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RESEARCH PAPER

AREAL LIGHT UTILIZATION EFFICIENCY OF A NATURAL COMMUNITY OF PELAGIC PHYTOPLANKTON IN A TROPICAL LAKE (LAKE BOSOMTWE, GHANA)

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ABSTRACT

The areal light utilization efficiency, one of the key factors in primary production, of a natural community of pelagic phytoplankton of Lake Bosomtwe (Ghana, West Africa), its seasonal signature and factors that influence it were investigated fortnightly from September 2005 to August 2006 by estimating the percentage of solar radiation utilized by phytoplankton of the lake in primary production. The results indicate an annual mean value of 0.28 ± 0.14% (n=25, CV=51.4 %) which lies at the lower end of values typical for lakes and reservoirs of the world. Mean light intensity within the mixed layer 166.03 ± 77.30 µE $m^{-2}s^{-1}$ (n=25, CV=51.4 %) did not reach a level that can potentially cause photoinhibition among the dominant phytoplankton groups viz, Cyanobacteria, Dinophyceae, and Chlorophyceae. Both the mean areal light utilization efficiency and mean irradiance in the mixed layer differed significantly between seasons at $p < 0.05$. Of the physicochemical factors investigated, changes in the mixed layer depth (r^2 = 29.3%, n=25), surface irradiance (r^2 = 36.5 %, n=25), mean irradiance in the mixed layer (r^2 = 23.3 %, n=25), surface water temperature (r^2 = 17.7%, n=23) and mean temperature in the mixed layer (r^2 = 22.8 %, n=23) significantly affected changes in the areal light utilization efficiency of the phytoplankton community at $p< 0.05$. However, of the biological factors measured, changes in the areal light utilization efficiency of the phytoplankton community had a significant predictive value only for the gross primary productivity (r^2 = 41.6%, n=25) at $p< 0.05$.

Keywords: Phytoplankton, light utilization efficiency, tropical lake, mixed layer depth, Lake Bosomtwe

INTRODUCTION

The primary productivity of aquatic ecosystems ultimately set limits on the overall productivity attainable in any ecosystem. One key factor that determines the limit of the primary production of an ecosystem is the efficiency with which resident primary producers capture light energy, a major resource, and accumulate it in the system in the form of organic matter. The extent of this process is one of the most important biological phenomena on which the entire diverse life depends on either directly or indirectly (Hecky, 984). Light energy is responsible for the state and for the circulation of water, nutrients and many features of the aquatic environment that determines the conditions of existence for aquatic organisms (Beadle, 1981). Schwaderer *et al* (2011), asserts that fluctuations in light is one of the key factors that affect the structure of phytoplankton communities based on differences in light utilization. From an anthropocentric point of view, knowledge of the light utilization efficiency of phytoplankton in aquatic systems is of great interest because of the desire to utilize aquatic systems as potential food sources of diverse forms (Kirk, 1994) and contribute to the sustainable development goal of eliminating hunger since the phytoplankton are major primary producers in lakes that sustains other organisms in them such as fishes which are the primary protein sources for many riparian communities.

Estimates of areal light utilization efficiencies by phytoplankton in aquatic ecosystems are generally low with much of the irradiance selectively and rapidly absorbed by the water itself and by dissolved and particulate matter contained in it (Kirk, 1994). Also, studies indicate that it varies over several orders of magnitude at the global level from very oligotrophic, high-altitude systems to eutrophic ones and also by season (Kirk, 1994; Marzetz *et al*., 2020). In lakes, variations in areal light utilization efficiency of phytoplankton are known to be affected by mixing and stratification cycles known to govern nutrient and light availability and changes in the species composition (Kaiblinger and Dokulil, 2006). In surface mixed layers of lakes, the light environment of phytoplankton may be modified as cells may be moved across large light gradients from very high intensities at the surface to darkness below the mixed layer (Kohler *et al*., 2018). Awortwi *et al* (2015) have observed the mixed layer depth in Lake Bosomtwe to be on average about twice that of the trophogenic zone in an annual cycle. This can lead to substantial modification of the light climate the phytoplankton experience and affect their light utilization efficiency, photosynthesis, composition, diversity, and growth rates (Kohler *et al*., 2018). On a more general scale, measurement of this parameter, permits a more direct comparison with photosynthetic efficiencies of other aquatic systems as well as terrestrial ecosystems (Dubinsky and Berman, 1981).

Several aspects of the phytoplankton of Lake Bosomtwe, a tropical meromictic lake in Ghana, West African have been studied such as their role as food organisms for fishes (Poste *et al*, 2008), temporal and seasonal variations in the wet biomass (Awortwi *et al*, 2015), the seasonality of the phytoplankton primary productivity (Awortwi *et al*, 2018), and species diversity (Addico *et al*., 2018) from which important information on these are documented. The present study is aimed at gaining an understanding of the efficiency with which the phytoplankton community of the lake utilize light energy. It is also desirable to have basic knowledge of the physicochemical and biological factors that can potentially affect or are affected by the light utilization efficiency of the phytoplankton of the lake and obtain an understanding of how they relate to each other. Thus, in this study, data collected from September 2005 to August 2006 based on fortnight sampling has been analyzed with the view to characterizing the extent of the light utilization efficiency of the phytoplankton of the lake, its seasonal (mixing-stratification) signature, as well as an understanding of its relationship with some key physicochemical and biological factors.

MATERIALS AND METHODS

Study area

Lake Bosomtwe, the only natural crater lake in West Africa is located at an altitude of 99 m amsl in the south-central part of Ghana (06°30'N; 01°25'W, Fig. 1) with a diameter of 8 km, surface area of 48.6 km^2 and has a drainage basin measuring 103.2 km^2 respectively (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 and annual precipitation is about 1136 mm (Puchniak *et al*., 2009).

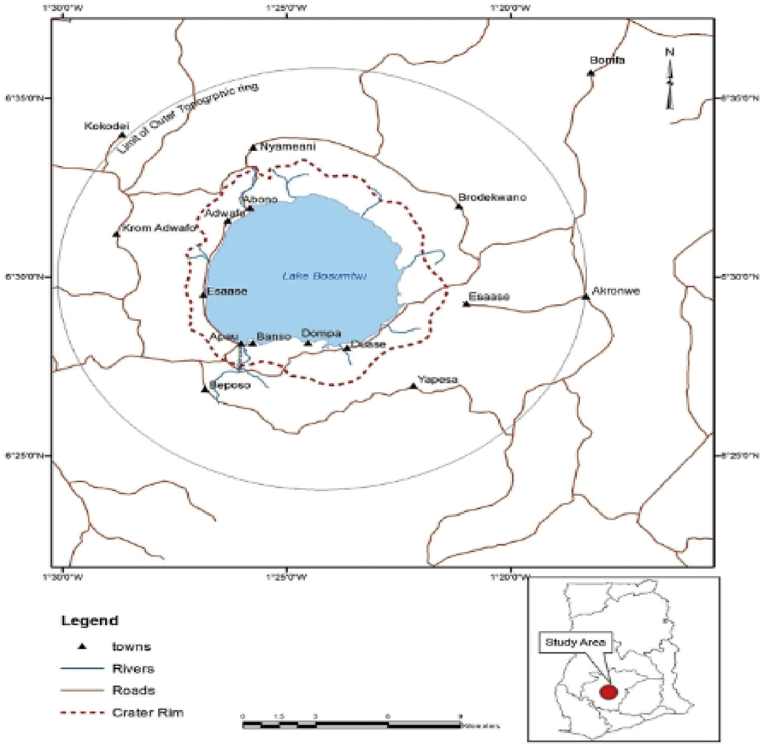

Fig. 1. Map of Lake Bosomtwe and its catchment area in Ghana (Loh *et al*., 2016)

It is closed-basin lake and the streams that flow into it are dilute compared to the lake's water (Karikari and Bosque-Hamilton, 2004). Groundwater flow is insignificant since the crater impact breccia tends to hinder it and hence, the lake obtains over 80 % of its water input from direct precipitation and 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; Awortwi *et al*., 2015; 2018). The lake's water conductivity ranges from 1182 to 1283 µScm^{-1} with alkalinity of 10320 mol L^{-1} and salinity of 0.32 g L^{-1} (Puchniak *et al*., 2009) whiles the pH ranges from 7.8 to 8.7 (Addico *et al*., 2018). At the base of the lacustrine foodweb, the chlorophytes dominate the species richness but the wet biomass is dominated by the cyanobacteria (Awortwi *et al*., 2015). The extant fish species in the lake are all cichlids (Post *et al*., 2008).

Sampling and monitoring of physico-chemical parameters

The data presented here were obtained at a central index station (6°30'609''N; 1°24'671''W) with maximum depth of 78 m representative of the pelagic zone of the lake. Fortnightly samples collected from this station were used for assessing the physicochemical and biological conditions of the lake and for estimating the light utilization efficiency of the phytoplankton. Bathythermographs providing the temperature-depth profile of the lake were obtained using a Hydrolab H2O Multiprobe 68SBP (Hydrolab Corporation, Austin, Texas, 1991) from which the mixed layer depth (Z_{mix}) was estimated as the depth from the top of the thermocline to the surface of the water. This was used to characterize sampling periods into stratified, mixing, and restratifying seasons following Awortwi *et al* (2015). Surface water temperature (T_o), mean temperature in the mixed layer (T_{mix}) and surface water conductivity (C_w) were also measured with this probe. The transparency of the lake water was measured using a 20 cm black and white Secchi disc (SD). A flat-plate LI-COR quantum metre (LI-COR Biosciences, Lincoln NB) was used to estimate the underwater irradiance in the photosynthetically active waveband (400-700 nm). This was used to determine the extinction coefficient (k_{PAR}; Kirk, 1994) and the euphotic depth (Z_{eu}) was subsequently estimated as depth at which irradiance was approximately 1 % that of incident irradiance following Talling (1986). Incident irradiance (Io) data were obtained as averages 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. Average irradiance in the Zmix (I_{mix}, expressed in µE m^{-2}s^{-1}) was determined according to Riley (1957). The water level of the lake (W_L) was measured using a water level gauge at Abono town.

Determination of the light utilization efficiency and other biological parameters

To determine the light utilization efficiency of the phytoplankton community, the in-situ light and dark bottle method for dissolved oxygen determination was employed during 4-hour incubations normally from 1000 – 1400 hours during each sampling period (Wetzel and Likens, 1979). From these, the gross photosynthesis (P_G) and estimates of community respiration (R_C) and net photosynthesis (P_N) were made. To change assimilated carbon to energy values, we used a factor of 1 gC to 10 kcal following Burgis and Dunn (1978) assuming all photosynthate is glucose.

The light utilization efficiency (eA) of the phytoplankton was then determined by obtaining the ratio between the P_G in kilocalories by the irradiance in kilocalories (Brylinsky and Mann, 1973; Dubinsky and Berman, 1981).

Using a Zeiss-type inverted microscope, the species composition and biomass of phytoplankton cells in a specific volume of the lake water (volumetric biomass) were determined at x400 magnification following the method of Utermohl (1958) and identifications were done mostly to species level (Prescott, 1978; Wehr and Sheath, 2003) and grouped into appropriate phytoplankton classes. Counts were converted to wet weight biomasses (P_B) 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_{mix} and obtained areal biomass by multiplying the mean volumetric biomass by the Z_{mix} on each occasion. Areal biomass was converted to carbon at a rate of 10 % (Lewis, 1974) and growth rates (r_g) in the Z_{mix} were estimated according to Petersen (1978).

Collection and analyses of total phosphorus and chlorophyll a samples

Samples for total phosphorus (ZTP) and chlorophyll a (Chl a) were also collected alongside phytoplankton sampling. Total phosphorus was analyzed using the phosphomolybdate colour development after persulphate digestion following spectrophotometric methods in Stainton *et al* (1977). Chlorophyll a was measured fluorometrically after extraction in 95 % acetone in a Turner 10 AU flourometer following spectrophotometric methods in Stainton *et al* (1977).

Statistical analyses

Simple linear regression analysis was used to determine the degree of relationship between the light utilization efficiency of the phytoplankton and the physicochemical and biological factors. These relationships were assessed for significance at $p < 0.5$ level. Analysis of Variance (ANOVA) was used to assess seasonal differences in the irradiance and irradiance-related parameters associated with the light utilization efficiency of the phytoplankton. Seasonal means were separated with LSD at 0.05 probability level whenever significant differences occurred. All statistical analyses were performed using the programmes contained in the Statistical Package for Social Scientists (2001).

RESULTS

Annual variations of mean irradiance in the mixed layer (I_{mix}) and the light utilization efficiency (eA)

Annual means of the irradiance in the mixed layer (I_{mix}) and the mean areal light utilization efficiency of the phytoplankton (eA) are presented in Table 1.

Table 1. Irradiance parameters and the light utilization efficiency of the phytoplankton of Lake Bosomtwe (Ghana) from September, 2005 to August, 2006; n = 25.

Parameter	Mean ± standard deviation	Maximum:Minimum ratio	CV (%)
I_{mix} ($\mu E\ m^{-2}s^{-1}$)	166.03 ± 77.30	4.2	46.5
eA (%)	0.28 ± 0.14	12.8	51.4

I_o is irradiance ($\mu Em^{-2}s^{-1}$) received at the surface of the lake; I_{mix} ($\mu Em^{-2}s^{-1}$) is mean irradiance within mixed layer column; eA (%) is the percentage light utilization efficiency of the phytoplankton

Mean irradiance within the mixed layer (I_{mix}) of the lake ranged over four folds from a low of 63.42 $\mu Em^{-2}s^{-1}$ during the mixing season (August) to a high of 293.11 $\mu Em^{-2}s^{-1}$ during the stratified season (March) with a mean of 166.03 ± 77.30 $\mu Em^{-2}s^{-1}$ (CV = 45.5 %; n=25; Table 1).

Mean areal light utilization efficiency (eA) within the mixed layer of the lake ranged close to 13-folds from a low of 0.06 % during the restratifying season (October) to a high of 0.77 during the mixing season (August) with a mean of 0.28 ± 0.14 (CV = 51.4 %; n=25; Table 1).

Relationship between physicochemical and biological parameters and the areal light utilization efficiency of the phytoplankton

The relationships between physicochemical parameters and the light utilization efficiency of the phytoplankton are presented in Table 2.

Table 2. Relationships between percentage light utilization efficiency (eA) and some physicochemical parameters in Lake Bosomtwe (Ghana) from September 2005 to August, 2006.

Parameters	r^2 (%)	p-value	n	Relationship
eA vs Io	36.5	0.001	25	eA = -0.0003*Io + 0.5831
eA vs Zmix	29.3	0.005	25	eA = 0.0226*Zmix + 0.0717
eA vs Zeu	4.9	0.282	25	eA = 0.0102*Zeu + 0.1325
eA vs Imix	23.3	0.014	25	eA = -0.0009*IZmix + 0.4308
eA vs Tmix	22.8	0.021	23	eA = -0.688*TZmix + 2.3133
eA vs To	17.7	0.045	23	eA = -0.046*To + 1.6674
eA vs Cw	17.3	0.054	22	eA = 0.0015*Cw - 1.5158

eA vs kPAR	14.8	0.057	25	eA = -0.1199*kPAR + 0.3971
eA vs SDD	9.3	0.138	25	eA = 0.1303*SD + 0.0847
eA vs Zeu:Zmix	8.3	0.162	25	eA = -0.2763* Zeu:Zmix + 0.4213
eA vs ZTP	8.3	0.220	20	eA = 0.0009*ZTP + 0.0012
eA vs WL	3.5	0.374	25	eA = 0.024*WL + 0.2124

I_o ($\mu E\ m^{-2}s^{-1}$) is the incident irradiance on the lake's surface; I_{mix} ($\mu E\ m^{-2}s^{-1}$) is mean irradiance within the mixed layer; Z_{mix} (m) is the mixed layer depth; Z_{eu} (m) is the euphotic depth; $Z_{eu}:Z_{mix}$ is the ratio of the mixed layer to the euphotic depth; To and T_{mix} are the surface water and mean water column temperatures (˚C) in the mixed layer respectively; C_w is the conductivity ($\mu S\ cm^{-1}$) of surface water; SDD (m) is the secchi disc depth; k_{PAR} (m^{-1}) is the extinction coefficient; Z_{TP} ($\mu mol\ l^{-1}$) is the total phosphorus concentration ($\mu mol\ L^{-1}$); WL (cm) is water level.

Increase in the physicochemical parameters, mixed layer depth (Zmix, r^2 = 29.3 %), euphotic depth (Zeu, r^2 = 4.9 %), ratio of mixed layer to euphotic depth (Zmix:Zeu ratio, r^2 = 21.5 %), surface water conductivity (Cws, r^2 = 17.3 %), secchi disc depth (SDD, r^2 = 9.3 %), total phosphorus concentration (ZTP, r^2 = 8.3 %), water level (WL, r^2 = 3.5 %) led to an increase in the areal light utilization efficiency of the phytoplankton but only the Zmix and Zeu had a significant relationship with it at $p < 0.05$. A simple linear regression of the Zeu:Zmix ratio on the Imix, (Fig 2) show strong positive and significant correlation at $p < 0.05$ (r^2 = 70.7 %, n=25).

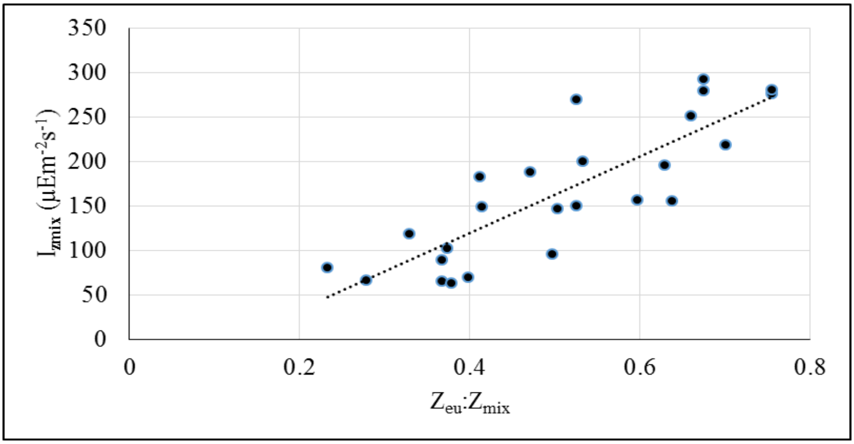

Fig. 2 Relationship between $Z_{eu}:Z_{mix}$ ratio and the mean irradiance in the mixed layer (I_{mix}) of Lake Bosomtwe (Ghana)

On the other hand, increases in the physicochemical parameters surface irradiance (I_o, r^2 = 36.5 %), mean irradiance in mixed layer (Imix, r^2 = 23.3 %), mean water temperature in the mixed layer (Tmix, r^2 = 22.8 %), surface water temperature (To, r^2 = 17.7 %), and the extinction coefficient (kPAR, r^2 = 14.8 %), led to a decline in the light utilization efficiency of the phytoplankton and all had a significant relationship with it except kPAR at $p < 0.05$ (Table 2).

Also, increases in the areal light utilization efficiency of the phytoplankton led to an increase in the biological parameters gross primary productivity (PG, $r^2 = 41.6$ %), net primary productivity (PN, $r^2 = 18.9$ %), chlorophyll a (Chl a, $r^2 = 17.7$ %), phytoplankton biomass (PB, $r^2 = 14.8$ %), and growth rate (r_g, $r^2 = 6.8$ %) but only the PG had a significant positive relationship with it at $p < 0.05$ (Table 3).

Table 3. Relationships between percent light utilization efficiency (eA), and some biological parameters in Lake Bosomtwe (Ghana) from September 2005 to August, 2006.

Parameters	r^2 (%)	p-value	n	Relationship
PG vs eA	41.6	0.0005	25	$P_G = 69.679*eA + 27.565$
PN vs eA	18.9	0.0300	25	$P_N = 69.64*eA – 15.864$
Chl a vs eA	17.7	0.0900	17	Chl a = 0.0109*eA + 0.1849
PB vs eA	14.8	0.0560	25	$P_B = 1.5336*eA + 1.4902$
r_g vs eA	6.8	0.2530	21	$r_g = 0.1402*eA + 0.0922$

Chl a (mg m^{-2}) is chlorophyll a concentration; P_B (kcal $m^{-2}d^{-1}$) is the biomass of the phytoplankton; P_G (kcal $m^{-2}d^{-1}$) is the gross primary productivity and P_N (kcal $m^{-2}d^{-1}$) is the net primary productivity; r_g (d^{-1}) is growth rate of the phytoplankton community.

Thus, the biological variable whose variation was most influenced by the variations in the areal light utilization efficiency of the phytoplankton was PG and the non-biological variable which explained best the variations in the areal light utilization efficiency of the phytoplankton was Io.

Both PG and Io (as well as Z_{mix}, Imix, Tmix, and To) were significantly related to the areal light utilization efficiency of the phytoplankton at $p < 0.05$. The rest had low correlation coefficients which were not significantly different from zero.

Seasonal variations in irradiance parameters and the areal light utilization efficiency of the phytoplankton

The mean irradiance in the mixed layer (I_{mix}) was lowest during the mixing season (88.46 ± 32.33 $\mu Em^{-2}s^{-1}$; CV = 36.5%; n = 6) and the highest occurred during the stratified season (226.03 ± 63.40 $\mu Em^{-2}s^{-1}$; CV = 28.0%; n = 11). It differed significantly between the stratified and the mixing seasons (df = 2, 15; Fig 3) and between the stratified and restratifying seasons (df = 2, 17; Fig 3) but not between the mixing and restratifying seasons (df = 2, 12; ANOVA, Fig 3) at $p < 0.05$. A simple linear regression of the Imix on the Io (Fig 4) showed a strong significant positive correlation at $p < 0.05$ (r^2 = 62.1 %, n = 25).

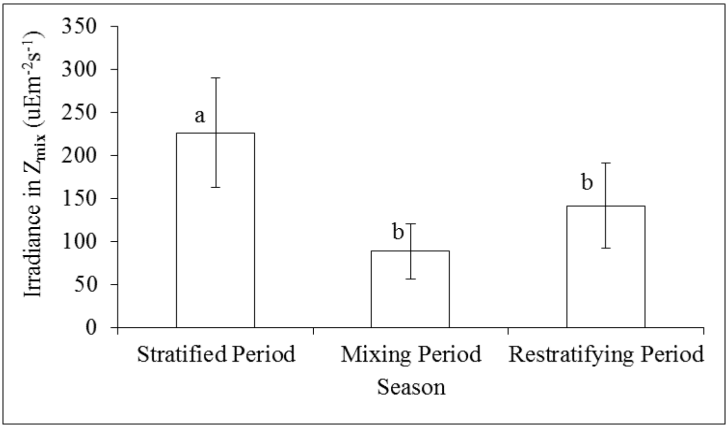

Fig. 3 Seasonal variation of the irradiance in the mixed layer (Imix) of Lake Bosomtwe (Ghana). Bars represent standard deviations. Bars for a season with different letters are statistically significant at p<0.05.

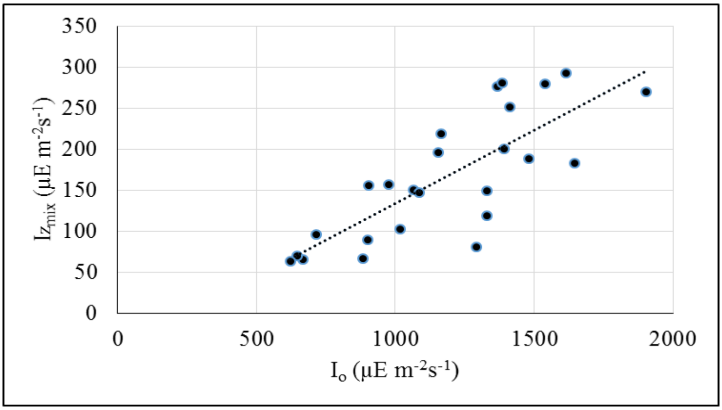

Fig. 4 Relationship between incidence irradiance (I_o) and the mean irradiance in the mixed layer (I_{mix}) in Lake Bosomtwe (Ghana)

The lowest mean areal light utilization efficiency (eA) of the phytoplankton of the lake occurred in the restratifying season (0.22 ± 0.11 %; CV = 51.5%; n = 8) and the highest occurred during the mixing season (0.44 ± 0.19 %; CV = 43.4%; n = 6). Mean areal light utilization efficiency also differed significantly between the mixing and stratified seasons (df = 2, 15; Fig 5) and between mixing and restratifying seasons (df = 2, 12; Fig 5), but not between the stratified and restratifying seasons (df = 2, 17; ANOVA, Fig 5) at $p < 0.05$.

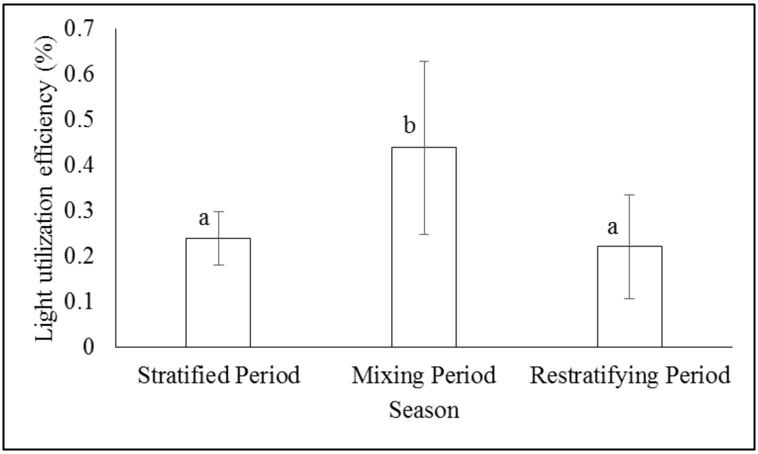

Fig. 5 Seasonal variation of the % light utilization efficiency in the mixed layer by the phytoplankton (eA) of Lake Bosomtwe (Ghana). Bars represent standard deviations. Bars for a season with different letters are statistically significant at p<0.05.

The seasonal composition of the phytoplankton community biomass during the study is shown in figure 6. In the stratified season, the phytoplankton community biomass appeared in the sequence: Cyanophyceae (58.0 %) > Dinophyceae (23 %) > Chlorophyceae (13.4 %) > Bacillariophyceae (3.6 %) > Cryptophyceae (1.5 %) > Euglenophyceae (0.4 %) > Chrysophyceae (0.1 %). In the mixing season, the phytoplankton community biomass was similarly appeared in the sequence: Cyanophyceae (54.0 %) > Dinophyceae (19.0 %) > Chlorophyceae (17.3 %) > Cryptophyceae (5.3 %) > Bacillariophyceae (3.2 %) > Euglenophyceae (1.0 %) > Chrysophyceae (0.3 %). But in the restratifying season, phytoplankton community biomass appeared in the sequence: Cyanophyceae (54.0 %) > Chlorophyceae (22.6 %) > Dinophyceae (19.4 %) > Cryptophyceae (2.0 %) > Bacillariophyceae (1.4 %) > Euglenophyceae (0.6 %) > Chrysophyceae (0.002 %).

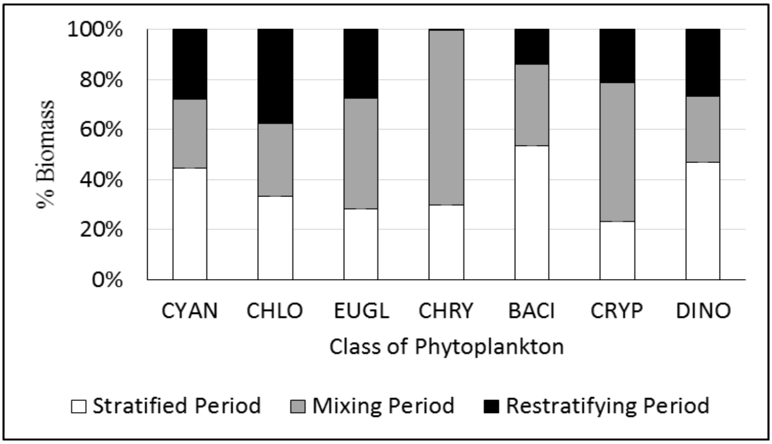

Fig. 6 Seasonal variation in the phytoplankton community biomass composition of Lake Bosomtwe (Ghana). CYAN is Cyanophyceae, CHLO is Chlorophyceae; EUGL is Euglenophyceae, CHRY is Chrysophyceae, BACI is Bacillariophyceae, CRYP is Cryptophyceae, and DINO is Dinophyceae

DISCUSSIONS

The areal light utilization efficiency of the phytoplankton of Lake Bosomtwe lies at the lower end of those typically observed for lakes and reservoirs of the world (Brylinsky, 1980) but below the biospheric average of 0.4 % (Odum, 1971). It is however similar to that obtained for composite photosynthetic organisms of the entire world of about 0.27 % (Hall and Rao, 1994). Talling *et al*., (1973) found very high values ranging from 0.5% to 3.3% associated with two Ethiopian soda lakes dominated by the cyanobacteria. Though the phtoplankton of Lake Bosomtwe is also dominated by the cyanobacteria (Awortwi *et al*., 2015), the areal light utilization efficiencies for these soda lakes even at their lower ends are close to twice that observed for the phytoplankton of Lake Bosomtwe. This may imply that, in an annual cycle, the phytoplankton of Lake Bosomtwe are less efficient at capturing and converting light energy into organic matter compared to that found in these lakes. One result is that the biomass of the phytoplankton that characterize these lakes are much higher, close to four times and up to over seven times, than that of of Lake Bosomtwe (Hecky and Fee, 1981; 1965; Awortwi *et al*., 2015). This may be due to the fact that at higher biomass of these lakes, higher competition may result in increased efficiency compared to the lower biomass of Lake Bosomtwe.

A number of factors have been noted to influence the efficiency of light utilization of phytoplankton in lakes. Some of these include changes in light intensity and condition, availability of nutrients, and the community composition of the phytoplankton (Marzetz *et al*., 2020). The negative relationship between light (i.e. both incident irradiance and the mean irradiance in the mixed layer) with the light utilization efficiency of the phytoplankton has also been observed in other lakes (Dubinksy and Berman, 1981; Morabito and Pugnetti, 2000; Marzetz *et al*., 2020) and is often attributed to light inhibition of phytoplankton at high light intensities. The range of light intensities that the phytoplankton community of the lake experienced within the mixed layer (63.42 to 293.11 $\mu Em^{-2}s^{-1}$) of the lake is within that expected for phytoplankton in the mixed layer of lakes (darkness to about 400 $\mu Em^{-2}s^{-1}$) as suggested by Horne and Goldman (1994). The significant negative relationship between the light utilization efficiency and mean irradiance in the mixed layer observed in this study, suggests that high light intensities tend to reduce the efficiency of light utilization of the phytoplankton community.

The variability in the mean irradiance in the mixed layer during the study period was quite wide (CV = 46.5 %). Wide variations in the light climate in aquatic systems are noted to affect changes in phytoplankton photosynthesis and growth rates (Marzetz *et al* 2020), parameters which are positively influenced by the light utilization efficiency as was observed in this study. The positive and significant relationship between the surface and mean irradiance in the mixed layer of the the lake (r^2 = 62.4%) may be an indication that other factors that are not energy-related may have less influence on the light conditions of the lake in an annual cycle. Guildford *et al* (2000), found a similar relationship in lakes Malawi and Superior but the influence of the changes in the mean irradiance in mixed layer were affected more strongly by the mixed layer depth than by the surface irradiance.

In Lake Bosomtwe, increases in the mixed layer depth and the euphotic depth were both positively influenced by the light utilization efficiency of the phytoplankton community though the relationship was only significant for the mixed layer depth. The secchi disc depth, a surrogate of light condition related to the euphotic zone, also had a positive relation with the light utilization efficiency of the phytoplankton though the relationship was also not significant. The strong positive relationship between the mixed layer depth and the areal light utilization efficiency may imply that during deep mixing, the phytoplankton may be utilizing light more efficiently on average comapared to a more stratified condition. Marra (1978) suggests that vertical turbulence may increase water column productivity of phytoplankton and inferred that the effect is due to the variations in light experienced by phytoplankton cells. But, Steelmann Nielsen and Hansen (1959) have also observed that during mixing seasons, the entire phytoplankton community is exposed to higher light levels than during thermal stratification. But the opposite is true in Lake Bosomtwe since the mixed layer is on average greater than that of the trophogenic zone (Awortwi *et al*., 2018) and light intensities in the mixed layer were higher during stratified conditions than in the mixing season. Tilzer and Goldman (1978) like Marra (1978), observed a similar relationship in Lake Tahoe. It may be that the availability of more nutrients in the mixing compared to the stratified period may be a more important factor affecting the efficiency with which the phytoplankton is able to utilize available light in Lake Bosomtwe. The mixed layer depth is considered as an environmental condition of fundamental importance to pelagic primary producers in lakes since it affects the phytoplankton production, biomass and loss rates (Diehl *et al*., 2002). This is corroborated in this study since the changes in the mixed layer depth significantly and positively influenced changes in the light utilitlzation efficiency of the phytoplankton community. However, a negative but weak relationhip between extinction coefficient and the areal light utilization efficiency may imply that there is an optimal range of light intensity between saturating intensities and intensities too low to enable the phytoplankton community to efficiently utilize it.

Increases in the ratio of the euphotic depth to mixed layer depth in the lake tends to reduce the areal light utilization efficiency due mostly to light inhibition. Increases in this ratio implies that light intensities are increasing which may reach inhbitory levels above staurating intensities and lead to a decline in the effciency with which the phytoplankton community is able to use available light.

Wood *et al*., (1978) asserts that changes in light climate as a result of fluctuations of this ratio affects the variability of photosynthetic rates which depends on the light utilization efficiency. Though changes in this ratio did not significantly affect changes in the light utilization efficiency of the phytoplankton community, this study shows a very strong positive relationship (r^2 = 70.6%) between this ratio and the mean irradiance within the water column both of which are considered good indices of the underwater light climate Naselli-Flores *et al* (2007).

The reduction in the areal light utilization efficiency with increases in temperature may be due to the adverse effects of higher temperature on enzymatic activities of the phytoplankton and increased respiartory rates at such temperatures. The high irradiance and associated high temperatures in the tropics that stimulate more photosynthesis also induce other energetically costly metabolic processes such as high respiration rates in photosynthetic cells (Kemp (1977, Beadle, 1981) and this acts to reduce their light utilization efficiencies. For instance, Awortwi *et al* (2018) estimates that phytoplankton community respiration in Lake Bosomtwe is on average close to 92% of the primary productivity.

Total phosphorus and nutrient related parameters such as conductivity and changes in water level of the lake generally led to an increase in the areal light utilization efficiency albeit to an insignificant extent. This imply that though nutrient and nutrient-related factors affects the light utilization efficiency, it may not limit the phytoplankton in Lake Bosomtwe. Several findings indicate that energy or light availability and its variations has a greater impact on phytoplankton communities than nutrients in nutrient-sufficient lakes (Brylinksy and Mann, 1973; Karikari and Bosque-Hamilton, 2004; Awortwi *et al*., 2018; Marzetz *et al*., 2020).

The positive relationship between the areal light utilization efficiency of the phytoplankton and all the other biological parameters implies that during periods of high light utilization efficiency, they make more efficient use of the light resource. Light as an important resource acts to stimulate these biological processes in the phytoplankton of the lake. Brylinsky and Mann (1973) found similar relationships between the light utilization efficiency and the biological parameters chlorophyll a and biomass of the phytoplankton during their studies of a large number of lakes across different latitudes.

Seasonally, the occurrence of the highest areal light utilization efficiency in the mixing period can be attributed to the low mean irradiance (88.64 $\mu Em^{-2}s^{-1}$) experienced by the phytoplankton which is below saturating intensities of between 100-500 $\mu Em^{-2}s^{-1}$ (Hecky and Fee, 1981) and high variability (Talmy *et al*., 2013). Hence, the phytoplankton can continue to increase their light utilization effciencies and reach optimal photosynthesis as light becomes increasingly available at sub-saturating intensities. Talmy (2013) observed that phytoplankton exposed to fluctuating light regimes typical of mixing seasons optimized photosynthesis compared to stratified conditions where phytoplankton are exposed to the same high light intensities. Awortwi *et al*., (2018), found levels of gross primary productivity and chlorophyll a to be highest during the mixing period. These parameters were positively influenced by increases in the light utilization efficiencies during this study. On the other hand, the high light intensities observed during the stratified and restratifying periods respectively, often inhibits photosynthesis of the phytoplankton with a resultant reduction in the light utilization efficiency (Marzetz *et al*., 2020). At high light intensities phytoplankton are noted to photoacclimate by increasing their carotenoid pigments relative to chlorophyll a which do not transfer energy to the reaction centres (Siefermann-Harms, 1985) or do so with reduced efficiency (Falkowsky and Raven, 1997). This, coupled with relatively low nutrient levels during these seasons (Awortwi *et al*., 2018) may be acting to reduce the light utilization efficiency of the phytoplankton.

In Lake Bosomtwe, changes in the light climate in the mixed layer and areal light utilization efficiency, did not lead to changes in the phytoplankton community composition. Different taxonomic groups of phytoplankton are known to differ in the antenna organization and pigment composition, which leads to differences in their light utilization efficiencies (Kunath *et al*., 2012) even though a high degree of acclimation to light by phytoplankton as was observed in this study, have been noted (Dimier *et al*.,2009). The community biomass of the Cyanobacteria, Dinophyceae, and the Chlorophyceae, made up more than 90 % of the biomass in all seasons. This may be attributed to the high functional versatility of these group especially the Cyanophyceae and Dinophyceae in been able to regulate their position in the water column to adapt to changing light intensities, quality and nutrient acquisition (Marzetz *et al*., 2020). All three groups experience photoinhibition at light intensities above 200 $\mu Em^{-2}s^{-1}$ (Horne and Goldman, 1994) and so are likely to experience this phenomenon and reduced areal light utilization efficiency in the stratified period where mean light intensity was over 226 $\mu Em^{-2}s^{-1}$ as the lowest areal light utilization efficiency as was observed in this season. On the other hand, in the mixing and restratified periods with lower mean light intensties of 88.64 and 141.34 $\mu Em^{-2}s^{-1}$ respectively, they will be expected to be less affected by photoinbition and therefore have comparatively higher areal light utilization efficiencies as was observed in this study.

CONCLUSIONS

The areal light utilization efficeincy of photosynthetic organisms is an important ecological parameter needed to understand many of the essential processes of phytoplankton in an aquatic ecosystems. The value for the phytoplankton of Lake Bosomtwe is relatively low and lie at the lower end of values typical for lakes and reservoirs of the world and may account for their lower biomass relative to similar soda lakes.

A clear seasonal signature of this efficiency associated with the mixing-stratification regime of the lake was observed with higher efficiencies achieved during the mixing season compared to the stratified and restratifying seasons. Low mean irradiance and high variability of light condition in the mixed layer of the mixing season, induced higher effciency compared to the stratified and restratifying seasons characterized by opposite conditions and resulted in lower efficiencies probably due to photoinhibition and higher respiration rates.

Physical factors especially surface irradiance and irradiance-related parameters seem to exert greater influence on the areal light utilization efficiency of the lake’s phytoplankton community compared to nutrient and nutrient-related factors. The gross primary productivity was the biological parameter that was most influenced by the areal light utilization efficiency.

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