Z_{eu} at

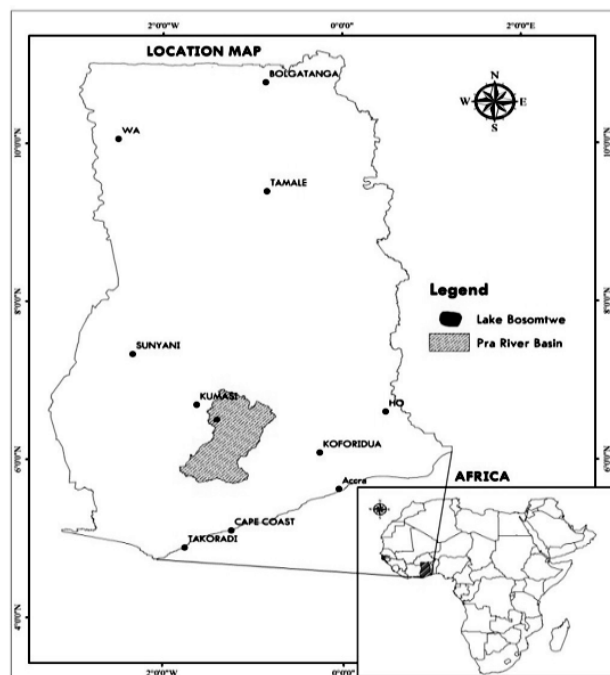


Fig. 1. Map of Ghana showing the location of Lake Bosomtwe and the Pra River Basin (Gardner, *et al.*, 1995)

the central index station after incubation for 4 hours usually between 1000 – 1400 hours on each sampling date. The oxygen content ($\text{mgO}_2 \text{ m}^{-3}\text{hr}^{-1}$) was determined and converted to carbon weight equivalent ($\text{mgC m}^{-3}\text{hr}^{-1}$) assuming one carbon atom assimilated for each molecule of oxygen released (Wetzel and Likens, 1979). The daily areal gross productivity was determined from the hourly values following Fee (1990) method. Surface irradiance (I), was obtained from a meteorological station situated along the north-eastern shore of the lake ($6^{\circ}31.138''\text{N}$, $1^{\circ}25.665''\text{W}$) as an average of total solar radiation during incubation periods. This was used to estimate the irradiance throughout the Z_{eu} generating a photosynthetic versus irradiance response that was interpolated to estimate the instantaneous photosynthetic rate for any depth in the Z_{eu} , resulting in an *in situ* photosynthetic profile. The gross photosynthesis (P_G) was subsequently calculated from these profiles as the double integral of the Z_{eu} to give instantaneous areal rates and over incubation time to give daily areal rates. Community respiration (R_C) per unit of water volume was likewise obtained by integrating through the Z_{eu} for 24 hours of a day to obtain areal values. Consequently, net primary productivity (P_N) in the Z_{eu} was derived by the difference between the P_G and the R_C . Annual production was estimated by summation of the daily areal values obtained. Water samples at each depth of incubation were immediately preserved with acid Lugol and used to determine the species composition and wet weight biomass (P_B) of the phytoplankton contributing to the productivity. Using a Zeiss-type inverted microscope, qualitative and quantitative analyses of phytoplankton cells were done at x400 magnification following

the method of Utermohl (1958). Counts were converted to wet weight biomasses by approximating cell volume obtained by routine measurements of at least 30 cells and the application of the geometric formula best fitted to the shape of cells (Rott, 1981). Since the Z_{eu} of Lake Bosomtwe is on average mostly situated in the Z_{mix} in an annual cycle (Awortwi *et al*, 2015), we assumed that phytoplankton were uniformly distributed within the Z_{eu} and obtained areal biomass by multiplying the mean volumetric biomass by the Z_{eu} on each occasion. Areal biomass was converted to carbon wherever relevant at a rate of 10 % (Lewis, 1974). Growth rates of the phytoplankton community were estimated according to Petersen (1978).

Collection and analyses of chlorophyll a and phosphorus samples

Samples for total phosphorus ($n = 20$) and chlorophyll a concentration ($n = 17$) were also collected alongside phytoplankton sampling whenever possible. Total phosphorus (Z_{TP}) was analyzed using the phosphomolybdate colour development after persulphate digestion following spectrophotometric methods in Stainton *et al* (1977). Chlorophyll a was analyzed using 500 ml of sampled water filtered through a $0.7 \mu\text{m}$ pore Whatman GF/F $\text{Ø} 47 \text{ mm}$ ($0.7 \mu\text{m}$ pore size) and extracted in 95 % acetone. The concentration of chlorophyll a in a water sample was then measured in a Turner 10 AU fluorometer following spectrophotometric methods in Stainton *et al* (1977).

Statistical analyses

Statistical Package for Social Scientists (2001) was used for statistical analyses of data. Analysis of Variance (ANOVA) and

the Least Significant Difference (LSD) were used to assess seasonal differences in the physicochemical and biological parameters associated with the phytoplankton primary productivity.

Results

Annual variations in physicochemical and biological parameters

Means of the physicochemical parameters measured are presented in Table 1. Mean mixed layer depth (Z_{mix}) during the period was 9.28 ± 3.47 m ($n = 25$) with a coefficient of variance (CV) of 37.36 %. Mean euphotic depth (Z_{eu}) during the period was 4.43 ± 1.76 m ($n = 25$; CV = 38.82 %). This resulted in a mean mixed layer depth:euphotic depth ($Z_{\text{mix}}:Z_{\text{eu}}$) ratio of 2.17 ± 0.74 ($n = 25$; CV = 34.29 %). Lake water transparency measured with Secchi disc (SD) recorded a mean of

1.52 ± 0.34 m ($n = 25$; CV = 22.40 %) while the extinction coefficient (k_{PAR}) had a mean of 0.97 ± 0.46 m^{-1} ($n = 25$; CV = 48.0 %). Mean irradiance (I) received per day at the lake's surface was 1180.21 ± 341.28 $\mu\text{E m}^{-2} \text{s}^{-1}$ ($n = 25$; CV = 28.92 %). Also, mean total phosphorus concentration (Z_{TP}) in the lake was 1.84 ± 0.49 $\mu\text{mol L}^{-1}$ ($n = 20$; CV = 26.43 %). Means of the areal gross productivity and related biological parameters measured are presented in Table 2. Mean areal gross primary productivity (P_{G}) was 4.72 ± 1.56 $\text{gC m}^{-2} \text{d}^{-1}$ ($n = 25$; CV = 33.1 %). Mean areal community respiration (R_{C}) was 4.34 ± 2.78 $\text{gC m}^{-2} \text{d}^{-1}$ ($n = 25$; CV = 64.0 %). This resulted in a mean areal net primary productivity (P_{N}) of only 0.37 ± 2.32 $\text{gC m}^{-2} \text{d}^{-1}$ ($n = 25$). Mean growth rate was 0.14 ± 0.33 d^{-1} ($n = 21$). Mean biomass of the phytoplankton was 0.41 ± 0.37 gC m^{-2} ($n = 25$; CV = 88.8 %) while mean chlorophyll *a*

TABLE 1

Physicochemical parameters and their variability in Lake Bosomtwe (Ghana) observed from September, 2005 to August, 2006. (Z_{mix} is mixed layer depth; Z_{eu} is euphotic depth; SD is secchi disc depth; k_{PAR} is extinction coefficient; I is surface irradiance; and Z_{TP} is total phosphorus; CV is coefficient of variance)

Parameter	Mean \pm Standard Deviation	CV (%)	n
Z_{mix} (m)	9.28 ± 3.47	37.36	25
Z_{eu} (m)	4.43 ± 1.76	38.82	25
$Z_{\text{mix}}:Z_{\text{eu}}$	2.17 ± 0.74	34.29	25
SD (m)	1.52 ± 0.34	22.40	25
k_{PAR} (m^{-1})	0.97 ± 0.46	48.00	25
I ($\mu\text{E m}^{-2} \text{s}^{-1}$)	1180.21 ± 341.28	28.92	25
ZTP ($\mu\text{mol L}^{-1}$)	1.84 ± 0.49	26.43	20

TABLE 2

Variability of gross primary productivity of phytoplankton (P_{G}) of Lake Bosomtwe (Ghana) and related biological parameters from September, 2005 to August, 2006. (R_{C} is areal community respiration; P_{B} is areal biomass; CV is coefficient of variance)

Parameter	Mean \pm Standard Deviation	CV (%)	n
P_{G} ($\text{gC m}^{-2} \text{d}^{-1}$)	4.72 ± 1.56	33.10	25
R_{C} ($\text{gC m}^{-2} \text{d}^{-1}$)	4.34 ± 2.78	64.0	25
Growth rate (d^{-1})	0.14 ± 0.33	86.13	21
P_{B} (gC m^{-2})	$0.41 \text{ gC m}^{-2} \pm 0.37$	88.80	25
Chlorophyll <i>a</i> (mg m^{-2})	52.11 ± 19.51	37.44	17

concentration was $52.11 \pm 19.51 \text{ mg m}^{-2}$ ($n = 17$; CV = of 37.44 %).

Seasonal variations in physicochemical and biological parameters

Stratified seasons were periods (November to December, March to June) when high atmospheric temperatures warmed the surface waters and resulted in vertical stratification of the water column for much of the year. On other hand, mixing periods were periods (late December, July to August) when reduced atmospheric temperatures cools surface waters and resulted in mixing of the water column. The restratifying seasons were periods (January to February, September to October), when the surface waters begin to warm again and vertical stratification is being re-established.

Seasonally, a higher mean Z_{mix} of $13.67 \pm 2.48 \text{ m}$ ($n = 6$) in the mixing period and a lower mean Z_{mix} of $6.75 \pm 2.25 \text{ m}$ ($n = 8$) in the restratifying period was observed (Table 3). There was a significant difference in the Z_{mix} between the mixing and restratifying period ($df = 2, 12$) on the one hand and also between the mixing and stratifying period ($df = 2, 15$) on the other hand at $p = 0.05$. No significant difference in the Z_{mix} occurred between the

stratified and restratifying period ($df = 2, 17$) at $p = 0.05$.

Also, mean Z_{eu} ranged from a high of $5.37 \pm 1.06 \text{ m}$ ($n = 11$) in the stratified period to a low of $3.10 \pm 1.03 \text{ m}$ ($n = 8$) in the restratifying period (Table 3). These were periods (November to December, March to June) when high atmospheric temperatures warmed the surface waters and resulted in vertical stratification of the water column for much of the year. There was a significant difference between the stratified and restratifying period ($df = 2, 17$) on the one hand and also between the mixing and restratifying period ($df = 2, 12$) on the other hand at $p = 0.05$. No significant difference occurred between the stratified and mixing periods ($df = 2, 15$) at $p = 0.05$.

For the $Z_{\text{mix}}:Z_{\text{eu}}$ ratio, a higher mean value of 2.96 ± 0.84 ($n = 6$) in the mixing period and a lower mean value of 1.67 ± 0.28 ($n = 11$) in the stratified period were noted (Table 3). There was however, no significant difference between the seasons at $p = 0.05$.

A higher mean SD of $1.67 \pm 0.27 \text{ m}$ ($n = 11$) in the stratified period compared to a lower mean SD of $1.21 \pm 0.29 \text{ m}$ ($n = 8$) in the restratifying period was noted (Table 3). There were significant differences in the mean SD between the stratified and restratifying periods

TABLE 3

Seasonal variation of some physicochemical factors in Lake Bosomtwe (Ghana) from September, 2005 to August, 2006 (Z_{mix} is mixed layer; Z_{eu} is euphotic depth; SD is the secchi disc depth; k_{PAR} is the extinction coefficient; and I is irradiance at lake surface)

Parameter	Mean \pm Standard Deviation		
	Stratified Period	Mixing Period	Restratifying Period
Z_{mix} (m)	8.73 ± 2.28 ($n = 11$)	13.67 ± 2.84 ($n = 6$)	6.75 ± 2.25 ($n = 8$)
Z_{eu} (m)	5.37 ± 1.06 ($n = 11$)	4.93 ± 1.65 ($n = 6$)	3.10 ± 1.03 ($n = 8$)
$Z_{\text{mix}}:Z_{\text{eu}}$	1.67 ± 0.28 ($n = 11$)	2.96 ± 0.84 ($n = 6$)	2.28 ± 0.58 ($n = 8$)
SD (m)	1.67 ± 0.27 ($n = 11$)	1.60 ± 0.28 ($n = 6$)	1.12 ± 0.29 ($n = 8$)
k_{PAR} (m^{-1})	0.75 ± 0.24 ($n = 11$)	0.82 ± 0.28 ($n = 6$)	1.37 ± 0.57 ($n = 8$)
I ($\mu\text{Em}^{-2} \text{ s}^{-1}$)	1358.92 ± 319.16 ($n = 11$)	924.83 ± 260.92 ($n = 6$)	1126.01 ± 309.40 ($n = 8$)
ZTP ($\mu\text{mol L}^{-1}$)	1.61 ± 0.19 ($n = 9$)	1.96 ± 0.54 ($n = 4$)	2.07 ± 0.67 ($n = 7$)

(df = 2, 17) and also between mixing and restratifying periods (df = 2, 12) at $p = 0.05$. No significant differences in the mean SD was found between the stratified and mixing periods (df = 2, 15) at $p = 0.05$.

A higher mean k_{PAR} of $1.37 \pm 0.57 \text{ m}^{-1}$ (n = 8) in the restratifying period compared to a lower mean k_{PAR} of $0.75 \pm 0.24 \text{ m}^{-1}$ (n = 8) in the stratified period was noted (Table 3). Mean k_{PAR} differed significantly between the stratified and restratifying periods (df = 2, 17) and also between mixing and restratifying periods (df = 2, 12), but no significant difference in the mean k_{PAR} was observed between the stratified and mixing periods (df = 2, 15) at $p = 0.05$.

A higher mean irradiance of $1358.92 \pm 319.16 \mu\text{E m}^{-2} \text{ s}^{-1}$ (n = 11) occurred in the stratified period compared to a low of $924.83 \pm 260.92 \mu\text{E m}^{-2} \text{ s}^{-1}$ (n = 6) in the mixing period (Table 3). There was a significance difference in the mean irradiance between the stratified and mixing periods (df = 2, 15) at $p = 0.05$. No significant differences were observed between stratified and restratifying periods (df = 2, 17), and between mixing and restratifying periods (df = 2, 12) at $p = 0.05$.

Mean Z_{TP} ranged from a high of $2.07 \pm 0.67 \mu\text{mol L}^{-1}$ (n = 7) in the restratifying period to a low of $1.61 \pm 0.19 \mu\text{mol L}^{-1}$ (n = 9) in the stratified period (Table 3). However, no significant differences in the mean Z_{TP} was

observed between seasons during the study at $p = 0.05$.

A higher mean P_G of $5.75 \pm 1.09 \text{ gCm}^{-2}\text{d}^{-1}$ (n = 6) occurred in the mixing period while the lowest P_G of $3.59 \pm 1.49 \text{ gCm}^{-2}\text{d}^{-1}$ (n = 8) occurred in the restratifying period (Table 4, Fig. 2). Mean P_G differed significantly only between the mixing and the restratifying period (df = 2, 12) but not between the stratified and mixing periods (df = 2, 15) or between the stratified and restratifying period (df = 2, 17) at $p = 0.05$.

A higher mean RC of $5.78 \pm 3.15 \text{ gCm}^{-2}\text{d}^{-1}$ (n = 11) was observed in the stratified period compared to the lowest of $2.31 \pm 1.60 \text{ gCm}^{-2}\text{d}^{-1}$ (n = 8) in the restratifying period (Table 4, Fig. 3). It differed significantly only between the stratified and the restratifying periods (df = 2, 17; $p < 0.05$) but not between the stratified and mixing periods (df = 2, 15) or between the mixing and restratifying periods (2, 12) at $p = 0.05$.

The highest seasonal mean growth rate of $0.14 \pm 0.10 \text{ d}^{-1}$ (n = 8) occurred in the restratifying period while the lowest growth rate of $0.12 \pm 0.06 \text{ d}^{-1}$ occurred in the mixing period (n = 6) (Table 4, Fig 4). However, it did not differ significantly between seasons at $p = 0.05$.

A higher seasonal mean PB of $0.59 \pm 0.50 \text{ gC m}^{-2}$ occurred in the restratifying period (n = 8) compared to a low of 0.28 ± 0.30 (n = 6)

TABLE 4

Seasonal variation of gross primary productivity (P_G) phytoplankton and related biological factors in Lake Bosomtwe (Ghana) from September, 2005 to August, 2006 (R_C is community respiration; rp is growth rate, P_B is wet biomass, Chl a is chlorophyll a)

Parameter	Mean \pm Standard Deviation		
	Stratified Period	Mixing Period	Restratifying Period
P_G ($\text{gCm}^{-2}\text{d}^{-1}$)	4.98 ± 1.40 (n = 11)	5.75 ± 1.09 (n = 6)	3.59 ± 1.49 (n = 8)
R_C ($\text{gCm}^{-2}\text{d}^{-1}$)	5.78 ± 3.15 (n = 11)	4.43 ± 1.59 (n = 6)	2.31 ± 1.60 (n = 8)
rp (d^{-1})	0.13 ± 0.10 (n = 7)	0.12 ± 0.06 (n = 6)	0.14 ± 0.09 (n = 8)
P_B (gCm^{-2})	0.35 ± 0.25 (n = 11)	0.28 ± 0.30 (n = 6)	0.59 ± 0.50 (n = 8)
Chl a (mg m^{-2})	50.68 ± 12.47 (n = 8)	60.21 ± 20.92 (n = 5)	33.60 ± 11.57 (n = 4)

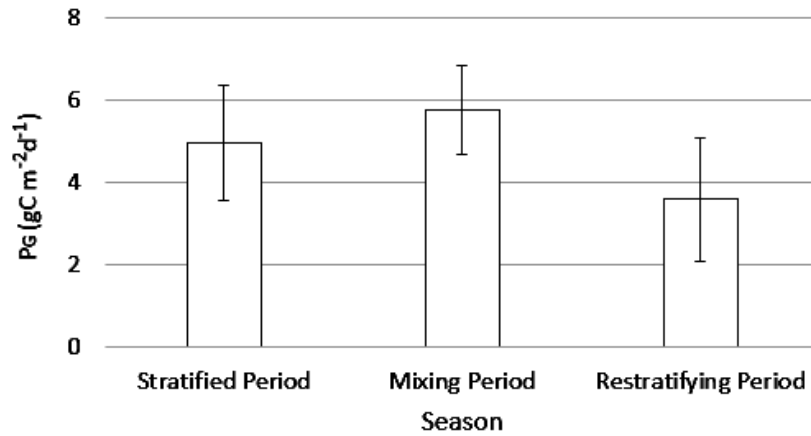


Fig. 2. Seasonal variation in the gross primary productivity of phytoplankton (PG) of Lake Bosomtwe (Ghana). Bars represent standard deviations

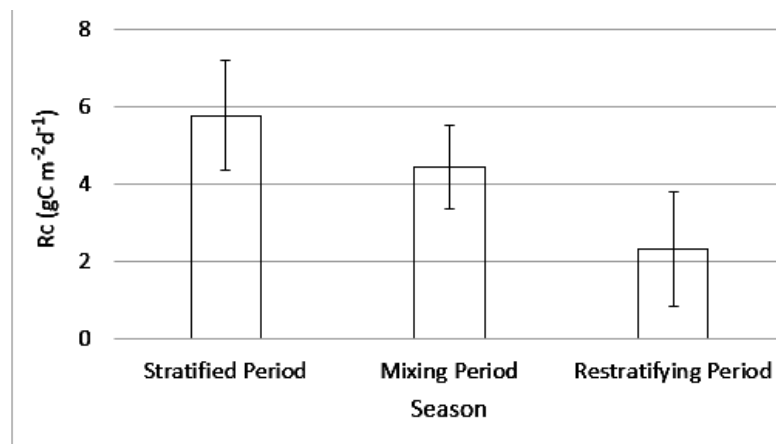


Fig. 3. Seasonal variation in the community respiration (RC) of phytoplankton of Lake Bosomtwe (Ghana). Bars represent standard deviations

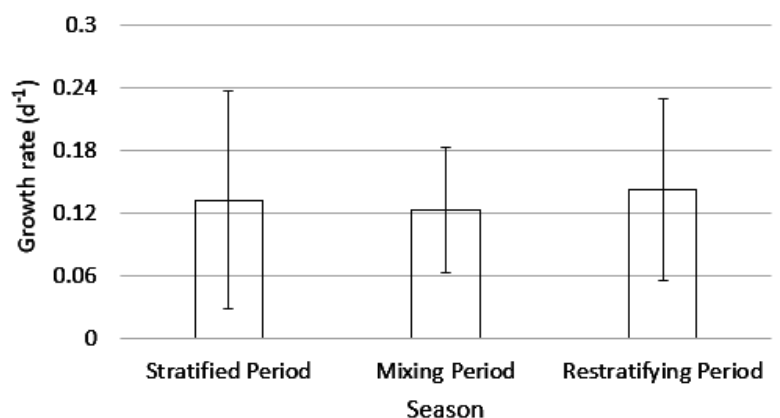


Fig. 4. Seasonal variation in the growth rates of phytoplankton of Lake Bosomtwe (Ghana). Bars represent standard deviations

in the mixing period (Table 4, Fig. 5). But P_B also did not differ significantly between the seasons at $p = 0.05$.

However, a higher seasonal mean chlorophyll

a concentration of $60.21 \pm 20.92 \text{ mg m}^{-2}$ occurred in the mixing period ($n = 5$) compared to a low of 33.69 ± 11.57 ($n = 4$) in the restratifying period (Table 4, Fig. 6). It

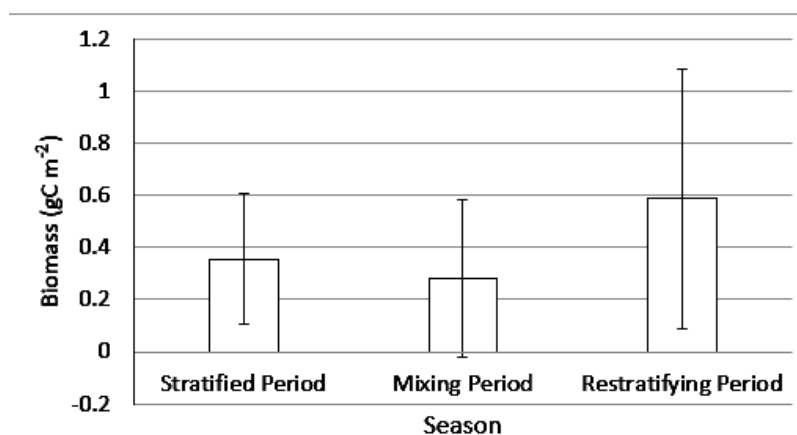


Fig. 5. Seasonal variation in the wet biomass (PB) of phytoplankton of Lake Bosomtwe (Ghana). Bars represent standard deviations

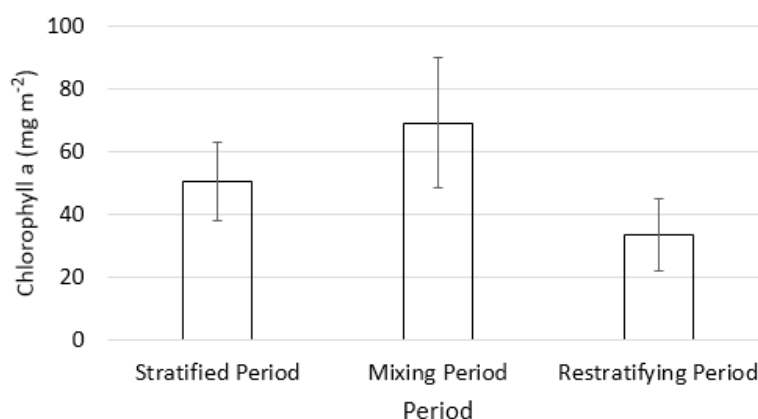


Fig. 6. Seasonal variation in the chlorophyll a concentrations of Lake Bosomtwe (Ghana). Bars represent standard deviations

differed significantly only between mixing and restratifying period ($df = 2, 7$) but not between the stratified and mixing periods ($df = 2, 11$) or the stratified and restratifying periods ($df = 2, 10$) at $p = 0.05$.

Relationships between physicochemical parameters and the phytoplankton productivity

The relationship between physicochemical parameters and the phytoplankton productivity is presented in Table 5. Increases in the physicochemical parameters Z_{mix} ($r^2 = 9.68\%$, $n = 25$), Z_{eu} ($r^2 = 6.58\%$, $n = 25$), SD ($r^2 = 12.42\%$, $n = 25$), solar radiation ($r^2 = 2.0\%$, $n = 25$) led to an increase in the P_G but all failed to significantly influence the P_G at $p = 0.05$. But increases in the $Z_{mix}:Z_{eu}$ ratio ($r^2 = 0.12$

$\%$, $n = 25$), k_{PAR} ($r^2 = 20.7\%$, $n = 25$), and Z_{TP} ($r^2 = 0.001\%$, $n = 20$) led to decreases in the P_G but again, none of these parameters could significantly influence the P_G at $p = 0.05$.

On the other hand, increases in the biological parameters R_C ($r^2 = 30.6\%$, $n = 25$), growth rate ($r^2 = 16.86\%$, $n = 21$), and chlorophyll a ($r^2 = 5.18\%$, $n = 17$) led to an increase in the P_G but none could significantly predict P_G except R_C at $p = 0.05$. Increases in the P_B however had a negative relation with P_G ($r^2 = 0.53\%$, $n = 25$) and failed to also significantly influence the P_G at $p = 0.05$.

Discussions

Mean areal gross primary productivity of Lake Bosomtwe's phytoplankton lie well

TABLE 5

Relationship between gross primary productivity (PG) phytoplankton and some physicochemical and biological factors in Lake Bosomtwe (Ghana) from September, 2005 to August, 2006 (Z_{mix} is mixed layer; Z_{eu} is euphotic depth; SD is the secchi disc depth; k_{PAR} is the extinction coefficient; and I is irradiance at lake surface; RC is community respiration; rp is growth rate, PB is wet biomass, Chl a is chlorophyll a)

Parameter	r ² (%)	n	Relationship
P _G vs Z _{mix}	9.68	25	$P_G = 0.14 * Z_{mix} + 3.4165$
P _G vs Z _{eu}	6.58	25	$P_G = 0.2276 * Z_{eu} + 0.0658$
P _G vs Z _{mix} :Z _{eu}	0.10	25	$P_G = - 1.0.073 * Z_{mix} : Z_{eu} + 4.872$
P _G vs SD	12.42	25	$P_G = 1.6277 * SD + 2.261$
P _G vs k _{PAR}	20.71	25	$P_G = - 1.5295 * k_{PAR} + 6.1955$
P _G vs I	2.0	25	$P_G = 1.0 \times 10^{-5} * I + 3.95$
P _G vs PB	0.53	25	$P_G = - 0.311 * P_B + 4.8435$
P _G vs Chl a	10.08	17	$P_G = 0.0237 * Chl a + 3.7481$
rp vs P _G	16.86	21	$rp = 0.0878 * P_G - 0.2653$
P _G vs R _c	30.61	25	$PG = 0.14 * RC - 0.3088$

within the range recorded for many tropical freshwater African lakes (Beadle, 1981; Robarts, 1984; Odour and Schargerl, 2007). A number of single factor theories such as, high water temperatures, relatively constant photoperiods, and the occasional supply of nutrients from deep mixing events, also features of Lake Bosomtwe, are usually used to explain such high productivities of tropical lakes (Odour and Schargerl, 2007).

However, the high irradiance and the associated high temperatures in the tropics that stimulate more photosynthesis are also known to induce other energetically costly metabolic processes such as high respiration rates from the phytoplankton and bacterial decomposition (Beadle, 1981). For instance, phytoplankton, like other organisms respire more in warm tropical waters but do not increase photosynthesis to the same extent. Hence, they are less efficient in warmer waters of tropical areas (Horne and Goldman, 1994). The areal community respiration of Lake Bosomtwe was consequently very high (over 90 % of the gross productivity) and resulted in a very low assimilable photosynthate of just

about 8 % of the gross productivity, making the lake just slightly autotrophic within the euphotic zone and leading to low growth rates compared to tropical lakes such as George, Tanganyika, Lanao, and Titicaca (Hecky and Fee, 1981). Respiration rates of phytoplankton are suggested to normally vary between 5 to 15 % of the gross productivity (Steelman-Nielsen, 1975) though in some tropical African lakes, it is between 35 to 92 % of the gross productivity (Ganf, 1974; Hecky, 1984). However, all bottle methods give an estimate of respiration not only of the phytoplankton but of all the community of organisms entrained with the phytoplankton in the bottle during the period of incubation (Reynolds, 2006). Thus, the net productivity and growth rate of the phytoplankton are usually underestimated when bottled methods measuring dissolved oxygen are used in estimating respiration Steelmann-Nielsen (1975).

Other reasons for the high respiratory rates observed for the lake may be attributed to the dominance of the Cyanobacteria and the Dinophyceae found during this study and also by Awortwi *et al* (2015), which are believed

to have high respiratory rates (Tilzer, 1989). Photoperiod truncations may occasionally contribute to the high respiratory rates. For instance, the phytoplankton spent close to 69 % of their time below the euphotic depth during the study period where only respiration but not photosynthesis occurs. This is likely to cause some light limitation even though it does not reach the critical value of about 80 % that totally limits phytoplankton production processes (Naselli-Flores *et al.*, 2007).

Fish yield records from Lake Bosomtwe are unavailable. Hence, following the method of Melack (1976), the potential fish yield was estimated using gross productivity at 384.12 kg ha⁻¹ yr⁻¹ that is relatively higher than tropical lakes such as George (136 kg ha⁻¹), Chad (14 kg ha⁻¹), Malawi (40 kg ha⁻¹), Tanganyika (125 kg ha⁻¹), Lanao (60 kg ha⁻¹) respectively (Hecky and Fee, 1981). However, Melack (1976) advises that interpretations of potential fish yields arising from the use of this equation should be done with caution since often the commercial catch records used in deriving the relationship usually represent fishing effort and not potential yield.

The variability of the gross productivity was high (CV = 33.1 %) similar to that of tropical lakes that show large variations associated with changes in the hydrological and hydrographical conditions (Melack, 1979). The similarly high variabilities observed in the physicochemical variables suggest that they may contribute to the high variabilities in the gross productivity.

In the mixing season, the occurrence of the highest gross productivity in the mixing season was influenced by high chlorophyll a concentrations, considerable light availability and abundant nutrients especially phosphorus, which are resources known to positively

influence primary productivity (Reynold, 2006). However, photoperiod truncations that lead to the mixing of phytoplankton below the euphotic depth led to considerably high community respiration (4.43 g Cm⁻²d⁻¹) compared to restratifying season and to reduced net productivity and growth rates of the phytoplankton during the mixing season. Hence, the lowest phytoplankton biomass was found during the mixing season. This however be attributed to the nature of the dominant phytoplankton groups in the lake, namely the Cyanobacteria and Dinophyceae which are known to be intolerant of mixing conditions (Paerl, 1996).

In the stratified season, gross productivity was comparable to that of the mixing season with possible influence by the high chlorophyll a concentrations and adequate supply of nutrients especially phosphorus. The abundant light during the stratified season which is influenced by high surface irradiance and within the water column is known to positively affect primary productivity (Post *et al.*, 1985; Reynold, 2006). However, the high irradiance and associated increases in water temperature also stimulated the observed high community respiration rates which exceeded the gross productivity (Beadle, 1981). If all the community respiration were attributable to the phytoplankton, there should not be accumulation of phytoplankton biomass. However, the phytoplankton biomass was about 1.3 times higher than that of the mixing season, indicating that the community respiration measures not only the respiration of the phytoplankton but also that of other microbes entrained within the bottles (Hecky, 1984). Also, the increase in the biomass compared to that of the mixing season may be due to the dominance of the Cyanophyceae and

the Dinophyceae known to adapt to stratified lake conditions when nutrients can be scarce and potentially growth-limiting, could also contribute to increased biomass. This is due to their ability to migrate between the light and nutrient fields to obtain these essential growth resources as well as the use of nitrogen fixation and mixotrophic feeding (Paerl, 1996; Reynolds, 2006). Cyanobacteria also have pigment adaptations that enable them to avoid photodamage from high irradiance at the lake's surface (Paerl, 1996).

During the restratifying season, the lowest gross productivity and equally low community respiration coupled with high phosphorus levels, resulted in the highest growth rates and phytoplankton biomass (Reynold, 2006). However, the low chlorophyll *a* concentration during the restratifying, did not adversely affect the gross productivity. But the high phytoplankton biomass during this period decreased the euphotic depth considerably due to self-shading.

In Lake Bosomtwe, physical factors influence phytoplankton productivity more than chemical factors. Nutrient factors usually exert limited control on phytoplankton production in nutrient-sufficient lakes (Cobeleas *et al.*, 1992), and the dominant phytoplanktons seem to be adapted in many ways to avoid nutrient limitation (Awortwi *et al.*, 2015). Positive correlation between irradiance and phytoplankton productivity are common (Morabito and Pugnetti, 2000) as was observed during this study. However, the lack of significant influence by irradiance and the irradiance-related secchi disc depth on the gross productivity suggest light adequacy for phytoplankton of tropical lakes (Brylinsky and Mann, 1973). The attenuation coefficient which is basically a function

of energy input and suspended particles including phytoplankton crop was however the best available non-biological variable for estimating the productivity. The negative relationship between productivity and the attenuation coefficient observed may be due to considerable light absorption by non-photosynthetic components or that the algae at high densities in Lake Bosomtwe exhibit low photosynthetic efficiencies (Kirk, 1994).

Biological factors also influenced the phytoplankton productivity of the lake. For instance, the positive correlation between chlorophyll *a* and productivity has been observed for several lakes (Enriquez *et al.*, 1996). The lack of significant influence by chlorophyll *a* on gross productivity has also been reported in other lakes (Henry *et al.*, 2006). However, a negative relationship between the gross productivity and biomass has also been reported for some lake (Morabito and Pugnetti, 2000). These observations may be attributed to the fact during stratified and restratifying seasons, the phytoplankton receives relatively higher irradiances compared to the mixing periods and may be producing pigments other than chlorophyll *a* that do not transfer excitation energy to the chlorophyll *a*. Such pigments act to reduce photosynthetic efficiency of the phytoplankton and consequently their productivity (Siefertmann-Harms, 1985) as was observed for these two seasons compared to the mixing period which had high chlorophyll *a* and productivity even on a lower biomass (Henry *et al.*, 2006).

Although not significant in this study, growth rates were positively affected by phytoplankton gross productivity. Periods of higher growth rates are important in supporting and maintaining secondary production including fisheries in biological systems (Enriquez *et al.*,

1996).

However, the best biological factor for predicting the productivity of the phytoplankton was the community respiration.

Conclusion

A real primary productivity of Lake Bosomtwe's phytoplankton is relatively high and lies well within that observed for many tropical African lakes. However, high community respiration rates per unit area within the water column greatly reduce its net productivity which negatively affects growth rates and biomass accumulation of the phytoplankton compared to other tropical lakes. The relatively high variability in the primary productivity is similar to those observed in other tropical African lakes characterized by pronounced seasonal fluctuations associated with seasonal variations in vertical mixing. High variabilities in physicochemical and biological parameters also drive the variability of Lake Bosomtwe's productivity.

With adequate levels of essential nutrients such as phosphorus and perhaps nitrogen, physical factors especially the attenuation coefficient exert more influence on the productivity of the phytoplankton.

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