
ANALYSIS OF THE RELATIONSHIP BETWEEN ABUNDANCE SURROGATES OF PHYTOPLANKTON OF LAKE BOSOMTWE (GHANA), AND THEIR RELATIONSHIP WITH THE PHYSICOCHEMICAL ENVIRONMENT

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ABSTRACT

Parallel determination of phytoplankton abundance surrogates viz, cell numbers, wet biomass, chlorophyll a and their derivatives were investigated in Lake Bosomtwe (Ghana) by collecting samples from an index station. In the laboratory cells were counted and fitted to geometric shapes for wet weight determination while chlorophyll a was estimated by fluorometry. No significant correlation was observed between the phytoplankton crop of cells and wet biomass ($r=+0.26$, $n=33$), chlorophyll a and cells ($r= -0.23$, $n=33$) and chlorophyll a and wet biomass ($r= -0.16$, $n=33$) respectively ($p>0.05$). Chlorophyll a content per unit cell ($0.34\pm0.24 \mu\text{g cell}^{-1}$, $n=33$; $\text{CV}=71.8\%$) and per unit wet biomass ($0.45\pm0.32 \%$, $n=33$; $\text{CV}=71.3\%$) were low and both decreased significantly with increase in cells ($r= -0.68$) and wet biomass ($r= -0.49$) respectively ($p<0.05$, $n=33$). Factors that significantly affected the variability of both chlorophyll a per unit cell and per unit wet biomass were mixed layer depth, ratio of mixed layer depth to euphotic depth, secchi depth and the extinction coefficient ($p<0.05$). In both cases, ratio of mixed layer depth to euphotic depth caused the most significant variability in chlorophyll a per cell ($r^2=59\%$; $n=33$) and chlorophyll a per unit wet biomass ($r^2=67\%$; $n=33$) respectively. The low chlorophyll a content per unit phytoplankton cell or wet biomass is attributed to cyanobacteria dominance which generally has low chlorophyll a content compared to other phytoplankton. The negative relationships between phytoplankton crop of cells or wet biomass and chlorophyll a per unit cell or per unit wet biomass is attributed to cell size reduction as abundance increase, physiological changes, light and hydrodynamic variability in the lake. Also, the chlorophyll a content per unit phytoplankton crop of cells or wet biomass seem to be controlled mostly by a combination of energy-related and hydrographic factors whiles nutrient-related factors appeared unimportant. Our study shows that the phytoplankton abundance surrogates of Lake Bosomtwe do not correlate well with each other and that the use of chlorophyll a as an abundance measure should be done with caution and all abundance surrogate measures should be measured in any study of the lake.

Keywords: Phytoplankton, abundance, surrogate, ratio of mixed layer to euphotic depth

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INTRODUCTION

Phytoplankton abundance estimation is one of the most useful and key measurements in the ecology of the pelagic ecosystem of lakes and oceans (Harris, 1986). This is because the abundance of phytoplankton has ecological implications for the evaluation of the quantum of chemical potential energy and its ready availability or otherwise for the productivity of aquatic ecosystems. Estimates of phytoplankton abundance also has implications for water quality management especially in the development and implementation of strategies to reduce the potential adverse effects due to the proliferation of nuisance and toxin-producing forms in drinking and recreational waters (Sandu *et al.*, 2003).

Since the carbon content of phytoplankton is very hard to measure directly, abundance of phytoplankton is usually estimated using other surrogates (Geider *et al.*, 1997). These surrogates include algal cell counts, biovolume-based wet weight biomass, and pigment concentration especially chlorophyll *a* (Smayda, 1978; Jeffrey *et al.*, 1997). Each of these have technical and ecological limitations even though Vollenweider (1969), posits that cells are perhaps the best quantitative expression of phytoplankton abundance. For instance, direct microscopic cell counting and species volume measurement are laborious and require taxonomic expertise and the use of preserved samples. Also, the chemical preservation process can affect cell volume and size and therefore the wet biomass depending on both the type of fixative and the concentration used, as well as the species

of phytoplankton involved (Montagnes *et al.*, 1994). Chlorophyll *a* is the most common and most abundant pigment in all oxygenic photosynthetic organisms and is relatively easy and rapid to quantify. Hence, because of the challenges associated with cell counting and subsequent conversion to algal biomass, chlorophyll *a* concentration has become popular as a quick and easy-to-measure alternative for phytoplankton abundance and is used extensively for estimating phytoplankton abundance in aquatic research. But, its concentration per unit of cell or wet biomass has been found to be affected by several external and internal factors, such as phytoplankton taxonomic composition, cell physiological conditions, efficiency of extractant solvent used, as well as several physicochemical conditions and resource needs (Meeks, 1974; Desortová, 1981; Reynolds, 1984; Riemann *et al.*, 1989; Vörös and Padisák, 1991; Kasprzak *et al.*, 2008). Chlorophyll *a* measurements also lacks any information on the community structure of phytoplankton (Kasprzak *et al.*, 2008).

The relationship between chlorophyll *a*, and other abundance surrogates of phytoplankton has been widely studied in phytoplankton ecology in lakes and oceans with most studies reporting positive relationships between them with varying strengths (Kalchev *et al.*, 1996; Tolstoy, 1979; Desortová, 1981; Vörös and Padisák, 1991; Jones *et al.*, 1996; Kalchev *et al.*, 1996; Rott, 1978; Vörös and Padisák, 1991). Given the varying relationships between these abundance surrogates in different lakes, it is ecologically important to establish these relationships for any particular lake of

interest to help improve our understanding of their relatedness and in taking management decisions regarding water quality and the evaluation of energy and matter in lake food webs.

Research work on phytoplankton abundance in Lake Bosomtwe have used one or the other of a particular surrogate. For instance, Awortwi *et al.*, (2015) used wet weight biomass while Addico *et al.*, (2018) used cell numbers. However, together, the relationship between these abundance surrogates, their variabilities, and the factors that affect them have not been the focus of any study on the lake to help provide the required knowledge and understanding needed in evaluating and interpreting them. Hence, in this paper, we provide an analysis of the relationship between phytoplankton standing stock of cells, biovolume-based wet weight biomass, and chlorophyll *a* concentration for Lake Bosomtwe. Specifically, we determined the relationships between the abundance surrogates of phytoplankton viz, cell numbers versus wet weight biomass, cell numbers versus chlorophyll *a*, and wet weight biomass versus chlorophyll *a* respectively and hypothesize that these abundance indices will positively and significantly be correlated with each other. Secondly, we assess the relationship between the chlorophyll *a* content per unit cell and per unit wet biomass as the cell numbers and wet biomass respectively change. In both cases, we hypothesize that increase in the phytoplankton stock of cells or wet biomass will lead to a decline in the chlorophyll *a* content per unit cell or wet per unit biomass respectively. Thirdly, we assess the relationship between the chlorophyll *a* content per unit cell or per unit wet biomass of the phytoplankton respectively with the physicochemical factors and hypothesize that these attributes will behave similarly with the variabilities in key physicochemical and nutrient factors which in turn will exert significant regulatory controls over their

variability. Fourthly, we determined the relationship between the chlorophyll *a* content per unit phytoplankton cell and the chlorophyll *a* content per unit phytoplankton wet biomass and hypothesize a positive and significant relationship between them.

We assumed that there is no significant effect of changes in the taxonomic composition of the phytoplankton on the chlorophyll *a* concentration since the community is dominated year-round by the cyanobacteria (Awortwi *et al.*, 2015) and consequently did not assess this aspect.

MATERIALS AND METHODS

The study was conducted in Lake Bosomtwe, a tropical meromictic lake located in the south central part of Ghana (06°30'N; 01°25'W) at 99 m above mean sea level (amsl). It has a surface area of 48.6 km², a maximum depth of 78 m and a mean depth of 45 m. A comprehensive description of its physical and chemical features can be found in Puchniak *et al* (2009), and Awortwi *et al* (2015). It is a dimictic lake with mixing periods that usually coincide with the harmattan winds in January and the cold dry season in August (Whyte, 1975; Puchniak *et al.*, 2009). Phytoplankton are key components of its pelagic plankton biomass and cyanobacteria are the most abundant group (Awortwi *et al.*, 2015; Addico *et al.*, 2018).

A central index area of the lake (06°30'609''N; 01°24'671''W; Fig. 1) was sampled 33 times at different periods from November 2004 to October 2006.

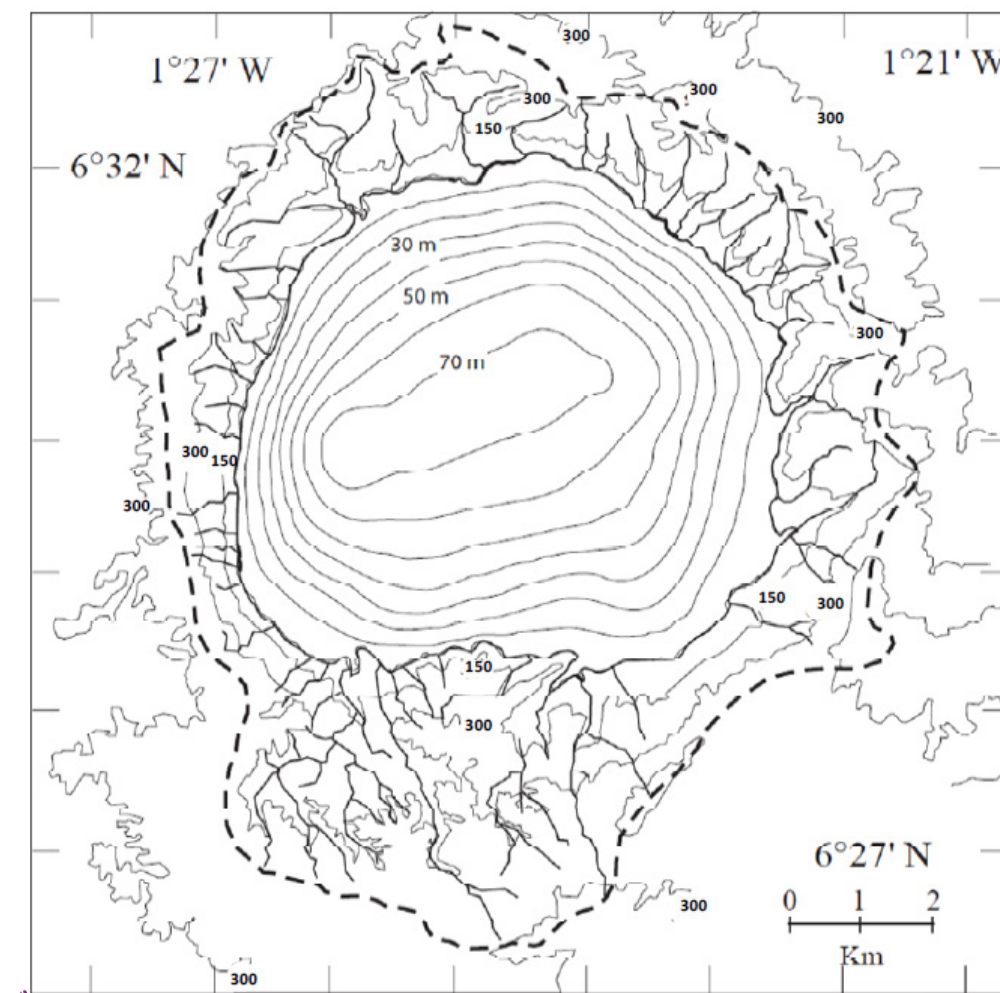


Fig.1 Basin map of Lake Bosomtwe (Adapted from Otu, 2010). Index station was 78 m deep.

Water samples were obtained at discrete depths within the water column at the central index station. All samples were split for parallel determinations of the phytoplankton standing stock of cells, biovolume-based wet weight biomass, and chlorophyll *a* concentrations.

Cell counts were done by the Utermöhl method after fixation with Lugol's solution (Utermohl, 1958). Species volume was estimated by shape assimilation to known geometric forms and direct measurement of the main cell dimensions in more than 25

randomly selected individuals (Smayda, 1978). Total algal biovolume in $\mu\text{m}^3\text{L}^{-1}$ was calculated by the addition of the biovolume of all species present and then converted to wet biomass in mg m^{-3} assuming a specific gravity of 1 g cm^{-3} (Kasprzak *et al.*, 2008). Chlorophyll *a* concentration was measured fluorometrically after extraction in 95 % acetone in a Turner 10 AU flurometer following methods in Havens *et al.* (2024). Chlorophyll *a* concentration, phytoplankton cell numbers, and wet biomass were then used to estimate the chlorophyll *a* per unit phytoplankton cell and chlorophyll

a per unit phytoplankton wet biomass respectively.

Water samples for assessing total phosphorus (TP) and total nitrogen (TN) were collected alongside phytoplankton sampling. Total phosphorus was analyzed using the phosphomolybdate colour development after persulphate digestion following methods in Havens *et al.* (2024). Concentrations of total nitrogen was determined using a reduction column of cadmium filings exposed to copper and the addition of a buffer solution (ammonium chloride, sodium tetraborate, and disodium dehydrate EDTA) and quantified by measuring absorption at 543 nm (Havens *et al.*, 2024).

Vertical temperature profiles were obtained from the central index station using a Hydrolab H2O Multiprobe 68SBP (Hydrolab Corporation, Austin, Texas, 1991) from which the mixed layer depth (Z_{mix}) was estimated. The transparency of the lake water (SD) was measured with

a Secchi disc. 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}) and the euphotic depth (Z_{eu}) following Kirk (1994) and Talling (1986) respectively. Mean irradiance in the mixed layer (I_z) was determined according to Riley (1957) whilst incidence irradiance (I_o) was obtained from a meteorological station near the lake shore at Abono (6°31.138''N, 1°25.665''W).

RESULTS

Relationship between phytoplankton abundance surrogates

A positive correlation between the phytoplankton crop of cells and wet weight biomass ($r = 0.23$) was found which was not significant ($p > 0.05$; $n = 33$; Fig. 2).

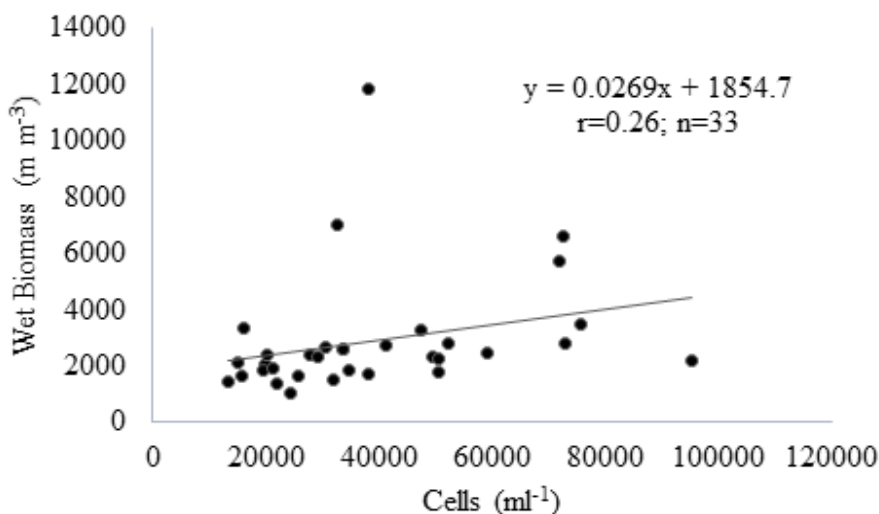


Fig. 2 Variability of phytoplankton cell numbers and wet biomass in Lake Bosomtwe, Ghana.

But, there was a wide variability of the cells and wet biomass relationship as is evident in the considerable scatter of values from the distribution of dots around the regression line (Fig. 2).

There were only four peaks of coincidence between the two variables out of the 33 sampling dates (Fig. 3).

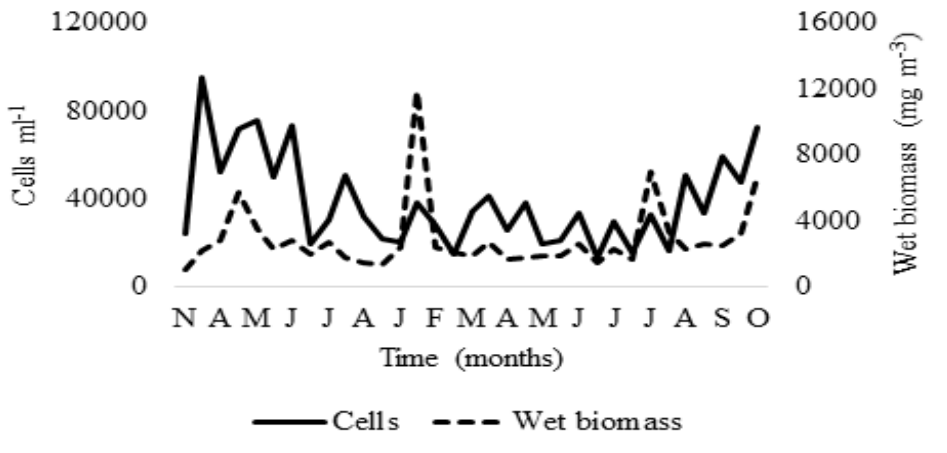


Fig. 3 Seasonal variability of phytoplankton cell numbers and wet biomass in Lake Bosomtwe, Ghana.

However, a negative correlation was found between both the chlorophyll *a* concentration

versus cell numbers ($r = -0.23$, $n=33$; Fig. 4).

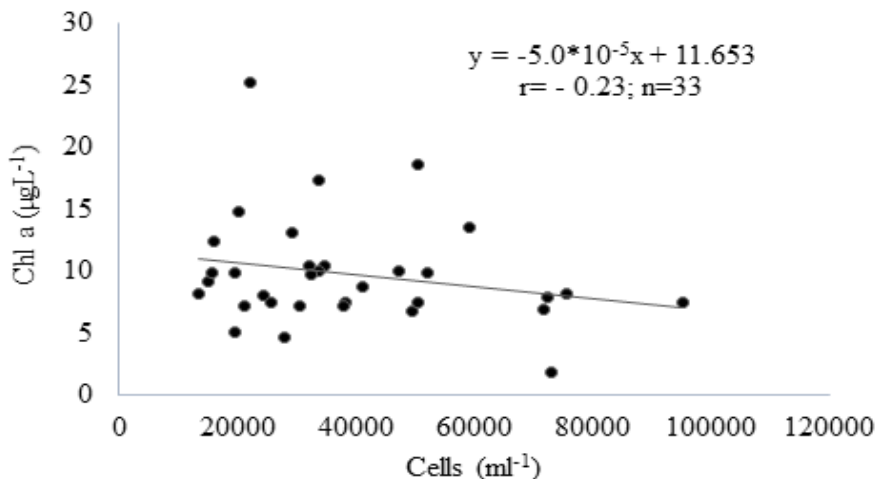


Fig. 4 Variability of chlorophyll *a* (chl *a*) concentration and phytoplankton cell numbers in Lake Bosomtwe, Ghana.

Again, a negative correlation was also found between both the chlorophyll *a* concentration

versus wet weight biomass ($r = -0.16$, $n=33$; Fig. 5).

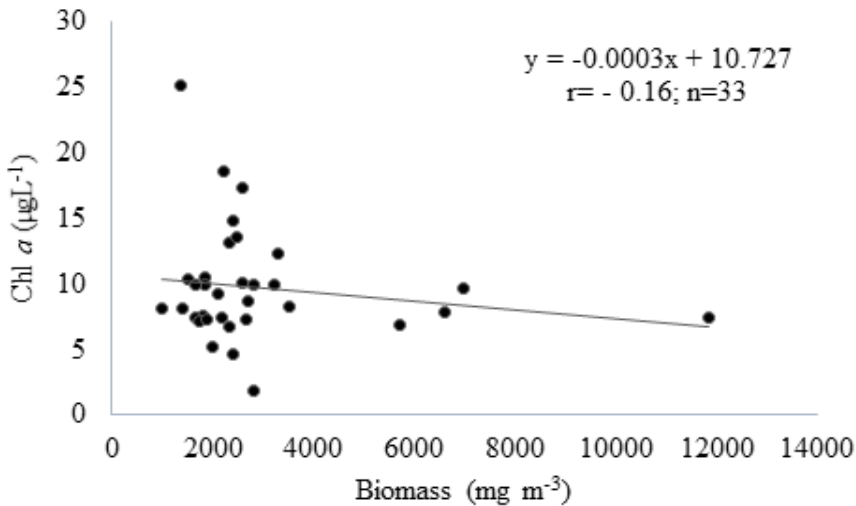


Fig. 5 Variability of chlorophyll *a* (chl *a*) concentration and phytoplankton wet biomass in Lake, Ghana.

These relationships were also not significant ($p > 0.05$; $n=33$). Again, considerable scatter of values in the distribution of dots around the regression lines for both relationships were observed. The negative character of the relationship between chlorophyll *a* and either

the phytoplankton crop of cells or wet biomass is supported by the roughly inverse course of the curves in the seasonal changes of cells, wet biomass, and chlorophyll *a* (Fig. 6 and 7).

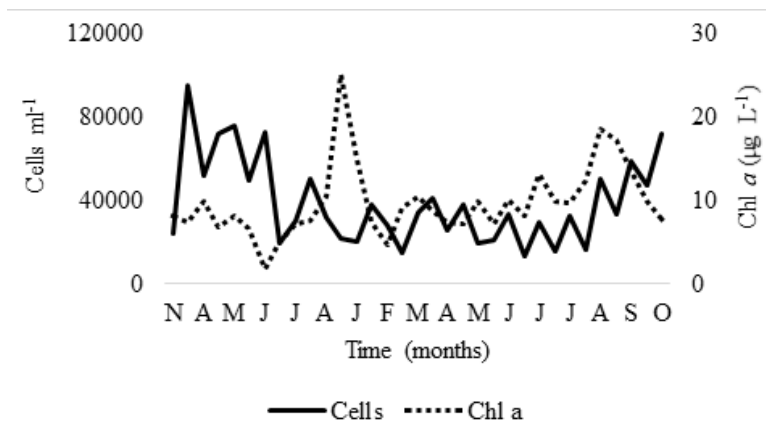


Fig. 6 Seasonal variability of phytoplankton cell numbers and chlorophyll *a* concentration in Lake Bosomtwe, Ghana.

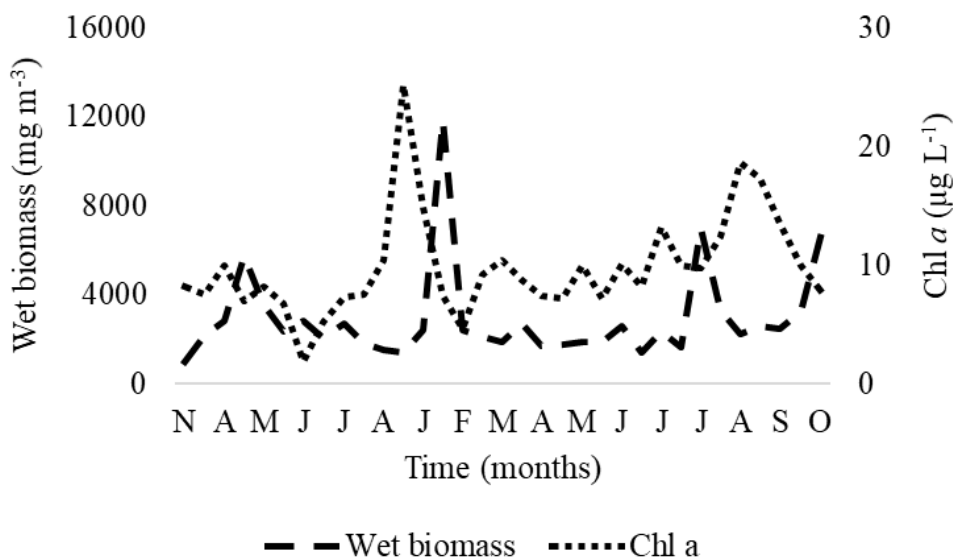


Fig. 7 Seasonal variability of phytoplankton wet biomass and chlorophyll *a* concentration in Lake Bosomtwe, Ghana.

There were only one peak of coincidence between the phytoplankton crop of cells and chlorophyll *a* (Fig. 6) but no coincidence between the phytoplankton crop of wet biomass and the chlorophyll *a* concentration (Fig. 7) out of 33 sampling dates respectively.

Relationship between chlorophyll content per unit phytoplankton cell and biomass

The chlorophyll *a* content per unit phytoplankton cell varied between 0.02 and 1.14 with a mean of 0.34 ± 0.24 µg cell⁻¹ (Table 1). On the other hand the chlorophyll *a* content per unit phytoplankton wet weight biomass varied from 0.06 and 1.81 with a mean of 0.45 ± 0.32 % (Table 1).

Table 1 Descriptors of some phytoplankton parameters observed during the study period

Parameter	Mean±SD	maximum	minimum	CV	n
Cells(mL ⁻¹)	3.8882±20722	95317	13532	53.30	33
Biomass(mg m ⁻³)	2898.90±2104.62	11834	1006	72.60	33
Chlorophylla(µg L ⁻¹)	9.76±4.38	25.15	1.79	44.81	33
Chl a per unit cell(µg cell ⁻¹)	0.34±0.24	1.14	0.02	71.62	33
Chl a per unit biomass(%)	0.45±0.32	1.81	0.06	71.31	33

The relationship between chlorophyll *a* content per unit phytoplankton cell and per unit phytoplankton wet biomass are shown

in figures 7 and 8 respectively. Within a range of 13532 to 95317 cells ml⁻¹ of phytoplankton, a significant decrease in the chlorophyll *a*

content per unit phytoplankton cells occurred from 1.14 to 0.02 $\mu\text{g cell}^{-1}$ ($r=-0.68$; $n=33$; $p<0.05$; Table 1; Fig. 8).

Also, within a range of 1006 to 11834 mg m^{-3} of phytoplankton, a significant decrease in the chlorophyll *a* content per unit phytoplankton

wet biomass occurred from 1.81 to 0.06 % ($r=-0.49$; $n=33$; $p<0.05$; Table 1; Fig. 9). However, considerable scatter of values evident from the distribution of dots around the regression lines were also observed in both cases (Fig. 8 and 9).

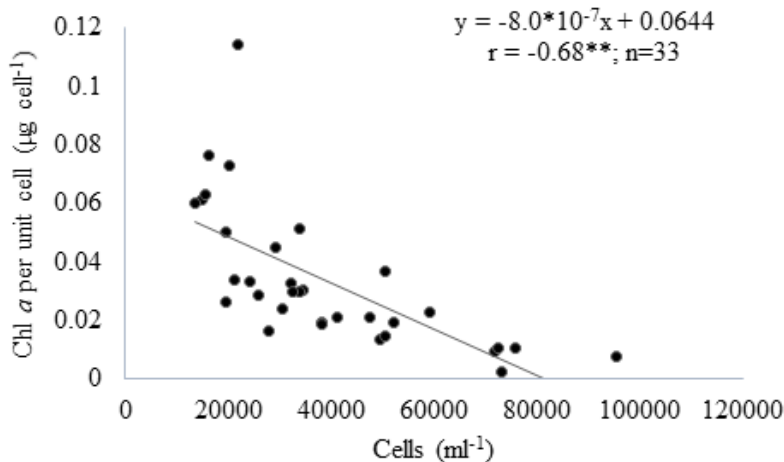


Fig. 8 Variability of chlorophyll *a* (Chl *a*) content per unit phytoplankton cell and phytoplankton cell numbers in Lake Bosomtwe, Ghana. Two asterisks express significance level higher than 0.05.

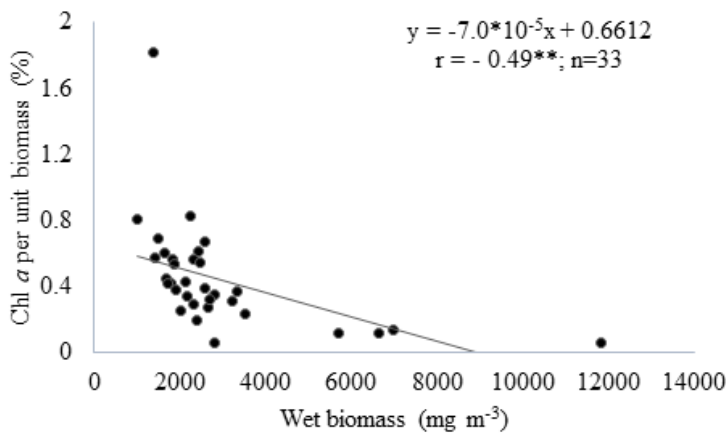


Fig. 9 Variability of chlorophyll *a* (Chl *a*) content per unit phytoplankton biomass and phytoplankton biomass in Lake Bosomtwe, Ghana. Two asterisks express significance level higher than 0.05.

However, a positive and highly significant correlation between chlorophyll *a* content per unit phytoplankton stock of cell and per unit wet weight biomass was found ($r=0.75$;

$p<0.001$; $n=33$; Fig. 10) with the variability in the chlorophyll *a* content per unit

phytoplankton cells explaining close to 57% of the variability in the chlorophyll *a* content per unit wet weight biomass.

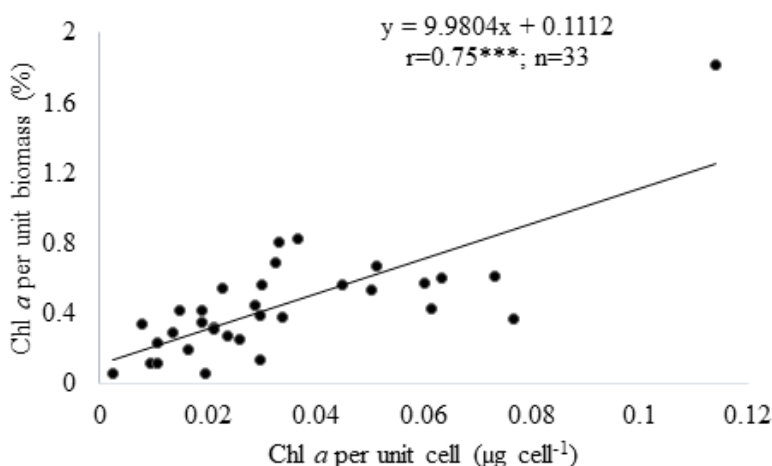


Fig. 10 Variability of chlorophyll *a* (Chl *a*) content per unit phytoplankton biomass and chl *a* content per unit phytoplankton cell in Lake Bosomtwe, Ghana. Three asterisks express significance level at $p = 0.001$.

Variability of chlorophyll *a* per unit cell and variability of physicochemical factors

The chlorophyll *a* content per unit phytoplankton cell increased significantly with increasing depth of the mixed layer (Z_{mix}), the depth of the mixed layer to euphotic depth ratio ($Z_{mix}:Z_{eu}$), and the extinction coefficient (k_{PAR}) respectively ($p<0.05$; $n=33$; Table 2),

but not with total phosphorus ($n=28$) and total nitrogen ($n = 23$) respectively ($p>0.05$).

Also, it decreased significantly with mean light intensity in the mixed (I_z), the euphotic depth (Z_{eu}), and secchi depth (SD; $p<0.05$; Table 2) but not with increasing incident light intensity (I_0), total phosphorus (TP) and total nitrogen (TN) respectively ($p>0.05$); Table 2).

Table 2. Relationship between chlorophyll *a* (chl *a*) per unit phytoplankton cell and physicochemical factors

Relationship	Equation	r	r ²	n	p
Chl <i>a</i> per unit cell vs I_0	$Y = -2.0 \times 10^{-4}x + 0.482$	-0.23	0.05	32	
Chl <i>a</i> per unit cell vs I_z	$Y = -0.001x + 0.485$	-0.46	0.22	32	**
Chl <i>a</i> per unit cell vs Z_{mix}	$Y = 0.0254x + 0.0638$	0.57	0.32	33	***
Chl <i>a</i> per unit cell vs Z_{eu}	$Y = -0.032x + 0.5374$	-0.41	0.17	33	**

Chl a per unit cell vs Z _{mix} :Z _{eu}	Y=0.1209x+0.0973	0.77	0.59	33	***
Chl a per unit cell vs SD	Y=-0.2781x+0.8281	-0.42	0.18	33	**
Chl a per unit cell vs kPAR	Y=0.3327x+0.1024	0.41	0.17	33	**
Chl a per unit cell vs TP	Y=-3.0x10 ⁻⁴ x+0.318	-0.03	0.001	28	
Chl a per unit cell vs TN	Y=-0.0021x+0.0637	-0.25	0.063	23	

n= number of samples on which the mean and standard deviations were estimated; r = correlation coefficient; r² = the coefficient of determination; p = the level of probability at which significance was estimated. Two and three asterisks express significance level higher than 0.05 and 0.001 respectively. No asterisk means the relationship is not significant (p>0.05).

Variability of chlorophyll a per unit wet biomass and variability of physicochemical factors

The chlorophyll *a* content per unit phytoplankton wet biomass increased significantly with increasing depth of the mixed layer (Z_{mix}), the depth of the mixed layer to euphotic depth ratio (Z_{mix}:Z_{eu}), and

the extinction coefficient (k_{PAR}) respectively (p<0.05; n=33; Table 3) but not with total phosphorus concentration (p>0.05; n=28; Table 3). However, it decreased significantly with increasing secchi depth (SD; p<0.05; Table 3) but not with increasing incident light intensity (I_o), light intensity in the mixed layer (I_z), the euphotic depth (Z_{eu}), and total nitrogen (TN) respectively (p>0.05; Table 3).

Table 3. Relationship between chlorophyll *a* (chl *a*) per unit phytoplankton biomass and physicochemical factors

Relationship	Equation	r	r ²	n	p
Chl a per unit biomass vs I _o	Y=-5.0x10 ⁻⁵ x+0.4916	-0.04	0.002	32	
Chl a per unit biomass vs I _z	Y=-0.0009x+0.5674	-0.27	0.08	32	
Chl a per unit biomass vs Z _{mix}	Y=0.0365x+0.0557	0.62	0.38	33	***
Chl a per unit biomass vs Z _{eu}	Y=-0.0334x+0.6604	-0.33	0.11	33	
Chl a per unit biomass vs Z _{mix} :Z _{eu}	Y=0.1712x+0.1034	0.82	0.67	33	***
Chl a per unit biomass vs SD	Y=-0.0009x+0.5574	-0.38	0.15	33	**
Chl a per unit biomass vs kPAR	Y=0.4449x+0.134	0.42	0.18	33	**
Chl a per unit biomass vs TP	Y=0.0002x+0.3956	0.01	0.0002	28	
Chl a per unit biomass vs TN	Y=0.0027x+0.0524	-0.26	0.069	23	

n= number of samples on which the mean and standard deviations were estimated; r = correlation coefficient; r² = the coefficient of determination; p = the level of probability at which significance was estimated. Two and three asterisks express significance level higher

than 0.05 and 0.001 respectively. No asterisk means the relationship is not significant ($p > 0.05$).

DISCUSSION

Relationship between phytoplankton abundance surrogates

Our findings indicate a positive but low correlation between the phytoplankton cell numbers and the biovolume-based wet weight biomass of Lake Bosomtwe which partly supports our hypothesis between these two abundance surrogates. A positive correlation indicates that both surrogates are true measures of the abundance of phytoplankton. Similar findings have been observed by others (Nabila *et al.*, 2021; Dubinsky and Stambler, 2009; Hillebrand *et al.*, 1999; Desortova, 1981). However, the lack of a significant relationship between these two surrogates may be due to fact that as the phytoplankton cell numbers increase, their biomass did not increase to the same extent. For instance, there were only four peaks of coincidence between these two surrogates out of the 33 sampling periods. This may be because the phytoplankton community composition and hence the biovolume may not change much with increasing cell numbers as has been observed by Awortwi *et al.* (2015). Selective grazing of larger celled phytoplankton to optimize efficiency can also lead to reduced correlation between these two phytoplankton surrogates (Marzetz *et al.*, 2020). Thus, though our results support other findings, the relationship is not strong with variations in the cell numbers explaining only close to 7% of the variation in the biovolume-based wet weight biomass of the phytoplankton.

On the other hand, the relationships between chlorophyll *a* concentration and both phytoplankton crop of cell and biovolume-based wet weight biomass respectively were negative and not significant and conflicted our hypotheses that both surrogates will have

positive and significant relationship with it. The phytoplankton crop of cells maxima and minima coincided temporally only once with the chlorophyll *a* concentration while the maxima and minima of the wet biomass did not coincide at all with that of the chlorophyll *a* concentration in 33 sampling periods respectively. These observations led to considerable variability in these relationships and the low coefficients of determination observed. The temporal decoupling of the phytoplankton crop of cells and wet biomass with the chlorophyll *a* concentration suggest that these relationships are examples of ontogenetic adaptations of the same phytoplankton community dominated by the cyanobacteria throughout the year induced by environmental factors (Felip and Catalan, 2000; Awortwi *et al.*, 2015). For instance, hydrodynamic factors such as changes in the mixed layer depth and reduced transparency can affect the light and nutrient conditions in a lake and cause changes in the chlorophyll *a* concentration (Huisman *et al.*, 2004) at constant cell numbers or biomass. Sterner and Elser (2000) attribute such negative relationship to nutrient depletion at high phytoplankton crops which will lead to a drop in the synthesis of chlorophyll *a* at constant cell numbers.

Also as an example, at high nitrogen limitation, cells may degrade chlorophyll *a* to reuse the nitrogen-containing components leading to a drop in chlorophyll *a* concentration (Mouget *et al.*, 2005). However, since the major nutrients, phosphorus and nitrogen are known to be sufficient for phytoplankton growth in Lake Bosomtwe (Karikari and Bosque-Hamilton, 2004; Awortwi *et al.*, 2015, 2018), nutrients may not significantly contribute to these observations.

Likewise, changes in composition of the phytoplankton community have similarly been suggested as a factor that can lead to a negative relationship between these abundance surrogates since different phytoplankton groups have different chlorophyll *a* concentrations on average (Litchman *et al.*, 2007). But, because the phytoplankton community of the lake is dominated by the cyanobacteria throughout the year (Awortwi *et al.*, 2015; Addico *et al.*, 2018), changes in community composition may also not significantly contribute to the negative relationships between these abundance surrogates.

Hence, we agree with Kaskitalo (1977) and Kasprzak *et al.*, (2008) in their conclusions that negative relationship between chlorophyll *a* and both the phytoplankton crops of cells and wet biomass may imply that pigment concentration alone cannot give a good indication of the temporal variations in the phytoplankton crop in lakes as is found for Lake Bosomtwe in this study.

Despite these observations, a considerable number of works have found a positive and significant relationship between phytoplankton abundance (cells and biomass) and chlorophyll *a* concentration in many lakes and reservoirs (Brylinsky and Mann, 1975; Willen, 1976; Desortiva, 1981; Felip and Catalan, 2000; Kasprzak *et al.*, 2008; Nabila *et al.*, 2021). These observations imply that the analysis of phytoplankton abundance should include as many surrogates as possible to help in the determination of the surrogate that can best represent lake-specific phytoplankton abundance (Ignatiades *et al.*, 1985).

Relationship chlorophyll *a* content per unit phytoplankton cell and wet biomass

Measurement of chlorophyll *a* content per unit cell ($0.34 \pm 0.24 \mu\text{g cell}^{-1}$) is rare in the literature but it was low compared to that

of Felip and Catalan (2000) estimate of 0.69 for a deep oligotrophic lake where flagellated chrysophytes are dominant. In the case of Lake Bosomtwe, it is dominated by the cyanobacteria year-round (Awortwi *et al.*, 2015). The cyanobacteria are generally known to have a lower chlorophyll *a* content per cell compared to most other phytoplankton (Saeed *et al.*, 2023).

Also, though the chlorophyll *a* content per unit wet biomass in Lake Bosomtwe ($0.45 \pm 0.32\%$) is within the range found in several other natural lakes in the literature of between 0.1 to 9.7% (Kasprzak *et al.*, 2008; Felip and Catalan, 2000; Desortova, 1981; Nicholls & Dillon, 1978; Keskitalo, 1977; Ahlgren, 1970), it is considered low since the most frequently reported values are between 3 - 4% (Desortiva, 1981). The reason for the low value may be attributed to the same reason why the chlorophyll *a* content per unit cell in the lake is low i.e. the dominance of the phytoplankton community by the cyanobacteria which tend to have lower chlorophyll *a* content compared to other phytoplankton (Saeed *et al.*, 2023). However, our value is consistent with that of Ahlgren (1970), who found values that ranged from 0.4 to 4.2 % for a cyanobacteria-dominated lake.

The chlorophyll *a* content per unit cell or per unit wet biomass both decreased significantly as the cells or wet biomass increased respectively confirming our hypotheses. At both low cells and low wet biomass respectively, chlorophyll *a* content per unit cell or wet biomass showed a wide range of values reducing the strength of these significant relationships. Several reasons have been attributed to these observations. These include cell size reduction as abundance increases to conserve resources with concomitant decline in chlorophyll *a* content per unit cell and hence wet biomass (Chen *et al.*, 2018), physiological changes that result in a reduced chlorophyll *a* synthesis or increased

chlorophyll *a* degradation in response to increased crop of cells or wet biomass (Liu *et al.*, 2018), as well as direct response to changes in environmental factors (Awortwi *et al.*, 2022). For instance, during the day times in which sampling was done, the phytoplankton may be adapting to high light intensities by reducing their chlorophyll *a* content and producing pigments such as carotenoids that act to protect them from photodamage (Marzetz *et al.*, 2020). This will result in lower chlorophyll *a* content even when cell numbers and associated wet biomasses are high. These are all plausible explanations for our observations in Lake Bosomtwe. Similar relationships have been found in other lakes (Kiss *et al.*, 2006; Sandu *et al.*, 2003; Felip and Catalan, 2000).

However, although nutrient limitations (Geider *et al.*, 1998) and changes in community composition (Felip and Catalan, 2000) have also been used to explain these observations, it is unlikely that they are significant factors for Lake Bosomtwe since nutrients are considered adequate and the phytoplankton are dominated by the cyanobacteria throughout the year (Karikari and Bosque-Hamilton, 2004; Awortwi *et al.*, 2015; Addico *et al.*, 2018).

Effects of physicochemical factors on the chlorophyll *a* content per unit phytoplankton cell and wet biomass

The chlorophyll *a* content of the phytoplankton per unit cell or wet biomass varied similarly with the physicochemical factors confirming largely our hypothesis. It also supports the positive relationship between the chlorophyll *a* content per unit cell and per unit wet biomass observed in this study.

The factors which significantly affected the variability of both the chlorophyll *a* content per unit cell and per unit wet biomass are the mixed layer depth, the mixed layer to euphotic depth ratio, the secchi disc depth, and the extinction coefficient of light. These factors

are all related to light and the light conditions in the water column.

The positive relationships between the mixed layer depth, the extinction coefficient of light, and the ratio of the mixed layer depth to the euphotic depth and the chlorophyll *a* content per unit cell or wet biomass is an often observed phenomenon in phytoplankton ecology (Desortova, 1981; Felip; Marzetz *et al.*, 2020; Catalan, 2000; Awortwi *et al.*, 2022) and is attributed to ontogenetic adaptation of the phytoplankton community to decreasing light availability as an attempt to harvest as much light available as is possible to avoid light limitation. Under such conditions, the dominant phytoplankton group in the lake, the cyanobacteria (Awortwi *et al.*, 2018), are able to use their different light-harvesting pigments which transfer excitation energy to chlorophyll *a* to broaden the photosynthetic efficiency and increase the general productivity of the lake (Marzetz *et al.*, 2020; Awortwi *et al.*, 2018). The high coefficient of determination between the ratio of the mixed layer depth to the euphotic depth and the chlorophyll *a* content per unit cell (59%) or wet biomass (67%) makes it the most useful predictor amongst the other significant physicochemical factors.

The light intensity at the surface and within the water column as well as the secchi disc depth (a surrogate of light intensity in the water column), all had a negative relationship with the chlorophyll *a* per unit cell or wet biomass but only the secchi depth significantly affected the variability of the chlorophyll *a* content per cell or wet biomass of the phytoplankton of the lake. Increases in the light intensity in the water column can photodamage the photosynthetic apparatus of phytoplankton (Marzetz *et al.*, 2020). Hence, phytoplankton communities often respond to high light intensities by reducing chlorophyll *a* synthesis and increasing the production of carotenoid and other accessory pigments that do not transfer excitation energy to

chlorophyll *a* to reduce the adverse effects of high light intensities (Marzetz *et al.*, 2020; Paerl, 1996; Siefertmann-Harms, 1985). Such periods often record reduced photosynthetic efficiencies (Falkowsky and Raven, 1997; Awortwi *et al.*, 2022). However, the extent to which light directly affected the variability of the chlorophyll *a* per unit cell or wet biomass was low compared to the ratio of the mixed layer to euphotic depth ratio pointing to the importance of hydrographic factors in explaining the variability of chlorophyll *a* concentration in phytoplankton ecology of the lake.

However, the chlorophyll *a* content per unit cell or wet biomass of the phytoplankton did not vary significantly with the nutrient factors. Generally, the key nutrients total phosphorus and total nitrogen have been found to be adequate for phytoplankton of Lake Bosomtwe (Karikari and Bosque-Hamilton, 2004; Awortwi *et al.*, 2015; 2018). Also, the lack of any significant and consistent relationship between the chlorophyll *a* content per unit cell and per unit wet biomass respectively and these nutrient factors suggest that nutrients may not be important enough in predicting phytoplankton cell-biomass-chlorophyll *a* relationships. Some studies also suggest, that in nutrient-sufficient lakes, light conditions generally have a greater effect compared to nutrient factors (Brylinsky and Mann, 1973; Marzetz *et al.*, 2020). Our study support this assertion.

Relationship between chlorophyll *a* content per unit cell and chlorophyll *a* content per unit wet biomass

The significant increase in the chlorophyll *a* content per unit biomass as the chlorophyll *a* content per unit cell increases can be explained by the scaling effect (Dubinsky and Stambler, 2009). In other words, as the chlorophyll *a* content per unit cell increases, the total chlorophyll *a* content per unit

biomass also increases as a direct contribution of each cell to the phytoplankton biovolume.

CONCLUSIONS

In summary, our study has established that, the relationship between the phytoplankton abundance surrogates are weak and not significant. The positive relationship between cell numbers and wet biomass imply they are true measure of phytoplankton abundance whilst the negative relationship between them and chlorophyll *a* implies that the variability of chlorophyll *a* is an ontogenetic phenomenon by the same phytoplankton community adapting to the changing physicochemical environment. This also imply that chlorophyll *a* measurement, a popular surrogate for estimating phytoplankton biomass, alone is not good estimate of the phytoplankton community of the lake and that it is essential to include other phytoplankton abundance surrogates to help in diagnosing what abundance index may truly represent a particular lake.

Secondly, the phytoplankton community of Lake Bosomtwe has low chlorophyll *a* content per unit cell or wet biomass. This is attributable to the dominance of the Cyanobacteria which have low chlorophyll *a* levels compared to other phytoplankton groups. Also, the significant negative relationship between the chlorophyll *a* and both the phytoplankton crops of cells and wet biomass respectively can be linked to the decrease in the chlorophyll *a* content due to cell size decreases as abundance due to cells or wet biomass increase as a way of conserving resources. It can also result from ontogenetic shifts due to hydrodynamic changes in the water column and changes in environmental conditions such as variabilities in light.

Thirdly, chlorophyll *a* content per unit cells or wet biomass related in a similar manner to the variabilities in the physicochemical

environment. Significant variabilities were driven largely the variabilities in hydrographic and light-related factors. The phytoplankton community were observed to respond to the varying light conditions by activating and enhancing their light harvesting complexes when light levels are low or producing more photo-protective pigments which prevent their photosynthetic apparatuses from photodamage. Overall, hydrographic factors, especially the ratio of mixed layer depth to euphotic depth, affected the variabilities of these two attributes much more than other factors while nutrient factors and changes in community composition, important in other lakes, seem unimportant.

Lastly, the positive and significant relationship between chlorophyll *a* content per unit cell and per unit wet biomass is traceable to scaling effect i.e. as the number of cells containing a certain amount of chlorophyll *a* increases, the chlorophyll *a* content in the biovolume of these same cells also increase by proportion. This also confirms that chlorophyll *a* may not be a good measure of the phytoplankton abundance in Lake Bosomtwe and that its concentration is regulated by the environmental conditions within the lake at any particular time.

Hence, we recommend that estimation of the abundance of phytoplankton in Lake Bosomtwe should be done with caution and that it should at the very least include all of these surrogates. This will help in improving our ability to better evaluate the productivity of the lake and also enhance management efforts. In addition, a spatial approach to sampling should also be considered to expand the scope and improve assessment.

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