Spatio-temporal variability of phytoplankton community species composition,

biomass and primary productivity of Lake Bosomtwe (Ghana)

By

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Declaration

I hereby declare that this thesis is my own work towards the PhD degree and that to the best of my knowledge, it contains no material previously published by another person(s) nor material which has been accepted for the award of any other degree of the University, except where due acknowledgement has been made in the text.



Abstract

In this thesis, the community composition, biomass and primary productivity of the phytoplankton of Lake Bosomtwe on spatio-temporal scales are presented for the first time in relation to the physico-chemical environment. Horizontal and temporal/seasonal variabilities in the wet weight biomass, chlorophyll a, gross productivities, and community respiration as well as growth rates are also assessed. Phytoplankton community composition and biomass were assessed from 14 different stations in spatial surveys and 1 index central station for temporal studies. Samples were collected biweekly (temporal study) and in stratified and mixing periods (spatial study) with a 6-Litre van Dorn sampler and preserved with acid Lugol. Samples were counted using inverted microscopy and converted to wet weight biomasses by approximating cell volume through routine measurements of 30-50 cells of an individual species and the application of the geometric formula best fitted to the shape of the cell. Identifications were performed on preserved whole and net (10 µm mesh) samples. The *in situ* light and dark bottle oxygen method was used for studying photosynthesis. An adapted version of the phytoplankton production model was employed to quantify phytoplankton photosynthesis and community respiration. Both chlorophyll *a* and total phosphorus were estimated. Coefficient of variance, t-test, ANOVA and the Levine test of homogeneity of variance were used to assess annual, inter-annual and seasonal variability of the means of physico-chemical and biological variables. Community species composition consisted of a total of 56 in horizontal and 75 in temporal studies in 7 major groups dominated by the Chlorophyceae. But the biomass dominated by the Cyanobacteria. Mean biomass of phytoplankton was 1570.0 in the first year (2004-2005)

iii

and 2262.3 mg m⁻³ in the second year (205-2006). Annual mean gross primary productivity of 4.73 gC m⁻²d⁻¹ is high but net productivity was very low i.e. 0.38 gC m⁻² 2 d⁻¹. This was due to the very high community respiration that represented 90 % of the gross primary productivity and may imply higher loss rates. Mean growth rate in the Z_{eu} of 0.13 d^{-1} is low and is commensurate with the low biomasses observed in the lake. Very weak relation between biomass and chlorophyll *a* and the little change in community composition in an annual cycle show that the changes in the chlorophyll a concentration are due to adaptation of the same community to differing conditions within the water column. Variabilities in the community biomass that range from a Coefficient of Variance of 28-79 % and that of the gross primary productivity of 33.1 % are high and seem to be regulated by the similarly high variabilities in the physicochemical parameters. Significant inter-annual differences in the community biomass were observed. Physical factors such as Z_{mix} and Z_{eu} seem to exert more control in the dynamics of the phytoplankton growth and productivity compared to chemical factors even though nitrogen limitation is suggestive because of the abundance of heterocystbearing filamentous Cyanophyceae. Selective grazing may also be contributing to some extent to the observed dynamics. W J SANE NO BADY

Title pagei	i
Declarationi	i
Abstractii	i
Table of contentsv	,
Table of symbols, units of measurements and definitionsv	i
List of Tablesvi	ii
List of Figuresvi	ii
Acknowledgementxi	v
Chapter One: General Introduction1	
Background	
Rational of study9	
Objectives of study	;
Chapter Two: Literature Review16	5
Phytoplankton studies in Africa	,
• Temporal and seasonal patterns of phytoplankton variability	5
Factors regulating phytoplankton growth dynamics	1
• Effects of some factors on the pattern of phytoplankton variability	ļ
• Spatial patterns of phytoplankton variability in lakes	7
 Spatial distribution of phytoplankton27 	,
 Vertical distribution of phytoplankton	
 Horizontal distribution of phytoplankton)
• Inter-annual variability of phytoplankton)

Table of Contents

• Primary productivity of phytoplankton	
Chapter Three: Materials and Methods35	
• Study area	
• Sampling sites	
• Physical parameters	
 Apparatus and procedure: Meteorology (Climatic characteristics	
 Apparatus and procedure: Water column characteristics	
 Measurements of Secchi discs depths, k_{PAR}, Z_{eu} and Z_{mix}40 	
Biological parameters42	
• Apparatus and procedure: Phytoplankton composition and biomass42	
 Apparatus and procedure: Phytoplankton primary productivity45 	
• Evaluation of seasonality	
• Statistical evaluation	
Chapter Four: Results	
 Horizontal distribution of physico-chemical parameters, phytoplank 	cton
community species composition and biomass	
 Secchi disc depth	
 Water temperature, dissolved oxygen and conductivity	
 Phytoplankton community species composition	
 Phytoplankton community biomass	
 Temporal and seasonal patterns of physico-chemical and biolog 	ical
parameters61	

 Physico-chemical characteristics of water column (Z_{eu}, Z_{mix}, Z_{mix}:Z_{eu} ratio
and total phosphorus)61
 Biological parameters
 Relationship between physic-chemical and biological parameters69
 Phytoplankton primary productivity
 Temporal trends and variability in the primary productivity
 Seasonal trends in the primary productivity
 Relationship with the physic-chemical variables
Chapter Five: Discussion
• Horizontal variability of the physico-chemical parameters
• Horizontal variability of community species composition and biomass101
• Temporal variability of phytoplankton community species composition and
biomass107
• Phytoplankton groups: Occurence and biomass contribution115
Phytoplankton primary productivity
• Seasonality of the phytoplankton primary productivity
Chapter Six: Conclusions and Recommendations
References133
Appendix 1168
Appendix 2171
Appendix 3

Parameter	Units	Definition					
Physico-chemical parameters							
SD	m	Secchi disc					
Zeu	m	Euphotic zone					
k _{PAR}	m ⁻¹	Extinction coefficient of PAR					
Z _{mix}	m	Mixed depth					
Z _{mix:} Z _{eu}	- 1	Ratio of Z_{mix} to the $Z_{eu.}$					
PAR	μS cm ⁻¹	Photosynthetically Available Radiation					
ТР	µmol L ⁻¹	Total phosphorus concentration					
Biological parameters							
P _G	gC m ⁻² d ⁻¹	Areal gross primary productivity					
P _N	$gC m^{-2}d^{-1}$	Areal net primary productivity					
R _C	$gC m^{-2}d^{-1}$	Areal community respiration					
P _B	mg m ⁻³	Phytoplankton wet weight biomass in Z _{mix}					
P _N :P _G	%	Assimilable photosynthate					
Chl a	μg L ⁻¹	Chlorophyll a concentration					

Table of symbols, units of measurements and definitions

List of Tables

Table of symbols, units of measurements and definitions......viii

Table 2 Daily areal gross primary productivity of some selected African Lakes......33

 Table 4.5 Means, standard deviations, coefficient of variances and maximum to

 minimum ratios for biological parameters.

 89

List of Figures

Fig. 3.1 Map of Ghana showing Lake Bosomtwe (Ghana web, 2008)......36

Fig. 3.3 Regression of inverse of SD depth versus k_{PAR} in Lake Bosomtwe......41

Fig. 3.4 Conceptual diagram of gross phytoplankton production model (A) Incident irradiance (B) In situ irradiance (C) Under water irradiance (D) P-I profile (E)......48

Fig 4.13 Percentage contribution of phytoplankton groups to wet weight biomass of Lake Bosomtwe in 1st-2004-2005 (A) and 2nd-2005-2006 (B) years respectively....78

Fig 4.19 Regression of chlorophyll *a* versus phytoplankton biomass of Lake Bosomtwe (Ghana) in from November 2004 to October 2006 (Simple regression)...84

Fig 4.20 Temporal variation of gross productivity, community respiration and net productivity of Lake Bosomtwe (Ghana) from September 2005 to August 2006.....90

Fig 4.21 Seasonal variation of the Areal gross primary productivity (A) and Community respiration (B) of Lake Bosomtwe, (Ghana)......91

Fig 4.24 Regression of gross productivity versus Z_{mix} : Z_{eu} (A) and Total phosphorus (B) of Lake Bosomtwe, (Ghana) from September (2005) to August (2006)......94

Fig 4.27 Regression of growth rates in the Z_{eu} versus gross productivity of Lake Bosomtwe (Ghana) from September (2005) to August (2006)......97



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CHAPTER ONE

GENERAL INTRODUCTION

1.1 Background

Lake Bosomtwe is situated in the south central part of Ghana (6°30'N, 1°25'W) about 32 km east of Kumasi, the regional capital of the Ashanti region. Some morphometric features of the lake are compared with some of the world's most famous lakes in Table 1.1. The maximum depth of the lake has fluctuated markedly in prehistoric times including an overflow event in a terrace along the crater rim at 210 m amsl (Talbot & Delibrias, 1980). The comparatively small catchment to surface area of the lake i.e. just over to 2:1- (Table 1.1) means that there may be a comparatively small impact of the catchment on the lake. However, the closed nature of the basin may also make the lake extremely sensitive to nutrient inputs from the catchment and therefore eutrophication. There are over 20 communities within the catchment of the lake which are administered by the Kuntenase and Bekwai districts. Most of them do not have direct road access to Kumasi, the regional capital, with the exception of Abono which also boasts of a modern hotel. Therefore, most tourist activities are centred at Abono.

 Table 1 Some morphometric features of Lake Bosomtwe compared to some selected lakes

Parameter Lake Bosomtwe		Lake Volta Lake Superior		Lake Baikal		
	(Ghana)		(Ghana)		(Tanzania)	(Russia)
Location	6°30'N, 1°25'W	6°30'N, 0.0'W	47.7°N, 87.5'E	53.5°N, 108.2'E		
Surface area (km ²)	48.6	8,482	82,100	31,500		
Maximum depth (m	n) 78	74	406	1,637		
Mean depth (m)	45	19	149	730		
Drainage basin (km	²) 103.1	385,180	128,000	540,000		

The origin of the crater, which Lake Bosomtwe occupies, has been described in literature since the late 19th century and was a subject of considerable debate (Hutchison, 1967). For example, Fergusson (1902) proposed that the crater was of volcanic origin, Kitson (1916) interpreted it as a subsidence feature whiles Rohleder (1936) preferred an explosive (endogenic) explanation but Maclaren (1931) was probably the first to suggest that the crater was of impact origin. However, since the 1960s several lines of evidence have supported an impact origin (Jones *et al.*, 1981; Koeberl & Shirey, 1993; Koeberl *et al.*, 1998). The crater is surrounded by steep-sided hills which rise to a maximum height of 460 m and the lowest is 210 m amsl (Jones *et al.*, 1981).

The geology, geophysics, geochemistry, hydrological and paleolimnological aspects of Lake Bosomtwe have received considerable research attention (Junner, 1937; Woodfield, 1966; Moon & Mason, 1967; Jones *et al.*, 1981; Reimold *et al.*, 1998; Wright *et al.*, 1985; Leube *et al.*, 1990; Taylor *et al.*, 1992; Hirdes *et al.*, 1992; Koeberl & Reimold, 2005; Feybesse *et al.*, 2006; Koeberl *et al.*, 2007; Talbot & Delibrias, 1977; Turner *et al.*, 1996a & b; Puckniak *et al.*, 2009). The crater has a complex geology. With the exception of recent clays, lakebeds, suevites and some basic dikes, the consolidated rocks of the area are of Precambrian age consisting of metamorphic, igneous rocks and different types of breccias (Koeberl & Reimold, 1998; Reimold *et al.*, 1998). The basement impact breccia from the initial meteoritic impact and overlying sediments are believed to inhibit ground water exchange (Koeberl *et al.*, 2007; Turner *et al.*, 1996a). As a result, the hydrological balance of the lake is driven by long-term fluctuations in rainfall relative to evaporation and reflected in changes in the lake water levels (Turner *et al.*, 1996a). The variability of the lake water level, correlates well with temporal

reorganizations in regional moisture balance (Talbot & Delibrias, 1977; Turner *et al.*, 1996a; Gasse, 2000) and a restricted catchment area means that the lake is maintained principally by precipitation (80%) and by numerous small streams (20%) that originate from the crater walls making it extremely sensitive to precipitation:evaporation balance (Turner *et al.*, 1996a & b; Whyte, 1975).

Annual precipitation within the lake basin seems to be decreasing. Talbot and Delibrias (1977) found it to be 1520 mm whiles Turner et al (1996a) and Puchniak et al (2009) observed 1380 mm and 1136 mm respectively a decrease of over 25 %. However, remnants of trees still standing in the lake and the historical fact that some communities had to move back or even relocate as a result of rising water levels give some credence to Talbot & Delibrias (1977) assertion that the overall hydrological balance is positive for the lake in the long term. Monthly rainfall maxima usually occur between March and June. Puchniak et al (2009) observed the highest rains in the month of May in both 2005 and 2006 whiles Whyte (1975) observed it in June. This observation is relevant to phytoplankton dynamics of the lake since it is likely that during such periods, nutrients may be brought in from the catchment to enhance growth. The biomass may also be diluted as a result of heavy rains but may later respond positively when the rains subside (Lind, 1968). Therefore, both positive and negative effects on the phytoplankton growth are possible. The community species composition may also be affected through the introduction of adventitious phytoplanktons during rainy seasons.

The paleoclimatic significance of Lake Bosomtwe was recognized early and a complex record of changes in lake level, lake chemistry, climate, and vegetation history

stretching back close to 28,000 years (Talbot & Delibrias, 1977; Talbot & Kelts, 1986) have been recognized. It is believed to be the most cited continuous paleoclimatic record in West Africa, one of few long sediment-rate varved sediment records in the world; proven record of hydrologic balance and terrestrial ecosystem variability, the only such record in West Africa that is varved; likely recorder of sahel aridity and tropical Atlantic sea surface temperature variations. Arguably the best preserved complex terrestrial impact crater of the approximately 95 confirmed terrestrial impact structures (Talbot & Delibrias, 1977; Talbot *et al.*, 1984; Scholtz *et al.*, 2002).

The lake is sited in the path of the Intercontinental Tropical Convergence Zone (ITCZ) a low pressure belt responsible for the regulation of the moisture balance between the northeasterly continental trade winds and the southeasterly trade winds (Nicholson, 1980; Janicot, 1992). Coupled with its high crater rims and the deep lake basin implies that wind mixing is restricted and in deeper waters bioturbation is absent i.e. the lake is meromictic (Almond & Hecky, 2000) providing the potential for high annual resolution necessary for paleoclimatic reconstruction (Koeberl *et al.*, 2007). This provided the premise in 2004 within the framework of an international and multidisciplinary drilling project led by the International Continental Drilling Program (ICDP) which recovered over 200 m long sediment core for investigations into paleo-environmental indicators during the over 1 million years since the formation of the crater (Koeberl *et al.*, 2007).

The lake lies in a close basin i.e. it has a radial drainage pattern that is wholely divorced from the general drainage system of the rest of Ghana due to the high crater rim surrounding it (Koeberl *et al.*, 2007). It has no outflows. According to Whyte (1975), 37 streams flowed into the lake during rainy seasons but only five namely

Abono, Abrewa, Ebo Kwakye, Twiwaa and Konkoma were believed to be permanent. Presently however only one of the supposed five permanent steams (Abrewa stream lying between Banso and Apewu villages) appears to be perennial. Without an outflow, the lake exhibits two different chemical environments- fairly dilute inflowing streams and a concentrated soda lake (Whyte, 1975; Karikari & Bosque-Hamilton, 2004). The main mineral constituents are the bicarbonates of sodium (McGregor, 1937; Karikari & Bosque-Hamilton, 2004). The concentration of solutes like sodium, potassium and chloride are relatively high compared to other water bodies in the country (Frempong, 1995; Karikari & Bosque-Hamilton, 2004). Ionic concentrations in the lake are quite similar to sea water compared to freshwaters especially with regards to sodium but are unique in its own way. It is in the order Na > K > Mg > Ca: $HCO_3^- > Cl^- > SO_4$ (Livingstone, 1963; Karikari & Bosque-Hamilton, 2004) contrasting the ionic dominance pattern of Ca > Mg > Na > K: HCO₃ > SO₄ > Cl⁻ for freshwaters and Na > Mg > Ca > K: $Cl^{-} > SO_{4} > HCO_{3}^{-}$ for seawater (Burton, 1976). The abundance of trace metals is found in the order; Cu > Zn > Fe > Cd (Karikari & Bosque-Hamilton, 2004).

Essential nutrients in the lake surface waters appear to be adequate for phytoplankton growth. Nitrate and orthophosphate concentrations are above the level of either P- or N-famine of 0.1 μ mol L⁻¹ and 0.2 μ mol L⁻¹ respectively (Reynolds, 2007). According to Karikari and Bosque-Hamilton (2004), the mean concentration in the first 5 meters was about 0.06 mg L⁻¹ (equivalent to 0.63 μ mol L⁻¹) for phosphate and 0.43 mg L⁻¹ (equivalent to 6.94 μ mol L⁻¹) for nitrate respectively at the middle portion of the lake. These concentrations are over 6 times and close to 35 times above the concentration of P and N-famine respectively and are likely to promote massive phytoplankton growth and productivity in the lake. However, these concentrations may

not reflect the whole range of concentrations in an annual cycle. This is because the timing of the 2004 Karikari and Bosque-Hamilton's research in October coincides with rainfall and also restratification periods which may make a lot of nutrients available from the catchment and from the hypolimnion respectively during this time.

The lake is thermally stratified for most part of the year except during the harmattan period i.e. usually from December-January and sometime including February, as a result of alternate heating and stratification in the day and cooling and destratification in the night and also between August and September referred to as the 'little' dry season by Talbot et al (1984) as a result of dense cloud developments, low atmospheric temperatures and also coincident with elevated wind speeds as well as low wedderburn numbers (Puchniak et al., 2009). This results in surface water temperature reductions and the water column becomes more or less isothermal and sometimes results in fish kills when it overturns (Beadle, 1981; Turner et al., 1996a; Puchniak et al., 2009). The occurrence of a fish kill in January, 2007 instead of the previous August which is usually the fish-kill month indicates the existence of inter-annual variabilities in this phenomenon in the lake. This is also an important aspect of the dynamics of phytoplankton whose distribution within the water column is mostly regulated by the thermal spectrum of the lake because of their microscopic sizes and is therefore central to this thesis. This is not to say that the phytoplankton are incapable of movement but partly because of their small sizes and partly because most of their movements are in the vertical plane, movement from place to place is limited (Boney, 1989). During such times when the mixed layer deepens, the phytoplankton are likely to be light limited since they are likely to be carried below the depth of the euphotic depth even though nutrients may be abundant in the overturn waters (Lewis, 1978). This is particularly so

since the lake seems to be turbid with secchi disc transparency, an index of eutrophication ranging between just about 1.1 m and 1.5 m (Koenings & Edmonson, 1991;Karikari & Bosque-Hamilton, 2004). Historically, an oxycline has been observed between 7-10 m (McGregor, 1937) and 15-20 m (Beadle, 1981) indicating variability in the oxygen structure of the water column associated with mixing and stratification events in the seasonal cycle (Puchniak *et al.*, 2009).

Mean pH is about 8.9 (Puchniak *et al.*, 2009) but can range between 8.74-9.04 giving it a high buffering capacity whiles water temperatures varies between 28.1-30.5 °C reflecting its tropical status (Karikari & Bosque-Hamilton, 2004; Hutchison, 1967). Mean conductivity is about 1150 μ Scm⁻¹, alkalinity of 10320 μ mol L⁻¹ and carbon dioxide concentration of about 59 μ mol L⁻¹ (Puchniak *et al.*, 2009). The lake is believed to show low conductivity for a close basin lake of such age, which tends to accumulate salts over time. According to Golterman (1979), conductivity of water bodies vary widely and range from between 10 to 100, 000 μ S cm⁻¹. However, most freshwaters have conductivities between 10-1000 μ S cm⁻¹ but may exceed 1000 μ S cm⁻¹ (Chapman, 1992; APHA, 1998) whiles dissolved oxygen has been noted to range from 1.9-5.0 mg L⁻¹ (Karikari & Bosque-Hamilton, 2004).

The level of pollution of the lake mainly from anthropogenic sources is still not well known but Karikari & Bosque-Hamilton (2004) found total and faecal coliforms to be high indicating pollution by human and domestic waste. This may also imply unsafe use of the lake water for domestic use without any form of treatment since coliform levels at all stations sampled were above W.H.O. standards for potability (Karikari & Bosque-Hamilton, 2004). Both domestic and recreational users of the lake may also be at risk of infections by these potentially harmful bacteria abundant in the lake water. However, isotopic studies of the fish biota of the lake by Poste *et al* (2008) has indicated that levels of total mercury conentrations in the fish do not approach the W.H.O. recommended guideline of 200 ng/g wet weight for "at risk" individuals, including children, pregnant women and frequent fish consumers (W.H.O., 1998). Consistent with proposed foodweb patterns, the highest concentration of total mercury was found in the invertivore (*Chromidotilapia guntheri*) and lowest in the phytoplanktivore (*Sarotherodon multifasciatus*).

Little knowledge exists on the biological aspect of the lake. The fish species and their ecology have been studied by Gunther (1902), Lelek (1968) and Whyte (1975). By far however, Whyte (1975) who described the distribution, trophic relationships and breeding habits of the fish species seems to have done the most detailed study of the biology of the lake on the fishes. Poste et al (2008) have also studied the foodweb structure of the lake using isotopes and found 3 trophic levels in the fish biota namely; a phytoplanktivore (Sarotherodon multifasciatus), 3 zooplanktivores (Tilapia busumana, T. discolor and Hemichromis fasciatus) and an invertivore (Chromidotilapia guntheri). No piscivore was found. Fish diversity seems to have decreased over 50 % (i.e. 11 to 5 species) in just over 3 decades (Whyte, 1975; Poste et al., 2008). The 5 remaining fishes are all cichlids, known to be tolerant of hypoxia (Melnychuk & Chapman, 2002) that live mainly in the lacustrine zone of the lake and feed mostly on the plankton. Typical riverine and estuarine species have become very rare and it is feared they may be extinct. This is supported by the observation that almost all the permanent streams with the exception of perhaps Abrewa where Poste et al., 2008 found the invertivore Chromidotilapia guntheri, have stopped flowing as a result of anthropogenic intrusion potentially depriving the estuarine and riverine forms their habitat.

Planktonic micro-organisms have received little attention. Whyte (1975) and Poste *et al.*, (2008), mentioned periphyton, phytoplankton and zooplankton as food organisms for the fish species and found the fish population to be distributed according to their food items with non-cichlids which fed on allocthonous food sources dominating in the estuarine and riverine zones whiles the cichlids which fed on authocthonous food sources dominated in the lacustrine zone. The cichlid, *Sarotherodon multifasciatus* which is one of the commonest fish species in the lake has a diet that consists of over 75 % phytoplankton (Whyte, 1975).

Fishing pressure is intense and as all the households within the 22 communities obtain their protein requirements, earn their livelihood and income by fishing almost everyday throughout the year from this small lake, current fishery efforts may not be sustainable and dwindling fish yields each year is already causing a lot of economic distress to the surrounding communities.

1.2 Rationale of thesis

African inland waters are ecologically diverse, and few are intensively studied, but their increasing economic and nutritional importance makes management of these lakes essential. To meet the need investigations of the fisheries have been expanding but seldom include adequate coverage of the limnology of the lower trophic levels (Melack, 1976). This statement aptly captures the state of biological research on Lake Bosomtwe where the most comprehensive biological research that has been done is on the fishes (Whyte, 1975). The situation is not different for most water bodies in the country. When interest in the aquatic resources in the country began over a century ago in the then Gold Coast, fish studies again dominated the research (Frempong, 1995 and references therein). At that time Gunther (1902) started documentation of the fishes based on the collection of specimen by R. B. N. Walker from 1898 to1900. From then on, the contribution of other collectors and the publication of the fish and fisheries of the Gold Coast by Irvin (1947) and others provide ample indication of the area of interest and concentration of pioneer workers (Frempong, 1995).

Historically, research on Lake Bosomtwe have tended to focused on aspects such as the general geology (Junner, 1937; Jones *et al.*, 1981), geochemistry (Turner *et al.*, 1996a), geophysics, paleolimnology (Beuning *et al.*, 2003) with some work on the hydrology, water column properties (Turner *et al.*, 1996a & b; Almond & Hecky, 2000; Puchniak *et al.*, 2009) and water quality (Karikari & Bosque-Hamilton, 2004). Very little work has been done on the biology of the lake and this was concentrated on the fishes (Whyte, 1975; Poste *et al.*, 2008). The planktonic communities of the lake have apparently never been the focus of any research.

However, at the base of the food web in lakes are microscopic, autotrophic, oxygenic photosynthesizing floating organisms referred to as phytoplankton whose species composition, biomass distribution and productivity drive the dynamics of other organisms in the food web including fishes. According to Wetzel (2001), they comprise diverse algae of almost every taxonomic group. The important role that phytoplankton play in the general productivity of lakes and their effect and implications for water quality and the fisheries resources as well as their importance in ecotourism development and scientific research cannot be overemphasized.

Phytoplankton provides an indication of water quality since virtually all the dynamics features of a lake such as taste, odour, colour, clarity and trophic state as well as quality are dependent to a lesser or greater extent on them (Fogg, 1975; Chorus &

Bartram, 1999; Hitzfeld *et al.*, 2000). Also as primary producers forming the base of the food web, they are important for the evaluation of energy and matter along aquatic trophic webs. For example Melack (1976) as well as Hecky and Fee (1981) have demonstrated that measurements of phytoplankton primary productivity can improve assessment of fish yields from tropical lakes. Moreover, detectable changes in the species composition, abundance and biomass are known to mirror changes in a lake's environment and the rapid turnover times of these organisms serves as sensitive indicators of environmental health which can serve as clues to fresh water managers on the adoption of appropriate and effective management strategies (Lee, 1989). In fact, the almost universal presence of phytoplankton in all waterbodies and the most extreme habitats indicates the important role they play in the ecological complex (Graham & Wilcox, 2000).

Therefore, the ecology of phytoplankton growth is of great importance to the character and history of lakes and to all other organisms that live in lakes. The major threat to lakes involves the excessive growth of these primary producers due to nutrient inputs caused by poor land-use management (Mazur-Marzec, 2006). The frequency, extent, intensity and duration of freshwater phytoplankton in recent times have been recognized as a world-wide problem in inland waters especially freshwaters and water supplies (Chorus & Bartram, 1999; Hitzfeld *et al.*, 2000; Mazur-Marzec, 2006). In freshwaters, the threat to water quality and eutrophication has been the development of harmful algal blooms (HABs) especially the toxins produced by several species of cyanobacteria (Mazur-Marzec, 2006). According to Graham and Wilcox (2000), 50-75 % of cyanobacteria blooms are considered toxic and over 40 cyanobacteria species are demonstrated or suspected toxin producers. Historically and in recent times, toxic algal

blooms have been confirmed as causing several problems in humans including gastroenteritis (Lepisto et al., 1993; Annadotter et al., 2001), dermatitis (Serdula et al., 1982) damaging effects on several body organs (Byth, 1980; Hawkings et al., 1997; Joachimsen et al., 1998) and even death (Teixera et al., 1993; Pouria et al., 1998; Carmichael et al., 2001; Mazur-Marzec, 2006). The W.H.O has even developed standard guideline values (toxins) and levels (cell concentrations) for domestic and recreational use of waters and advised that all algal blooms be considered harmful until proven otherwise (Chorus & Bartram, 1999). In Ghana, Addico et al (2006) found treatment methods for the removal of cyanobacteria cells from the Weija and Kpong reservoirs to be ineffective. Their preliminary investigations also revealed that toxic microcystin concentrations in these reservoirs are over three times above the level required for no observable adverse effect level (Chorus & Bartram, 1999). Massive fish kills are also linked with algal blooms through their population crashes which results in massive deoxygenation and asphyxiation of fish (Carmichael et al., 2001). Moreover, epidemics of cholera have also been linked with certain species of cyanobacteria notably, Anabaena and Nostoc which act as reservoirs of the causative agent Vibrio cholerae (Colwell et al., 1977; Islam et al., 2004).

Furthermore, as Vollenweider (1969) aptly put it, aquatic systems which the phytoplankton occupy differ from terrestrial systems which in general are relatively easy to define as sociological units, the structure of which is given by a few dominating species which persists on the same place over a long period of time. The character of an aquatic system, at least at the primary production level, is much more ephemeral and is dependent upon an array of changing environmental factors including meteorological, hydrological, nutritional and other biological factors which also change with time and space (Vollmer *et al.*, 2002; Verburg *et al.*, 2003; Lewis, 1978). The conceptualization of the spatio-temporal dynamics of the phytoplankton therefore needs to project the complex interplay between these hydrodynamic features and foodweb interactions. To get a fair idea about the character of the species present in a water body and their biomass and productivity dynamics therefore, spatio-temporal studies within short intervals of time are relevant because of the rapid growth rates of these organisms in order of days (Reynolds, 2007). Changes in phytoplankton community composition may for in stance affect photosynthetic rates, assimilation efficiencies, rates of nutrient utilization and grazing all of which are subject to considerable seasonal and spatial fluctuations even in the tropics where conditions are deemed stable (Wetzel & Likens, 1979).

Therefore, a study that seeks to characterize the species composition, biomass and productivity dynamics of phytoplankton on spatial and temporal scales in Lake Bosomtwe is worth it because of its socio-economic, cultural and scientific relevance. It is from this background that the objectives of this research were conceived as apparently no study to the best of my knowledge has focused on these important biological components of the biological community of the lake. There are few studies examining limnological parameters relevant to phytoplankton dynamics and none directly examining the spatio-temporal aspects of the phytoplankton community species composition, biomass and productivity of Lake Bosomtwe (Turner *et al.*, 1996a; Whyte, 1975; Almond & Hecky, 2000; Karikari & Bosque-Hamilton, 2004).

The **general objective** of this study was to assess the spatio-temporal variability of the phytoplankton community species composition, biomass and primary productivity of Lake Bosomtwe (Ghana). The **specific objectivies** of the study are:

- 1. To assess the horizontal and temporal variability in the phytoplankton community species richness composition;
- 2. To investigate the horizontal and temporal variability of the phytoplankton community biomass, and
- 3. To investigate the seasonal variability of the phytoplankton primary productivity.

This research spans a two year period from November, 2004 to December, 2006 during which the spatial and temporal aspects of the phytoplankton community species composition, biomass and productivity of Lake Bosomtwe were examined and related to meteorological as well as other limnological parameters of the water column relevant to phytoplankton dynamics. The scope of the research itself is set out in the organization of the chapters below. Treatment of individual phytoplankton species are outside the scope of this thesis i.e. horizontal and temporal trends for specific taxa of the phytoplankton species will not be treated.

Chapter Two, deals generally with a mostly descriptional background literature of phytoplankton dynamics with focus on tropical African lakes. Spatio-temporal variabilities of phytoplankton species, biomass and productivities are sought together with their causes. Also intra- and inter-annual aspects of phytoplankton variabilities are established.

Chapter Three deals with the apparatus, materials, methods and procedures in the field and the laboratory, models as well as the statistical tools employed in estimating and evaluating data generated. Limitations and precautions are also noted.

In Chapter Four, the results section, the horizontal variability of some physicochemical limnological parameters are presented in relation to the variability of phytoplankton community species composition and biomass based on data collected in a mixing season in August 2006 and stratified periods in November and December 2006 at 14 different stations along two transects based on synoptic sampling of subsurface water to evaluate horizontal patchiness. Also results on temporal and seasonal patterns of variability of the phytoplankton community species composition and biomass as well as chlorophyll *a* distribution in relation to the variability in the physico-chemical environment are examined based on data collected from November 2004 to October 2006 at biweekly intervals at the offshore index station. Furthermore, results are presented from this offshore index station on the seasonal gross phytoplankton productivity, community respiration and growth rates. The variability in the productivity and community respiration of the lake is also related to the variability of some physicchemical variables to determine possible controlling factors.

Chapter Five discusses the horizontal and temporal aspects of phytoplankton communityspecies composition, biomass and productivity as well as physic-chemical parameters measured alongside phytoplankton by integrating, explaining and comparing with other works.

In Chapter Six, conclusions of general findings and implications as well as suggestions for further studies are also made. To facilitate complete understanding of the thesis, materials that are relevant but which otherwise obstruct the flow of the manuscript are placed after the main chapters including the various literature reviewed in this thesis followed by appendices.

CHAPTER TWO

LITERATURE REVIEW

2.1 Phytoplankton studies in Africa

Phytoplankton patterns of variability is a well investigated phenomenon in aquatic ecology and several studies have described the importance, patterns and underlying mechanisms driving them (May & MacArthur, 1972; Colwell, 1974; Petersen, 1975; Abele, 1976; Sommer *et al.*, 1986; Talling, 1986; Marshal & Peters, 1989; Vanni & Temte, 1990). These patterns are usually similar in lakes having analogous climatic conditions, morphometric characteristics and trophic status (Reynolds, 1976a).

In Africa, although some study of phytoplankton began in 1899 during the Fulleborn expedition, wide ranging information from water bodies in the continent only became available after 1950 (Talling, 1986; Lewis, 1987). Several authors have worked on various aspects of phytoplankton in Africa throughout its long historical development including their taxonomy, abundance and productivity on spatio-temporal scales (Schmidle, 1902; Ostenfeld, 1909; Schuurman, 1932; Abdin, 1948; Fish, 1952, 1957; Gayral, 1954; Ganf, 1974; Harbott, 1982; Kalff, 1983).

2.2 Temporal and seasonal patterns of phytoplankton variability

The temporal patterns of phytoplankton community structure are an important and familiar aspect of the biology of temperate lakes. These patterens usually bears some obvious relation to seasonal weather changes that affect the availability of light and nutrients in the water column (Melack, 1979). Such temperate lakes go through large seasonal variations in light, nutrients and temperature. Tropical lakes likewise experience seasonal weather changes that induce physico-chemical changes of various kinds in lakes and that differ in amplitude and periodicity from those of temperate lakes but because climatic conditions especially insolation and temperature are less variable near the equator, it is often assumed that there is less variability (Beadle, 1981; Talling, 1986). Despite this, temporal changes can be very dramatic in these lakes (Lewis, 1978) and nutrient supply and hence hydrography is thought to play an accentuated role (Melack, 1979).

At higher latitudes in Africa, pronounced algal seasonality is a common observation and is influenced by marked changes in radiant energy income, water temperature and seasonal water input (Talling, 1986; Schuurman, 1932; Gayral, 1954). In Africa generally, including the tropical belt, annual phytoplankton seasonal patterns are usually dominated by hydrological or hydrographic features or a combination of the two (Talling, 1986; Melack, 1979; Biswas, 1969, 1972, 1977). Hydrological responses in closed basin lakes are known to be strong (Harbott, 1982). In such lakes cyanobacteria usually dominate during non-flood periods whiles after initial dilution, several diatoms may rise to ascendancy (Gras *et al.*, 1967; Iltis, 1977; Compere and Iltis, 1983). Lind (1968) however, cautioned that for lakes (especially smaller ones) that are strongly influenced by increased run-off during the wetter seasons, both positive and negative effects on algal growth are possible depending on the nutrient status of run-off water.

Seasonal studies of phytoplankton productivity have been done in a variety of lakes (Nauwerk, 1963; Lewis, 1978; Dokulil, 1984; Tilzer & Beese, 1988; Robarts, 1984). In a comparative study of tropical and temperate lakes, Melack (1979) observed significantly greater temporal variability in gross photosynthetic rates in high latitude lakes compared to low latitude lakes. Seasonal differences are known to be more marked the farther a lake is situated away from the equator, as do changes in the plankton (Moss, 1969). Reduced variability in solar radiation associated with decreasing latitude is believed to depress seasonal amplitudes in gross (Odum, 1971) and net (Lewis, 1987) photosynthetic rates. Melack (1979) and others (Cobelas *et al.*, 1992; Talling, 1971; Jewsen & Wood, 1975; Carpenter *et al.*, 1987; Tilzer, 1989) attribute the variability in the photosynthetic rates of phytoplankton as a response to variations in the physical (irradiance, mixing and temperature), chemical (e.g. nutrient supply rates) and biological (e.g. grazing and mineralization) factors. In general, the primary causes of variability have been attributed to the high annual irradiances, the low variation in irradiances as well as the low Coriolis Effect in the tropics which makes tropical lakes more prone to mixing by wind of a particular strength compared to temperate lakes (Lewis, 1987).

Melack (1979) has observed three patterns of temporal change in the abundance and/or photosynthetic rates of phytoplankton in most tropical lakes. In the first pattern, most tropical lakes exhibited pronounced seasonal fluctuations that usually corresponded with variations in increased rainfall, river discharges and associated turbidity or wind induced vertical mixing (Talling, 1965b; Melack, 1979; Lemoalle, 1973b) in a similar pattern to typical changes in middle and high latitude lakes (Kalff & Knoechel, 1978). Coefficients of variances (CVs) usually exceed 25 % in such lakes and the species composition changes as the environmental conditions change. In the second pattern, the CV is lower (less than 20 %) and there is little coupling of the fluctuations in the phytoplankton productivity to the seasonality of the weather (Melack & Kilham, 1974; Vereschi, 1978) as a result of perennial rivers and sufficient internal recycling of nutrients. Also, lakes with fringing swamps obtain buffer from the impact of seasonal rains and river discharges (Melack, 1979). In lakes with this muted seasonality, the amplitude of the diel fluctuations often exceeds the month to month changes and because the same phytoplankton assemblages usually persist for many days in these lakes, they must be adapted to the full range of environmental variations. This contrasts with the seasonal succession of phytoplankton typical of temperate lakes and tropical lakes with pattern 1 above. In contrast to the continuation of regular seasonality of pattern 1 and near constancy i.e. pattern 2, in some lakes an abrupt shift from one persistent algal assemblage and level of photosynthetic activity to another pattern occurs (Melack & Kilham, 1974; Melack, 1976; Vereschi, 1978).

Moreover, the proportion of epilimnetic water of a lake in contact with its sediments has been suggested as a regulatory factor determining the amplitude of annual biomass change of phytoplankton (Kalff & Watson, 1986). For instance, Lake George with almost daily mixing and intimate contact between epilimnetic waters and its sediments has annual biomass amplitude of 2 (Ganf, 1974). But in Lake Victoria with about 50 % of the sediment surface in contact with epilimnetic waters (Hecky & Kling, 1981), the annual biomass ratio increased to 4 (Talling, 1966) whiles In Lake Lanao with just 20 % of sediment in contact with the epilimnion, the annual biomass change rose to 10 (Lewis,1978). Moreover, in Lake Tanganyika with only about 10 % of the sediment in contact with the ratio rose to 45 (Hecky & Kling, 1981).

A number of detailed taxonomic investigations have been made of phytoplankton communities in tropical Africa. Few of these however, deal with both species composition and algal biomass (Lemoalle, 1981) on sufficient temporal scales (Lewis 1978a; Kalff & Watson, 1986). Seasonal changes in the species composition and biomass have been described for some African lakes, including lakes Victoria (Talling, 1966), George (Ganf, 1974), Tanganyika (Hecky & Kling, 1981), Sibaya (Hart & Hart, 1977), Chad (Compere & Iltis, 1983), Awassa (Kebede & Belay, 1994) and Elmenteita (Melack, 1988).

According to Kalff (2002), normally between 70 to 200 species of phytoplankton are likely to be observed in any particular lake but long term examination in temperate lakes usually yield over 700 species even though in tropical lakes this number is expected to be lower even in the long term. However, despite this generic hypothesis, species richness in some tropical lakes can be considerable. For instance, several observations from tropical lakes from Africa show that between 9 to over 900 species can be found (Kalff & Watson, 1986; Kebede & Belay, 1994). On temporal basis, most tropical lake phytoplankton taxa seem to be dominated by the Chlorophyceae but several shallow and saline lakes such as George, Sonachi, Elmenteita, etc are dominated by the Cyanophyceae while other phytoplankton groups contribute varying number of taxa to the percentage community species composition of tropical lakes (Kalff & Watson, 1986; Ganf, 1974). One reason why the Chlorophyceae and Cyanophyceae dominate the species richness of tropical lakes is their ability to tolerate high irradiances but they share this characteristic with the Dinophyceae (Paerl, 1996; Sterner, 1989). The Cryptophyceae and the Chrysophyceae are known to be richer in taxa in relatively oligotrophic lakes and cold waters (Hecky & Kling, 1981; Kalff & Watson, 1986).

Most studies on phytoplankton use chlorophyll *a* as an index or surrogate of the phytoplankton standing crop or biomass. Few of such studies used surrogates based on the biovolume and the situation is not different for most African lakes (Hecky & Kling, 1987; Sarmento *et al.*, 2006). However, mean summer biovolume-based phytoplankton biomasses are known to range over 3 orders of magnitude from about 100 to 100, 000
mg m⁻³ (1 mg L⁻¹ to 100 mg L⁻¹) wet weight biomass between the most oligotrophic and eutrophic temperate as well as saline lakes (Kalff & Knoechel, 1978) but as much as 3,360,850 mg m⁻³ of phytoplankton biomass has been recorded in a tropical reservoir (Kotut *et al.*, 1998). In a survey of tropical lakes, Kalff & Watson (1986) found phytoplankton biomass to range from 100 mg m⁻³ in an oligotrophic lake to 43, 000 mg m⁻³ in a closed basin saline lake. A similar range of <0.5-1.0 µg L⁻¹ (mg m⁻³) for oligotropic lakes and 15-100 µg L⁻¹ (mg m⁻³) for eutrophic lakes is found for chlorophyll *a* (Wehr & Sheath, 2003). In most tropical lakes, the phytoplankton biomass seems to be dominated by both Chlorophyceae and the Cyanophyceae but the contribution of the other groups are usually small (Kalff & Watson, 1986; Kebede & Belay, 1994).

2.3 Factors regulating phytoplankton growth dynamics

Several authors (e.g. Lewis, 1978; Paerl, 1996) consider four main factors as important in the control and regulation of phytoplankton growth. These include nutrient (mostly phosphorus and nitrogen), light availability, and metabolic rates as affected by temperature. Nutrient and light availability are in turn controlled by a number of operational factors (Lewis, 1987) such as Z_{mix} , Z_{eu} , and the ratio Z_{mix} : Z_{eu} , nature of inflowing waters, etc. For instance, the Z_{mix} : Z_{eu} ratio is considered a good descriptor of under-water light climate that phytoplanktons experience (Naselli-Flores & Barone, 2007). Optimal increases in phytoplankton biomass therefore occur when these three factors are jointly maximized (Lewis, 1978).

Mixing processes are known to affect species interactions and availability of nutrients (Levin, 1974; Hulot & Huisman, 2004) especially for planktonic species whose spatio-temporal distributions are to a large extent governed by physical mixing processes

(Riley et al., 1949; Hutchinson, 1967; Spigel & Imberger, 1987; Reynolds, 1997; Abraham et al., 2000; Diehl et al., 2002). A change in the Z_{mix} is therefore critical in regulating nutrient supply, light availability and indirectly zooplankton grazing pressure. According to Lewis (1978), when Z_{mix} shows no change, nutrients incorporated into phytoplankton biomass move from the mixed layer into the stagnant layer below, depleting the nutrient pool within the Z_{mix} . Increases in Z_{mix} thus represent an improvement of nutrient supply by return of nutrients to the surface waters even though it may reduce light availability by carrying phytoplankton far below the Zeu but it also reduces sinking rate to a minimum (Lewis, 1978; Talling, 1971). When Z_{mix} decreases however, nutrient supply is restricted by limiting the nutrient pool from which the phytoplankton can draw so that deficiencies may occur more rapidly (Lewis, 1978; Talling, 1971). Also, during stratification in tropical lakes, high rates of organic decomposition may deplete hypolimnetic oxygen forming an oxic-anoxic interface (Hecky et al., 1996) below which bioavailable nitrogen can be lost through denitrification (Seitzinger, 1988; Hecky et al., 1996) and bioavailable phosphorus is enriched through its release from reduced iron oxide complexes making nutrients scarce in the surface waters.

Turbulence which is generated by wind strength, also affects nutrient availability as nutrients are rapidly supplied to the zone of light optimum from all parts of the Z_{mix} and it also facilitates nutrient uptake by renewing nutrient supply at the sites of uptake on cell surfaces (Lewis, 1978; Huisman *et al.*, 2004). In many lakes, nutrient supply from the watershed is an additional factor affecting nutrient availability (Lewis, 1978; Melack, 1979). Also, light availability is considered a major controlling factor in phytoplankton growth. Variations in light result from the availability of light, depth of mixing and transparency of the lake (Lewis, 1978). Growth inhibition can occur especially during mixing periods even though the amount of incident light is high (Lewis, 1974; Talling, 1971; Huisman *et al.*, 2004). The ratio of the Z_{mix} to the Z_{eu} can sometimes limit phytoplankton growth and production (Talling, 1971). Some authors believe that below a given a critical value of this ratio i.e. about 4 to 5 (Strickland, 1965; Wood *et al.*, 1978; Naselli-Flores *et al.*, (2007), light limitation is expected to prevail.

In addition to nutrient and light availability, temperature potentially affects metabolic rates and thus growth (Lewis, 1978). The greatest thermal change in the water column of a tropical lake is however likely to occur during seasonal mixing which may also be coincident with light limitation as a result of deep mixing which might be considerably more important to the phytoplankton than the accompanying slight thermal change (Lewis, 1978). The potential controlling role of temperature variation therefore appears to be much lower in tropical lakes as the range of variation is slight by comparison with variations of other factors (Lewis, 1978).

Also, loss control factors play key role in the regulation of growth of phytoplankton dynamics. Losses are often attributed to grazing by zooplankton and herbivorous fishes, sinking or sedimentation, respiration and other factors such as senescence, attack by parasites, viruses and bacteria (Lewis, 1978; Reynolds, 2007). Losses may also occur through allelopathy and cell lysis as a result of programmed cell death or apotosis or death through some other unknown means that may be intimately related to the nutritional state of the population in question (Canter & Lund, 1953; Shilo, 1971; Lewis, 1978; Reynolds, 2007). If grazing is selective, it may affect community

species succession and dominance (Lewis, 1978). Sinking which varies between species and nutritional states is an important mechanism of biomass loss (Hutchinson, 1967; Smayda, 1970). The principal factor directly affecting sinking is turbulence, which is controlled by wind speed, and the density profile of the upper water column (Lewis, 1978).

2.4 Effect of some factors on the pattern of phytoplankton variability

The population dynamics and distribution of the phytoplanktons are a consequence of complex interactions among environmental resources, the needs and tolerance of each species or group, and the competition among species or groups (Cox, 1990; Branco and Senna, 1996). The inter-relationships between phytoplankton and their physico-chemical and biological environment are well documented in temperate lakes (Lewis, 1978; Lind, 1984; Willen, 1976). Some definite patterns in the abundance of certain phytoplankton groups in relation to the Z_{mix} and turbulence, which are related to both nutrient and light availability as well as zooplankton grazing rates, have been documented (Lewis, 1978; Huisman *et al.*, 2004).

Diatoms (Baccilariophyceae) peak coincide with periods of marked depression of the thermocline and the duration of the peaks are controlled by the duration of the deep mixing (Talling, 1966; Lewis, 1978; Jones & Gowen, 1990; Harris & Baxter, 1996; Kaiblinger *et al.*, 2007). The usually low biomass of diatoms in most lakes during calm weather have been attributed to their poor tolerance of low nutrient levels especially, silicon depletion, and rapid sinking rates (Lewis, 1978; Lund, 1950; Stoermer *et al.*, 1972). Willen (1991) found that diatoms are good competitors at low light conditions when the ratio of Z_{mix} : Z_{eu} is high during mixing periods.

The Cyanophyceae and the Chlorophyceae also show clear but complicated relationships to the depth of mixing with both declining when conditions are suitable for diatom growth during periods of deep mixing (Lewis, 1978; Paerl, 1996). Maxima usually occur when the Z_{mix} is thin, though it is not coincident for both groups (Lewis, 1978; Howard, 1994). According to Lewis (1978), the Cyanophyceae appear to increase when nutrient depletion is pronounce while the Chlorophyceae increase under less severe conditions. The establishment of a high thermocline following nutrient enrichment thus usually leads to marked growth of the Chlorophyceae (Lewis, 1978). The nitrogen-fixing capability of some Cyanophyceae gives them an advantage when nitrogen sources are depleted (Horne et al., 1972; Paerl, 1996). The success of other cyanophyceae incapable of nitrogen fixation under pronounced nutrient depletions may be due to other factors such as buoyancy regulation (Reynolds & Walsby, 1975; Ibelings, 1996; Paerl, 1996) or carbon uptake ability (Shapiro, 1973). For instance Reynolds (1972) reports that Cyanophyceae show dramatic vertical migration speeds of between 20 and up to 140 m day⁻¹. The Cyanophyceae therefore do well under rather extreme conditions, and clearly succeeds at times when the Chlorophyceae cannot (Lewis, 1978; Hecky & Kling, 1981). Weak mixing may thus generate asymmetric interactions that may shift the competitive balance in phytoplankton communities (Huisman et al., 2004).

The Cryptophyceae and Baccilariophyceae show an ecological alliance and are favoured by turbulent conditions and minimum sinking rates (Lewis, 1978; Talling, 1986). Baccillaiophyceae are large and are weighted by their silicified frustules, so their need for turbulence seems obvious; this reasoning does not apply to the cryptophytes, which are motile (Huisman *et al.*, 2004). At very high turbulences, motility is of no

value to the Cryptophyceae in maintaining position (Lewis, 1973). However, at minimum turbulence, the limited motility of some cryptophytes will be of value. During such times, turbulence will be enough to move non-motile species to undesirable portions of the water column, but not powerful enough to override the limited powers of movement of a cryptophyte (Lewis, 1978). The capacity for mixotrophy in the Cryptophyceae also serves as an advantage in nutrient depleted waters although zooplankton preference for them as superior food compared to other algae may substantially reduce their biomass especially during stratified periods in lakes (Graham & Wilcox, 2000; Carpenter *et al.*, 1987).

The Dinophyceae seem to produce high biomasses only when nutrient depletion is more severe because of their nutritional flexibility and motility just like the Cryptophyceae but in addition are usually bigger in size and are also not a superior zooplankton food (Hutchinson, 1967; Lewis, 1978; Reynolds, 2006; Graham & Wilcox, 2000). They are specialists and thrive under conditions of extreme nutrient limitation and compete poorly unless turbulence is minimal (Lewis, 1978; Lee, 1989; Jacobson & Anderson, 1996). Motility is thus, an effective defense against sinking. But motility must occur with other adaptations compensating for extreme nutrient scarcity if it is to be of value when turbulence is minimal. This is true of both the Cryptophyceae but more so of the Dinophyceae because of their relatively large sizes.

The competitive abilities of the different groups of phytoplankton at different conditions are therefore important factors in their presence and dominance in a community assembly (Cox, 1990). Baccilariophyceae, Cryptophyceae and some Chlorophyceae occupy the ideal positions and therefore dominate during periods of high to moderate productivity. Deterioration of overall conditions for phytoplankton leads to a shift favouring species or groups with special adaptations that compensate for changes in one or more of the growth or loss control factors which in the Cyanophyceae include buoyancy regulation and nitrogen fixation and in the Dinophphyceae, mixotrophy and motility (Lewis, 1978) and generally for these two groups unpalatability to zooplankton (Carpenter *et al.*, 1987).

In the end, algal communities develop as a result of the variable capacity of different species to colonize, grow, compete, tolerate multiple stresses and resist loss processes. The net result is the production of different community structures in different water bodies (Cox, 1990) and different community structures at different times in the same water body (Lund, 1965).

2.5 Spatial patterns of phytoplankton variability in lakes

Non-uniform spatial distributions of phytoplankton have been observed on many occasions, in both the vertical and horizontal planes over water bodies and are important in the understanding of the ecology of phytoplankton (George & Heaney, 1978).

2.5.1 Spatial distribution of phytoplankton

Aquatic ecosystems are manifestly heterogeneous owing to spatial differences in temperature, solute content, wind stress, etc. Each of these drivers is also subject to almost continuous variation (Reynolds, 2006). The changes in temperature, insolation, hydrological exchanges and the delivery of essential nutrients affecting a given stretch of water also occur on simultaneously differing scales of temporal oscillation. For instance over minutes, hours, night-day alternations, with changing season, interannually and over much broader scales of climatic change (Reynolds, 2006). JuhaszNagy (1992), has observed that the relative uniformity or heterogeneity within an ecological system depends mainly upon the spatio-temporal scale at which it is observed.

2.5.2 Vertical distribution of phytoplankton

The vertical distributional behaviour of phytoplankton is usually viewed in relation to the physical structure of the water and is expected to conform to the kinetic structure of the water column (Reynolds, 2006). Non-motile negatively buoyant phytoplankters are destined to be lost from the surface waters. Numerous studies have demonstrated the sensitivity of Baccillariophyceae distribution to water movements and to the onset of thermal stratification in water bodies (Ruttner, 1938; Findenegg, 1943; Lund, 1959; Nauwerck, 1963; Margalef, 1958, 1978; Smayda, 1973, 1980).

Positively buoyant phytoplankters especially planktonic, gas-vauolate Cyanobacteria are also sensitive to the mix layer depth except that here they float rather than sink through the more stable layers (Reynolds, 1989). Buoyant Cyanobacteria are known to form in still windless conditions (Reynolds & Walsby, 1975). Neutrally buoyant phytoplankters are the most easily entrainable. These are usually unicells of the nanno- and picoplankton which are non-motile and also lack gas vacuoles. These are usually distributed uniformly through the epilimnion (Happey-Wood, 1988; Reynolds, 2006).

Motile phytoplankters such as dinoflagellates, cryptophytes and euglenophytes which are capable of directed movements can usually cause discontinuous vertical distribution in lakes and seas (Nauwerck, 1963; Moss, 1969; Cloern, 1977; DonatoRondon, 2001; Reynolds, 2006). Klaveness (1988) has demonstrated this phenomenon in Cryptophyceae and Hader (1986) in Euglenophyceae.

2.5.3 Horizontal distribution of phytoplankton

It is a generally agreed that assumptions of horizontal homogeneity have no place in modern plankton science because of the myriad of causes that may be responsible (Welch, 1952; Reynolds, 2006). A well established fact concerning the horizontal distribution of phytoplankton is its irregularity when any area of fair size is considered (Welch, 1952). This lack of uniformity extends not only to large areas but also to relatively small lakes and regions of lakes though in general phytoplankton are more uniformly distributed compared to the zooplankton (Welch, 1952) and this is important in lake managament. George & Heaney (1978), divide the factors that affect horizontal distribution of phytoplankton into those that produce local changes in the rate of population increase or decrease (e.g. grazing, nutrient and temperature differences) and those bringing about spatial redistribution of the population (e.g. wind induced water movements). Welch (1952) lists action of wind, nature of inflowing streams, general flowage areas, currents and undertow currents, action of predators, indirect results of diurnal migration of certain phytoplankters, etc.

Winds may cause drift of upper waters and under these conditions, phytoplankton may become concentrated in the vicinity of the shore which faces into the wind (Welch, 1952; George & Heaney, 1978). This will result in the corresponding thinning of the phytoplankton on the opposite side. Patchiness is strongest when winds are light but weakens as winds start to exceed 3 ms⁻¹, disappearing altogether at greater than 5 ms⁻¹ (Heaney, 1976; Heaney & Talling, 1980a).

Inflowing streams either increase the phytoplankton quantitatively, qualitatively or both or can dilute them (Welch, 1952). Also, irregularities in the horizontal distribution of phytoplankton may result from shorelines which have various bays and coves sufficiently protected to provide better conditions for developing phytoplankton than does the open water (Welch, 1952).

Also, although not directly applicable to lake conditions, theoretical models developed by Steele (1974) and Platt & Denman (1975) for turbulence and phytoplankton growth rates in the open sea, suggest that differential production can only be expected to occur on scales ranging from 10-100 km.

2.6 Inter-annual variability of phytoplankton

Considerable inter-annual variabilities have also been recognized by aquatic ecologists in the seasonal dynamics of phytoplankton (Jassby *et al.*, 1990, 1992; Goldman *et al.*, 1968; Anneville *et al.*, 2002; Sarmento *et al.*, 2006), and this is believed to be driven by strong inter-annual variation in the physical, chemical and biological characteristics of lakes (Archonditsis *et al.*, 2004; Baines *et al.*, 2000). Much direct and indirect evidence suggest that nutrients have a dominant influence on the mean abundance of phytoplankton at any given latitude (Schindler, 1978). Carpenter *et al* (1987) provided experimental evidence that trophic interactions can result in interannual variation of phytoplankton. Grazers can suppress biomass if nutrients are already limiting or can affect the species composition of phytoplankton by selective feeding (Reynolds, 1984).

2.7 Primary productivity of phytoplankton

Phytoplankton standing crop refers to how much phytoplankton cells or biomass is already present in a given water body. Primary productivity on the other hand refers to the new organic matter being formed by the phytoplankton and is an important biological process with an influence on many chemical reactions throughout a lake and on all trophic levels (Melack, 1976). Biological differences may be expressed both qualitatively and quantitatively i.e. as the abundance of composite biomass or as diversity of kind. For many purposes however, the factor of greatest importance is the rate at which organic matter is formed from inorganic matter and accumulated in the system under study. The basic process involved is the photosynthesis of plants which in lacustrine environments of lakes is largely performed by the phytoplankton. Phytoplankton productivity in lakes, estuaries and oceans plays an essential role in element cycling and food supply to heterotrophs (Cloern, 1977).

Several studies of primary productivity of phytoplankton have been made and there are some evidence that tropical lakes are highly productive (Talling, 1965a; 1966). Experiments by Deevey (1955; 1957) in Central America, indirect evidence from survey of Indonesian lakes (Ruttner, 1931, 1952) and studies in the Philippines (Frey, 1969; Lewis, 1973) suggest that tropical lakes are universally more productive than their temperate counterparts.

According to Melack & Kilham (1974), in lakes not enriched by human activities, gross photosynthetic rates of 11 gCm⁻²day⁻¹ or greater are rare. But, Odum (1956; 1957) have observed that as much as between 15.0-17.25 gCm⁻²d⁻¹ may be realized in the most fertilized communities if conditions are favourable. The mean gross photosynthetic rate for the streams and lakes of the world is about 0.6 gCm⁻²day⁻¹

(Whitaker & Likens, 1975). Annual productivity of phytoplankton is known to vary over 3 orders of magnitude between 1.5 gCm⁻²yr⁻¹ in ultraoligotropic Antarctic lakes to about 2250 gCm⁻²yr⁻¹ in hypereutrophic low latitude lakes (Goldman *et al.*, 1968).

The most productive systems on an annual basis are shallow, extremely nutrientrich lowland lakes where the combination of year-round high irradiances and shallow water column's yields a high effective light climate (Beadle, 1981; Wetzel, 2001). This combined with high water temperatures and high nutrient levels yield very high biomasses and results in high areal production rates (Kalff, 2002). High water temperatures in inland waters at low latitudes allow a high rate of microbial decomposition and recycling of nutrients contained within the organic matter respired, making them quickly available for uptake and growth by algae (Kalff, 2002). Ultraoligotrophic lakes on the other hand, experience very short growing seasons, low temperatures and very low nutrient inputs from their drainage basins (Kalff, 2002; Beadle, 1981).

Several studies in tropical lakes have shown that the upper limits of areal gross productivity of phytoplankton can be very high (Table 2.1) and several exceed the rates given by Melack & Kilham (1974). Goldman (1968) characterized aquatic primary production of temperate lakes and estimated it to range from about 0.012 gCm⁻²d⁻¹ to 3.6 gCm⁻²d⁻¹ from the most oligotrophic to the most hypertrophic. Kalff (2002) reports the most productive lake on areal bases as Haartbeesport Dam in South Africa with a maximum of about 115.88 gCm⁻²d⁻¹ and a mean rate of about 15.65 gCm⁻²d⁻¹ but Robarts (1984) reports a mean of 30.9 gCm⁻²d⁻¹ for the same dam. Areal rates as high as 21.38 and 21.34 gCm⁻²d⁻¹ in Lake Aranguandi (Talling, 1973), and an Indian reservoir (Sreenivasan, 1965) respectively have been reported. Some other lakes in Africa have

gross areal values greater than 11 gCm⁻²d⁻¹ (Table 2.1). These studies also reveal that in the tropics, the range of daily integral fixation is also wide. For instance, Beaver and Crisman (1991) estimated that tropical lakes between 0° to 10° had a mean CV of 37 %.

 Table 2 Daily areal gross primary productivity of some selected tropical lakes

Lake D	Daily integral fixation (gC m ⁻² d ⁻¹)	Reference (s)
Haartbeesport Dam (South	Africa) 30.90	1
George (Uganda)	14.00	2
Edward (Uganda)	13.80	2
Aranguandi (Ethiopia)	13-22	3
Ayyangulam (India)	9.00	4
Rashitani (Tanzania)	7.50	5
Mariut (Egypt)	4.81	6
Nasser (Egypt)	4.41	7
Nakuru (Kenya)	3.90	13
Elmenteita (Kenya)	3.19	13
Victoria (Uganda)	2.78	2
Albert (Uganda)	2.66	2
Bogoria (Kenya)	2.55	13
Volta (Ghana)	2.25	8
Naivasha crater (Kenya)	1.84	9
Chad (Chad)	1.69	11
Kivu (Kenya)	1.44	12
Tanganyiaka (DRC &Tanz	ania) 0.80	12

1. Robarts, 1984. 2. Talling, 1965a 3. Baxter *et al.*, 1965 4. Sreenivasan, 1964 5. Melack & Kilham, 1974 6. Aleem & Samaan, 1969. 7. Samaan, 1971. 8. Viner, 1970. 9. Melack 1979. 10. Lewis, 1974. 11. Lemoalle 1973. 12. Hecky & Fee, 1981. 13. Odour & Schagerl, 2007.

The mechanisms by which high productivity is sustained in the tropics are still unclear because of lack of published comprehensive seasonal observations on tropical lakes but productivity has been shown to increase with standing crop (Lewis, 1974). Lewis (1974) further lists high productivity per unit standing crop, high sustained standing crop per unit area and maximum transparency per unit of production as been related to high productivity of tropical lakes. Tropical lakes are also known to show more intra-seasonal variation in the thickness of the Z_{mix} as a result of the low Coriolis Force (Melack, 1980). This periodic intra-seasonal deep mixing followed by restoration of the thinner mixed layer, results in efficient recycling of microbial nutrient regeneration. The combination of efficient nutrient cycling, higher mean water temperatures and greater stability of solar irradiance results in higher phytoplankton production (Lewis, 1976; Kalff, 2002). However if the Z_{mix} exceeds the thickness of the Z_{eu} , algae are transported into darkness where respiration, but not photosynthesis continues (Tilzer & Goldman, 1978). This may reduce total productivity.

Beadle (1981) has noted that the continuous high temperatures in the tropics that induce more productivity also stimulate all processes in the metabolic cycle of the phytoplankton that will ultimately result in high oxygen consumption. Thus, although gross primary productivity and the circulation of energy and materials may be more rapid at higher temperatures, the net productivity is not necessarily increased (Ryther, 1963).

Ganf (1974) has observed that respiration increases with increasing photosynthesis. Also, the relative respiration rates for blue-green (Bindloss, 1974) and dinoflagellates (Tilzer *et al.*, 1977) are found to be high whiles a linear relation seems to exist between respiration and photosynthesis in some Chlorophyceae dominated lakes (Dokulil, 1983). Respiration rates in phytoplankton are however generally found to vary between 5 to 15 % of gross photosynthesis at light optimum (Ryther, 1954; Steelmann-

Nielsen & Hansen, 1959; McAllister *et al.*, 1964). Juday (1922) also estimates that the best available respiratory coefficient for lacustrine producers is about 33.3 %. But Ganf (1974) estimated community respiration in Lake George to be 92 % of gross productivity whiles Bunt (1965) recorded community respiration values of between 20 to 100 % in bacteria-free algal cultures.



CHAPTER THREE

MATERIALS AND METHODS

3.1 STUDY AREA

Lake Bosomtwe is situated in the Ashanti Region of Ghana (06°30'N, 01°25'W), West Africa, about 32 km from Kumasi, the regional capital (Boamah & Koeberl, 2007) within the semi-deciduous forest/savanna potential zone of West Africa (Hall & Swaine, 1981; Fig. 3.1). According to Hall & Swaine (1981), prior to severe degradation of the natural vegetation by settlement and cultivation, the Bosomtwe region was dominated by semi-deciduous rain forest. The major macrophyte is a species of *Typha*. Today, the catchment is partly cultivated and partly forested. Agricultural practices by the over 22 communities within the catchment include cocoa, plantain and palm nut plantations. Tomato, cabbage, okro and other vegetables are also cultivated.



Fig. 3.1 Map of Ghana showing Lake Bosomtwe (Ghana web, 2008)

The crater (Fig. 3.2) which the lake occupies is of meteoritic impact origin (Jones *et al.*, 1981; Koeberl & Shirey, 1993; Koeberl *et al.*, 1998) and is known to form in hard

crystallined target rocks that inhibit ground water exchange (Turner *et al.*, 1996a). As a result, the hydrological balance of the lake is driven by long-term fluctuations relative to evaporation and reflected in changes in the lake water level (Turner *et al.*, 1996a).



Fig. 3.2 A bathymetric map of the Lake Bosomtwe (Google Map, 2008).

The lake has a diameter of 8 km and a maximum depth of 78 m (Turner *et al.*, 1996a). The mean depth is about 45 m (Welcome, 1972). The lake lies in the path of the seasonal migration of the Inter Tropical Convergence Zone (ITCZ), an atmospheric boundary between N-E continental trade winds (Harmatten winds) and S-W onshore winds (Nicholson, 1980) and responds to climatic variations by significant changes in the lake water levels (Turner *et al.*, 1996b) and water chemistry (Talbot *et al.*, 1984; Talbot & Johannessen, 1992; Talbot & Kelts, 1986). The present-day water budget of the lake is believed to be slightly positive (Talbot & Delibrias, 1980). Average monthly temperature is about 26 °C and annual precipitation varies between about 1136 mm to

1520 mm with a pronounced dry season from November to February (Turner *et al.*, 1996b; Puchniak *et al.*, 2009).

It is a closed basin lake which is stratified most year round except during the Harmattan and also during the 'little dry season' in August. It has one perennially flowing stream (Abrewa). It is also meromictic. The pH averages around 8.9 implying that most of the carbon is in the bicarbonate from. In fact, the chief mineral constituents are the bicarbonates of sodium and potassium (McGregor, 1937; Karikari & Bosque-Hamilton, 2004; Puchniak *et al.*, 2009) whiles conductivities range between 1182-1283 μ Scm⁻¹ (Puchniak *et al.*, 2009; Karikari & Bosque-Hamilton, 2004). Moreover, the essential nutrients, phosphates and nitrates appear to be adequate for phytoplankton growth (McGregor, 1937; Karikari & Bosque-Hamilton, 2004).

3.2 Sampling sites

Sampling for phytoplankton temporal studies (i.e community species composition, biomass and productivity) was done at a single location in the deepest central portion of the lake (CSTN-Fig 3.1B) whiles horizontal studies were done at 14 different stations along two transects of the lake (Appendix 1D). Some morphometric features of the 5 stations used for inshore-offshore comparison are shown in Table 3.1 below.

Station	Approximate distance	Latitude	Longitude	Depth (m)
	from village			
ABONO	200 m	6°31'595''N	1°25'650''W	11.4
APEWU	200 m	6°28'620''N	1°26'185''W	11.5
ASISIRIWA	200 m	6°31'853"N	1°23'564''W	6.7
DOMPA	200m	6°28'432''N	1°24'668''W	1.8
CSTN	4 km	6°30'609''N	1°24'671"W	78

 Table 3 Location, distance, depth and proximal bathymetry for 5 stations during horizontal surveys

3.3 Physical data

3.3.1 Apparatus and Procedure: Meteorology (climatic characteristics)

Meteorological variables {air temperature (°C), precipitation (mm), wind speed (ms⁻¹), relative humidity (%) and barometric pressure (mbar)} were monitored with a remote meteorological station HOBO[®] Weather station (6°31.138"N, 1°25.665"W) near the lake shore at Abono (© 2001-2003 ONSET Computer Corporation part H21-001). The meteorological station was launched to measure the various variables every 10 minutes for the period (from November 2004 to October 2006) monitored with the aid of the computer programme BoxCar[®] Pro.

3.3.2 Apparatus and Procedure: Water column charateristics

A multiprobe 6SBP Hydrolab H2O[®] Water Profiler (Hydrolab Corporation, 1991) fitted with sensors for measuring conductivity (μ S m⁻¹), temperature (°C), dissolved oxygen (% saturation) and pH was used for online *in situ* measurements of

these variables at the CSTN i.e. an index offshore station approximately 4 km from the lake shore and 78 m deep. The conductivity and temperature sensors are very sensitive and highly stable. However, the dissolved oxygen sensor required frequent calibration: the internal electrochemistry of the oxygen sensor changes with successive measurements making recorded values to undergo a gradual linear departure from actual concentrations if recalibrations are not done (Carlson, 2002). The Profiler was then deployed on a suspension line by holding it at the water surface for at least two minutes to allow it to stabilize and then lowered through the water column at approximately 15 cms⁻¹ up to 50 m. This was done each sampling period fortnightly alongside phytoplankton sampling for two years for temporal studies and at 14 different stations during 4 horizontal studies on 2 transects at two different seasons.

3.3.3 Secchi Disc (SD) depth, k_{PAR} , Z_{eu} and Z_{mix}

Water transparency measurements using SD depths were performed at the CSTN biweekly and at 14 different stations comprising inshore and offshore areas during horizontal studies (Table 3.2; Appendix 1A &1B) alongside phytoplankton sampling. This was done with a 25 cm black and white secchi disc (SD) as the average depth at which the disc was no longer visible upon lowering and when it just becomes visible upon raising it in the water column on the shaded side of the sampling boat.

Inshore areas are defined here as 4 stations with relatively shallow depths compared to the middle portion of the lake and 200 m away from the shore and offshore areas as stations situated more than 200 m away from the lakeshore with relatively

deeper maximum depths compared to inshore areas. Data for meteorological and some physico-chemical water column variables have been published (Puchniak *et al.*, 2009).

A flat-plate LI-COR quantum sensor (LI-COR Biosciences, Lincoln NB) was initially used to estimate the under water irradiance in the photosynthetically active waveband (400-700 nm). Measurements were taken above and below the air-water interface to ascertain surface reflection, and at different depths thereafter until irradiance was approximately 1% of surface irradiance to determine k_{PAR} following the method of Kirk (1994). Due to technical problems however, only measurements on 11 sampling dates could be completed. However, seechi disc (SD) depths and the k_{PAR} estimated at the same time were highly positively correlated (Eqn. 3.1; Fig 3.3) and had a coefficient of determination of approximately 0.84 (r = 0.92; p < 0.01, n = 11).



Fig. 3.3 Regression of inverse of SD depth versus k_{PAR} in Lake Bosomtwe (Ghana)

Subsequently, all k_{PAR} values were estimated from this relationship (Eqn 3.1).

Eqn. (3.1)
$$SD^{-1} = 0.4262 * k_{PAR} + 0.291$$

The calculation of k_{PAR} from SD enables a good approximation of the euphotic depth (Z_{eu}) which is taken to be the depth of penetration of 1% of surface light (Kirk, 1991). The euphotic depth was then estimated according to Talling (1986) as,

Eqn. (3.2)
$$Z_{eu} = 3.7/k_{PAR}$$

The Z_{mix} of the lake at any time was determined from online *in situ* measurements of the depth profiles of temperature taken with a 6SBP multiprobe H20[®] Water Profiler (Hydrolab Corporation, Austin, Texas, 1991) as the length from the top of the thermocline to the surface of the water column. This was estimated by manual inspection of temperature versus depth curves for the first prominent break.

3.4 Biological Parameters

3.4.1 Horizontal and temporal variability of phytoplankton community species composition and biomass: Apparatus, field and laboratory procedure, data analysis

Horizontal sampling of phytoplankton species composition and biomass was done synoptically at 2 m depth within the Z_{eu} and Z_{mix} at 14 different stations (Table 3 & Appendix 1B) along 2 horizontal transects in a mixing season in August 2006 and during stratified seasons in November and December of 2006. Samples for temporal studies were taken at a single central index station-CSTN (Fig 3.1B) at biweekly intervals for two consecutive years (November 2004- October 2006) except between December and January when the sampling interval was about a month. Ten depths (surface, 1, 2, 5, 8, 10, 12.5, 15, 20 and 30 m) were sampled during each biweekly sampling. Samples were taken with a 6-Litre van Dorn water sampler. This was subsampled into 125 ml glass bottles and preserved immediately with 1 ml acid Lugol solution and then stored in a dark, cool container for further analysis in the laboratory.

In the laboratory, 2 ml of a water sample were usually concentrated by allowing the phytoplankton to settle for 2 hours at room temperature in a 2 ml capacity chamber of the Utermohl (1958) type. This usually gave large count sizes that were usually uniformly distributed. Counts were made at x 400 using a Zeiss inverted microscope. Total counts of viable cells for any one sample within the mixed layer usually exceeded a minimum of 400-600 cells which is usually required to assure that the count is representative of the sample (Findlay & Kling, 2004). Taxa were counted as cells on a single transect 200 µm wide across the centre of the counting chamber. Cell fragments were not counted.

Counts of single cells, colonies and filaments were converted to wet weight biomasses of individuals by approximating cell volume. Estimates of cell volume for each species was done by routine measurements of 30-50 cells of an individual species and the application of the geometric formula best fitted to the shape of the cell (Vollenweider, 1968; Rott, 1981). A specific gravity of 1 was assumed for cellular biomass. Average biomasses of the phytoplankton in the Z_{mix} were used in further analysis of the data. This was calculated by determining the Z_{mix} of the water column of each sampling date and averaging the biomass from the top of the thermocline up to the water surface.

Identifications were performed on preserved whole and net (10 μ m mesh) samples. Most of the phytoplankton taxa were identified to species level except where it was impossible. Also, some colourless spindle and spiral-shaped organisms were present in all samples and at most depths sampled. These were morphologically similar to the

Monoraphidium spp (green algae) also present in the lake. However, the absence of chlorophyll *a* in their fixed state made identification impossible and were therefore not counted. The identity of these organisms may rest upon examination of fresh samples through fluorescence microscopy.

Taxonomic keys employed in the identification of species include: Meel, 1954; Fritsch, 1956; Prescott, 1978; Gerrath & Denny, 1980; Caljon, 1987; Komarek, 1989; Caljon & Cocquyt, 1992; Conforti, 1994; Komarek & Novelo, 1994; Williamson, 1994; Romo *et al.*, 1995; McGregor & Fabbro, 2001; Komarek & Komarkova, 2002; Komarek & Komarkova, 2003; Wehr & Sheath, 2003; Komarek, 2005; Komarek & Komarkova, 2006.

The sedimentation-inverted microscopy (Utermohl, 1958) employed is usually free from interferences but suspended sediments sometimes obscure phytoplankton in samples. Chambers were cleaned with distilled water and then by alcohol and again with distilled water before reuse to ensure that residues from previous sample were completely removed. Convection currents and air bubbles, which interfere with sedimentation, were avoided by filling the chamber without trapping any gas bubble and at room temperature.

For chlorophyll *a*, water samples within the Z_{mix} were collected with a 6-L van Dorn siphoned into 5-L carboys and used for analysis on each occasion alongside phytoplankton sampling. In the lab, 500 ml of the water was usually filtered through 0.7 μ m pore Whatman GF/F Ø 47 mm filters and extracted in 95 % acetone. The fluorescence of chlorophyll *a* was then measured in a Turner 10 AU flourometer following spectrophotometric methods in Stainton *et al* (1977) to determine the final concentration of chlorophyll a in the water sample.

For total phosphorus analysis, water samples within the Z_{mix} were collected with a 6-L van Dorn and siphoned into 20 ml vials on each occasion alongside phytoplankton sampling. In the laboratory, total phosphorus was analyzed by the ascorbic acid method after persulphate digestion following spectrophotometric methods described in Stainton *et al* (1977).

Chlorophyll *a* and total phosphorus samples were taken only during the temporal studies.

3.4.2 Phytoplankton primary productivity

3.4.2.1 Duration

Phytoplankton productivity measurements were also performed at the central station (Fig. 3.1B) biweekly for a year (September 2005- August 2006).

3.4.2.2 Apparatus, field and laboratory procedure and data analysis

In situ light and dark bottle oxygen method was employed to quantify phytoplankton photosynthesis and community respiration. At the central station, the Z_{eu} was determined. Seven (7) depths within the Z_{eu} were then chosen for incubation (Vollenweider, 1969). A 6-L van Dorn discrete water sampler was used to collect samples from these predetermined depths and sub-sampled introducing water via siphon into the bottom of 2 light and 1 dark 300 ml BOD (biochemical oxygen demand) bottles. This was done away from light water was allowed to overflow to exclude air bubbles. One light bottle was immediately fixed with 2 ml each of manganese sulphate and alkaline iodide azide solution. Reagents were prepared following Wetzel & Likens (1979). A 125 ml glass bottle was also filled with this water and preserved immediately with acid Lugol to determine the biomass and species of phytoplankton contributing to the productivity. All fixed and unfixed samples were then placed in cool dark containers until samples from all depths were collected and treated likewise. The unfixed light and dark bottles from the 7 depths were then suspended on a metered suspension line and incubated at their respective depths for 4 hours usually between 1000 – 1400 hours. After the incubation, the samples were removed and fixed as before for the initial bottles and placed in the cool dark container for further analysis in the lab.

In the lab, the methodology of Wetzel & Likens (1979) was followed to determine the final dissolved oxygen concentration in the BOD bottles. Primary productivity was then expressed as the quantity of oxygen released (mgO₂ m⁻³hr⁻¹) or carbon assimilated (mgC m⁻³hr⁻¹) on the assumption of one carbon atom assimilated for each of the molecule of oxygen released. (Productivity quotient = 1).

The P_G and R_C of a vertical column of water 1 m² in cross-section (mgO₂ m⁻²t⁻¹) was then determined from the surface of the lake to the bottom of the Z_{eu} using an adapted version of a model of integration originally developed by Fee (1990). Fig 3.3 below provides the concepts behind the model with relevant equations. The first step involves quantifying underwater irradiance (I) along user-specified time (t) and depth (z) intervals (Fig 3.3C grey lines). Equation (3.3) quantifies I at each interval of t and z as a function of I₀ (the initial or surface irradiance) and k_{PAR} (Fig 3.3C).

Eqn. (3.3): $I_{[t,z]} = I_{0[t]} \cdot e^{-k \cdot z}$

 I_0 (Watt/m²/s) was obtained from the meteorological station (6°31.138"N, 1°25.665"W) situated along the N-E shore of the lake as an average of total solar radiation during incubation periods and converted to $\mu E \text{ m}^{-2}\text{s}^{-1}$ according to Biggs (1986).

 P_G was was subsequently calculated as the double integral (Eqn. 3.4) of $P_{(t,z)}$ through the Z_{eu} (0 $\rightarrow Z_{eu}$) and time ($t_0 \rightarrow t_1$).

Eqn. (3.4):
$$P_G = {}^{t1} \int_{t0} {}^{zeu} \int_0 P_{[t, z]}$$

 R_C was likewise obtained by integrating through the Z_{eu} and Z_{mix} for 24 hours of a day and consequently P_N in the Z_{eu} (Eqn 3.5) and Z_{mix} (Eqn. 3.6) were derived by subtracting R_C in the Z_{eu} and Z_{mix} from P_G .

Eqn. (3.5):
$$P_{N [Zeu]} = P_G - R_{C[Zeu]}$$

Eqn. (3.6): $P_{N [Zmix]} = P_G - R_{C[Zmix]}$

Oxygen weight units were converted to carbon weight equivalents by multiplying by 0.375 (Wetzel & Likens, 1979).

Mean areal biomasses of phytoplankton were converted to carbon wherever relevant at a rate of 10 % (Lewis, 1974). Growth rates were estimated according to Petersen (1978) as,

Eqn. (3.7): growth rate $[Zeu] = Ln (C_0 + P_N)/t^*C_0$

Eqn. (3.8): growth rate $_{[Zmix]} = Ln (C_{o} + P_{N})/t^{*}C_{o}$

Where $C_0 = 10$ % of organic matter or wet weight in gC m⁻² and

 P_N = the net productivity in the $Z_{eu} \mbox{ or } Z_{mix}$ in gC $m^{-2} \mbox{ d}^{-1}$



Fig. 3.4 Conceptual diagram of gross phytoplankton production model. Incident irradiance (A) In situ irradiance (B) Under water irradiance (C) P-I profile (D)

A number of authors have commented on the biases introduced into the production estimates because of the unnatural conditions caused by the confinement of phytoplankton in bottles. General and specific assumptions, limitations, precautions and interferences with the *in situ* light and dark method of primary productivity of phytoplankton are described in Vollenweider (1969), Steelmann Nielsen (1975), Strickland (1960), Saijo & Ichimura (1960), Gessner (1959), and Winberg (1960) and are summarized in Appendix 3A. According to Odum (1956), although some of these biases tend to compensate for one another, bottle techniques are generally considered to lead to underestimates of primary productivity.

3.4.3 Evaluation of seasonal variability

Sampling periods were divided into three periods namely,

1. Stratified periods which refer to periods when the mixed layer was stable and shallow for a relatively long period,

2. Mixing periods which refer to periods when the mixed layer deepened following prolonged stratification, and

3. Restratifying periods which refer to periods immediately following mixing periods during which stratification is re-established.

From 2004 to 2005 (1st year), the stratified period occurred from November-December and from March-June, the mixing period was observed in January and also from July-August while the restratifying periods occurred in February and from September-October. From 2005 to 2006 (2nd year), the stratified period occurred from November-mid December and then from March-June as in the 1st year (2004-2005). The mixing period instead of January as in first year occurred in late December and from July-August as in the 1st year (2004-2005). The restratifying period occurred from January-February and from September-October.

Thermal stratification of water masses permits phytoplankton to maintain their vertical distribution while at the same time not interfering with the migration of some forms. In contrast, vertical mixing distributes phytoplankton throughout the water column and transports nutrients from enriched to previously depleted layers. Stratification and mixing therefore control the two most important factors in phytoplankton ecology: phytoplankton light climate and nutrient availability. Grazing by zooplankton is also known to be affected by the stratification-mixing process. This was the rationale for the seasonal periods chosen for this study.

3.4.4 Statistical evaluation

Both descriptive (means, standard deviations, coefficient of variances) and inferential statistics (t-test, One-Way ANOVA and simple correlations) were used to analyze the data generated using the statistical package SigmaPlot 10 (Syst. Inc, USA). Means, standard deviations and coefficient of variances were estimated for physico-chemical and biological data to estimate the central tendency and extent of variability of the data. T-test was used to infer variability between the 2 years' biomass and other physico-chemical variables while One-Way ANOVA was used to analyze variabilities between and within seasons for the various physico-chemical and biological parameters. Simple reression analysis between the biomass/chlorophyll *a*/productivity and the physico-chemical parameters was employed individually as predictors of the factors that may potentially be controlling the biomass and/or productivity of the phytoplankton of the lake.

CHAPTER FOUR

RESULTS

4.1 Horizontal distribution of some physico-chemical parameters and phytoplankton community species composition and biomass

4.1.1 Lake-wide (horizontal) physico-chemical characteristicsal variables

Physico-chemical parameters of the lake water column measured include lake transparency using the Secchi disc, temperature, conductivities and dissolved oxygen.

 $\langle | | \rangle$

4.1.1.1 Secchi disc (SD) depths

Seasonal lake-wide mean transparencies as measured by the SD depth ranged from 1.1 m to 1.6 m during the entire period (mixing and stratified periods). It was higher during the stratified period (mean SD depth of 1.6 m, n = 14) compared to the mixing period (mean SD depth of 1.3 m, n = 14-Table 4.1). The variability in the lake-wide mean SD depth though generally low, was however slightly higher during the mixing season (1.5-fold change and a CV of 9.6 %) compared to the stratified period (1.2-fold change and a CV of 6.8 %; Table 4.1). Horizontally, SD depths at all stations were higher in the stratified compared to the mixing period. The highest SD transparencies occurred at the central station and at 2 inshore areas of Abono and Apewu (SD of 1.4 m; Fig 4.1) during the mixing season but was highest in the central station compared to all inshore stations during the stratified period (SD of 1.6 m; Fig 4.1). Comparison of SD depths of the 2 seasons indicates a clearer inshore-offshore pattern in the stratified period compared to the mixing season (Fig 4.1).

4.1.1.2 Water temperature, dissolved oxygen and conductivity

Lake-wide (i.e. horizontal) mean water temperatures ranged from 27.6 °C to 30.4 °C during the period. It was higher during the stratified period (mean of 30.1° C, CV = 0.8 %, n =14) compared to the mixing period but the variability is generally very low for both seasons (mean of 27.9 °C, CV = 0.6 %, n=14; Table 4.1). Horizontally, water temperatures were higher at all stations during the stratified period compared to the mixing period (Fig 4.2). It was highest in the inshore area near Abono (30.4 °C) and lowest at the CSTN (27.8 °C) during the stratified and highest at inshore areas of Apewu and Asisiriwa (28.1 °C) and lowest again at the CSTN (27.8 °C) during the mixing periods (Fig 4.2).

Lake-wide horizontal mean dissolved oxygen (DO in %) ranged from 47.2 % to 86.1 % during the period. It was higher and more variable in the stratified (mean of 66.2, CV = 23.7 %, n =14) than in the mixing period (mean of 57.3, CV = 11.2 %, n =14; Table 4.1). In the stratified season, dissolved oxygen concentrations were highest at inshore areas of Abono (80.4 %) but both inshore area of Asisiriwa and offshore CSTN had comparable DO concentrations (51.7 and 53.6 % respectively; Fig 4.3). In the mixing season, DO was highest at the CSTN (72.4 %) and lowest in the inshore station of Asisiriwa (49.8 %, Fig 4.3).

Lake-wide mean horizontal water conductivity ranged from 1106.4 μ S cm⁻¹ to 1312.9 μ S cm⁻¹. Mean conductivity in the stratified period (mean of 1294.8 μ S cm⁻¹, n = 14) though slightly higher was comparable to that of the mixing season (mean of 1275.3 μ S cm⁻¹, n = 9; Table 4.1). Variabilities were generally very low but slightly higher in the mixing period (CV = 3.8 %, n =14) compared to the stratified period (CV = 2.3 %, n = 9; Table 4.1). In the stratified period conductivity was highest at inshore station of Asisiriwa (1312.9 μ S cm⁻¹) but comparable with that of CSTN (1307.5 μ S cm⁻¹) and lowest at inshore station of Abono (1297.3 μ S cm⁻¹, Fig 4.4). During the mixing period, the conductivities were comparable at all sites except at inshore Dompah where the lowest (1106.4 μ S cm⁻¹) occurred (Fig 4.4). No clear offshore-inshore trends were observed in both seasons, but it was higher at all stations in the stratified compared to the mixing period where comparisons were possible.

4.1.2 Horizontal distribution of phytoplankton

4.1.2.1 Community species composition

A total of 56 phytoplankton species comprising 44 genera and representing 7 major groups were identified. The groups which include the Chlorophyceae (19 species representing 33 %), Cyanophyceae (17 species representing 30 %), Bacillaryophyceae (7 species representing 13 %), Dinophyceae (6 species representing 11 %), Cryptophyceae (4 species representing 7 %), Euglenophyceae (2 species representing 4 %) and Chrysophyceae (1 species representing 2 %) were observed during a deep mixing period in August and stratified periods in November and December respectively lake-wide. The highest number of species for a single taxon was 3 and was observed in the genus *Chroococcus* Naegeli (*C. disperses, C. minimum, C. turgidus*), a coccal cyanobacterium and *Tetraedron* Kuetzing (*T. minimum, T. minimum var granulata and T. trigone*), a chlorophyte (Appendix 1C).

Total species richness did not follow any inshore-offshore trend during both periods (Fig 4.5A) and lake-wide mean species richness in both seasons was about the same (approximately 22 species). Total species richness in both the stratified (49 species) and the mixing (50 species) seasons were also comparable with the stratified period having a higher percentage of Dinophyceae, Cryptophyceae and Chlorophyceae compared to the mixing period while the mixing season had higher percentage of Baccillariophyceae, Cyanobacteria and Euglenophyceae.

The highest species richness during the stratified period occurred at inshore station of Apewu (30 species) and the lowest occurred at inshore station of Dompah (15 species; Fig 4.5A). However, inshore station of Abono and CSTN had comparable number of species (Fig 4.5A). The cyanobacteria dominated the species composition at all sites except at inshore Apewu where the Chlorophyceae had just one species more than that of the Cyanobacteria (Fig 4.5B). Offshore- inshore observations of the community species composition during this period indicate the cyanobacteria and Euglenophyceae to be more prominent in the species richness at the offshore station CSTN (Cyanobacteria-51 %, Euglenophyceae- 4 % respectively) compared to the inshore stations (Cyanobacteria-44 %, Euglenophyceae- 0 % respectively; Fig 4.5B). At the same time, the Dinophyceae had higher % species richness at inshore stations (16 %) compared to that of the offshore CSTN (8 %). The Bacillariophyceae, Cryptophyceae and Chlorophyceae however contributed almost the same quata to the percentage to the total species richness at both inshore and offshore stations (Fig 4.5B).

In the mixing season, species richness was comparable at all stations being just over 20 except at inshore station of Apewu which had the lowest of 18 species (Fig 4.5A). Similar to the stratified period, the Cyanophyceae dominated the species richness of all stations during this period. Offshore- inshore observations during this period indicate a greater % contribution to species richness in the offshore CSTN by the Dinophyceae (9 %), Bacillariophyceae (9 %), Cryptophyceae (9 %) and Euglenophyceae (3 %) compared to the inshore areas where the Dinophyceae, Bacillariophyceae and Chrysophyceae contributed 4 % each, 8 % by the Cryptophyceae and 0 % by the Euglenophyceae. The Chlorophyceae however, contributed a higher percentage to the inshore areas (32 %) compared to offshore areas (23 %; Fig 4.5C). The percentage contribution of the Cyanophyceae was however comparable between the inshore (48 %) offshore (46 %) areas (Fig 4.5C).

4.1.2.2 Community biomass

Lake-wide phytoplankton community biomass for both stratified and mixing periods ranged from 1462.22 mg m⁻³ to 7214.02 mg m⁻³. It was higher and more variable during the stratified period (mean of 5032.42 mg m⁻³, CV = 45.3 %, n =14) compared to the mixing period (4515.84 mg m m⁻³, CV = 31.2 %, n =14; Table 4.1). No obvious offshore-inshore trend was observed in both seasons since the highest and lowest biomasses both occurred at inshore areas (Fig 4.6A).

In the stratified period, the highest biomass occurred at an inshore station of Apewu (7214.02 mg m⁻³) and the lowest at an inshore station of Assisriwa (1462.22 mg m⁻³; Fig 4.6A). During this period the sequence of decreasing dominance of the biomass by phytoplankton groups lake-wide was in the order Cyanophyceae (54.4 %) > Dinophyceae (26 %) > Chlorophyceae (14.2 %) > Cryptophyceae (2.2 %) > Euglenophyceae (1.9 %)> Chrysophyceae (0.9 %) > Bacillariophyceae (0.4 %). The inshore biomass was dominated in the sequence Cyanophyceae (52 %) > Dinophyceae (32 %) > Chlorophyceae (14 %) > Cryptophyceae (2 %) > others (0 %) whiles offshore biomass was dominated in the sequence Cyanophyceae (64 %) > Chlorophyceae (34 %) > Bacillariophyceae /Chrysophytes (1 % respectively) > others (0 %; Fig 4.6B).

In the mixing period, the highest biomass occurred at inshore areas of Abono (6250.66 mg m⁻³) and the lowest again at inshore area of Asisiriwa (2840.63 mg m⁻³;

Fig 4.A). The sequence of decreasing dominance of the community biomass by phytoplankton groups lake-wide was in the order Cyanophyceae (43 %) >Dinophyceae (20 %) > Euglenophyceae (17 %) > Chlorophyceae (9 %) >Cryptophyceae (8 %) > Bacillariophyceae (2 %) > Chrysophyceae (1 %). During this period inshore phytoplankton biomass was dominated in the sequence Cyanophyceae (39 %) > Euglenophyceae (29 %) > Dinophyceae (14 %) > Chlorophyceae (8 %) >Cryptophyceae (7 %) > Bacillariophyceae (2 %) > Chrysophyceae (1 %). In the offshore areas the sequence was in the order Cyanobacteria (38 %) > Dinophyceae (36 %) > Chlorophyceae/Cryptophyceae (8 %) > Euglenophyceae (4 %) >Bacillariophyceae = Chrysophyceae (0 %; Fig 4.6C).


Table 4.1 Means and CVs of lake-wide phytoplankton biomass and some physico-chemical parameters of Lake Bosomtwe during mixing

 and stratified periods

Parameter	Mean Mixing period Stratified period		Coefficient of Variance (%) Mixing period Stratified period		Maximum:minimum biomass Mixing period Stratified period	
Phytoplankton biomass	4515.84	5932.42	31.20	45.30	3.30	7.20
SD depth (m)	1.30	1.60	9.60	6.80	1.02	1.02
Temperature (°C)	27.91	30.10	0.59	0.84	1.20	1.02
Dissolved oxygen (%)	57.30	66.17	11.20	23.70	1.50	1.02
Conductivity (µ E cm ⁻¹)	1275.34	1294.76	3.84	2.30	1.90	1.40





Fig 4.1 Horizontal variation of secchi disc (SD) depth of Lake Bosomtwe (Ghana) in mixing and stratified seasons at one central station and 4 inshore stations.



Fig 4.2 Horizontal variation of water temperature (°C) of Lake Bosomtwe (Ghana) in mixing and stratified seasons at one central station and 4 inshore stations.



Fig 4.3 Horizontal variation of dissolved oxygen (%) of Lake Bosomtwe (Ghana) in mixing and stratified seasons at one central station and 4 inshore stations.



Fig 4.4 Horizontal variation of water conductivity (μ S cm⁻¹) of Lake Bosomtwe (Ghana) in mixing and stratified seasons at one central station and 4 inshore stations.



Fig 4.5 Horizontal variation of total species richness (A), % contribution of phytoplankton groups to the species richness in the stratified (B) and mixing (C) period of Lake Bosomtwe (Ghana) at one central station and 4 inshore stations.



Fig 4.6 Horizontal variation of total phytoplankton biomass (A), % contribution of phytoplankton groups to the phytoplankton biomass in the stratified (B) and mixing (C) period of Lake Bosomtwe at one central station and 4 inshore stations.

4.2 Temporal and seasonal patterns of physico-chemical and biological parameters 4.2.1 Physico-chemical characteristics of the water column (Z_{mix} , Z_{eu} , Z_{mix} : Z_{eu} and total phosphorus)

Temporal trends in Z_{mix} for the 2 years (2004-2006) are depicted in Fig 4.7. Mean Z_{mix} in the 1st year (2004-2005) was 9.90 m, n = 26 and for the 2nd year (2005-2006) it was 9.52 m, n = 25. Mean Z_{mix} were comparable between the two years (Table 4.2) and did not differ significantly in between the two years (t {49} = 0.345, *p*> 0.05; 2-tailed test). Mean Z_{mix} had a CV of 63.9 % in the 1st year whiles in the 2nd year the CV was 34.02 % (Table 4.2). Also, homogeneity of variance test shows that the variability between the 2 years' Z_{mix} did not differ significantly (Levine's statistic, 2-tailed test, p=0.055, df = 2, 49).

Seasonally, mean Z_{mix} differed significantly among seasons (One-way ANOVA, F (2, 24) =15.431, *p*<0.01) in the 1st year being higher during the mixing period (17.7 m, n = 7) and lowest in the restratifying period (6.3 m, n = 6; Fig 4.8A). Mean Z_{mix} differed significantly between mixing and stratified periods (Tukey HSD, p = 5.34 x 10⁻⁵, df = 2, 16) and between mixing and restratifying periods (Tukey HSD, p = 3.3 x 10⁻⁴, df = 2, 11) but not between stratified and restratifying periods (Tukey HSD, p = 0.910, df =2, 17). The variability in Z_{mix} also differed significantly between the 3 seasons (Levine's statistic, F (2, 23) = 5.540, *p*<0.01). In the 2nd year, mean Z_{mix} again differed significantly among the 3 seasons (One-way ANOVA, F (2, 23) = 15.017, *p*<0.01) been higher during the mixing period (13.7 m, n= 6) and lowest in the restratifying period (7.5 m, n = 8; Fig 4.8A). Mean Z_{mix} again differed significantly between mixing and stratified periods (Tukey HSD, $p = 4.12 \times 10^{-4}$, df = 2, 17) and between mixing and restratifying periods (Tukey HSD, $p = 1.13 \times 10^{-4}$, df = 2, 10) but not between stratified and restratifying periods (Tukey HSD, p = 0.910, df = 2, 17).

Temporal trends in the Z_{eu} for the 2 years are depicted in Fig 1.1. Mean Z_{eu} in the 1st year (6.63 m, n = 26) was higher than the 2nd-2005-2006 (4.73 m, n = 25) year-2004-2005 (Table 1.1) and it differed significantly between the 2 years (t {49} = 2.407, p<0.01; 2-tailed test). The mean Z_{eu} varied over 10-fold with a CV of 55.8 % in the 1st year whiles in the 2nd year it varied close to 3-fold with a CV of 32.5 % (Table 4.2).

Seasonally, mean Z_{eu} differed significantly among seasons (One-way ANOVA, F (2, 24) = 7.359, *p*<0.01) in the 1st year (2004-2005) been highest during the stratified period (8.2 m, n =13) and lowest in the restratifying period (2.6 m, n = 6; Fig 4.8B). Mean Z_{eu} differed significantly between stratified and restratifying periods (Tukey HSD, p= 0.003, df = 2, 19) and between mixing and restratifying periods (Tukey HSD, p = 0.029, df = 2, 11) but not between stratified and mixing periods (Tukey HSD, p = 0.987, df = 2, 16). In the 2nd year (2005-2006), mean Z_{eu} did not differ significantly among the 3 seasons (One-way ANOVA, F = (2, 23) = 2.326, *p*> 0.01).

Mean Z_{mix} : Z_{eu} differed significantly between seasons in the 1st year-2004-2005 (One-way ANOVA, F (2, 24) = 5.623, *p* <0.01) being highest during the mixing period (3.2, n = 7) and lowest in the stratified period (1.02, n =13; Fig 4.10A). Only 32.8 % of the variance in the mean Z_{mix} : Z_{eu} can be attributed to the between seasonal variability whiles the remaining 76.6 % represent within seasonal variability. Mean Z_{mix} : Z_{eu} differed significantly only between the stratified and mixing periods (Tukey HSD, p=0.018, df = 2, 16) but not between stratified and restratifying periods (Tukey HSD, p = 0.058, df = 2, 19) and restratifying and mixing periods (Tukey HSD, p = 0.690, df = 2, 11). In the 2nd year (2005-2006), $Z_{mix}:Z_{eu}$ again differed significantly between seasons {One-way ANOVA, F (2, 23)} = 9.038, *p*<0.01) being highest during the mixing period (3.13, n = 6) and lowest in the stratified period (1.67, n = 11; Fig 4.10A). Variance of the mean between the seasons (45.1 %) and within the seasons (54.6 %) was comparable. Mean $Z_{mix}:Z_{eu}$ again differed significantly between the stratified and mixing periods (Tukey HSD, p = 0.001, df = 2, 17) and the mixing and restratifying periods (Tukey HSD, p = 0.556, df = 2, 17).

Temporal trends in the total phosphorus concentration for the two years are depicted in Fig 1.2. Mean total phosphorus in the 1st year-2004-2005 (2.21 μ mol L⁻¹, n = 21) was higher than the 2nd year-2005-2006 (1.91 μ mol L⁻¹, n = 20; Table 4.2) but it did not differ significantly between the two years (t = {49} = 1.706, *p* > 0.05; 2-tailed test). The mean total phosphorus concentration varied over 5-fold with a CV of 24.0 % in the 1st year (2004-2005) whiles in the 2nd year (2005-2006), it varied close to 3-fold with a CV of 30.7 % (Table 4.2). Homogeneity of variance test show that the variability between the 2 years' total phosphorus concentration did not differ significantly (Levine's statistic, 2-tailed test, p = 0.817, df = 2, 39).

Seasonally, mean total phosphorus concentration did not differ significantly among seasons (One-way ANOVA, F (2, 19) = 0.911, p>0.05; Fig 1.1) in the 1st year (2004-2005). In the 2nd year (2005-2006) however, mean total phosphorus concentrations differed significantly among the 3 seasons (One-way ANOVA, F (2, 17)

= 4.999, p<0.01) being highest during the restratifying period (2.27 µmol L⁻¹, n = 7) and lowest in the stratified period (1.61 µmol L⁻¹, n = 9; Fig 4.10B). Only 37 % of the variance in the mean total phosphorus concentration can be attributed to the between seasonal variability whiles the remaining 63 % represent within seasonal variability. Mean total phosphorus concentrations differed significantly between stratified and restratifying periods (Tukey HSD, p =0.015, df = 2, 16) but not between stratified and mixing periods (Tukey HSD, p = 0.509, df = 2, 15) and between mixing and restratifying periods (Tukey HSD, p = 0.293, df = 2, 9).

4.2.2 Biological parameters

4.2.2.1 Phytoplankton biomass and chlorophyll *a*

Temporal trends in the phytoplankton wet weight biomass for the 2 years are shown in Fig 4.9 and Fig 4.11. In the 1st year (2004-2005), during the prolonged stratified periods between November and December and also between March and June, phytoplankton biomass was low (Fig 4.9). During the mixing periods in January, July to August biomass was also low (Fig 4.9). However, in the restratifying period (February, September to October), the biomass is observed to increase and reached the maximum during this period in October. In the 2nd year (2005-2006), the peak biomass observed in October of the 1st year (2004-2005) declined steadily following prolonged stratification up to late December when the lake mixed again (Fig 4.9). As the lake begun to restratify between January and February, the biomass was observed to increase but was low during the prolonged stratification from March to July when the next mixing occurred (Fig 4.9). Again as the lake begins to restratify between September and October, the biomass was observed to increase (Fig 4.9). Mean phytoplankton wet weight biomass in the 2nd year (2262.30 mg m⁻³, n = 25) was higher than the 1st year-2004-2005 (1570.01 mg m⁻³, n = 26; Table 4.2) and differed significantly between the 2 years-2004-2005 (t{49} = 2.52, p<0.01; 2-tailed test). It varied over 15-fold with a CV of 78.9 % in the 1st year (2004-2005) whiles in the 2nd year (2005-2006) it varied close to 3-fold with a CV of 28.4 % (Table 4.2). Homogeneity of variance test show that the variability between the 2 years' phytoplankton wet weight biomass differed significantly (Levine's statistic, 2-tailed test, p = 0.003, df = 2, 49).

Seasonally, mean phytoplankton wet weight biomass did not differ significantly among the seasons (One-way ANOVA, F (2, 24) =1.190, p>0.05; Fig 1.1) in the 1st year (2004-2005). But in the 2nd year (2005-2006), it differed significantly among the 3 seasons (One-way ANOVA, F (2, 23) = 4.944, p<0.01) being highest during the restratifying period (2726.8 mg m⁻³, n = 8) and lowest in the mixing period (1984.1 mg m⁻³, n = 6; Fig 4.12A). Only 31 % of the variance in the mean phytoplankton wet weight biomass could be attributed to the between seasonal variability whiles the remaining 69 % represent within seasonal variability. It differed significantly between stratified and restratifying periods (Tukey HSD, p = 0.026, df = 2, 17), mixing and restratifying periods (Tukey HSD, p = 0.899, df = 2, 10) but not between mixing and stratified periods (Tukey HSD, p = 0.899, df = 2, 17).

Temporal trends in the chlorophyll *a* concentration for the 2 years are shown in Fig 4.9. Generally, higher chlorophyll *a* concentrations were observed during the mixing periods compared to either the stratified or restratifying period of both years. Mean chlorophyll *a* concentration in the 2nd year-2005-2006 (10.90 μ g L⁻¹, n = 21) was higher than that of the 1st year-2004-2005 (7.14 μ g L⁻¹, n = 9; Table 1.2) and it differed

significantly between the 2 years (t {27} = 2.128, p<0.01; 2-tailed test). It varied over 5-fold with a CV of 33.93 % in the 1st year-2004-2005 and over 5-fold in the 2nd year-2004-2005 with a CV of 48.6 % (Table 1.2). Homogeneity of variance test show that the variability between the 2 years' chlorophyll *a* concentration did not differ significantly (Levine's statistic, 2-tailed test, p = 0.097, df = 2, 29).

Seasonally, mean chlorophyll *a* concentration did not differ significantly among seasons (One-way ANOVA, F (2, 8) = 1.20, p>0.05; Fig 1.1) in the 1st year (2004-2005) just like the biomass. But in the 2nd year (2005-2006) however, it differed significantly among the 3 seasons (One-way ANOVA, F (2, 22) = 4.245, p<0.01) being highest during the mixing period (15.4 µg L⁻¹, n = 5) and lowest in the stratified period (8.41 µg L⁻¹, n = 8; Fig 4.12B). Only 32 % of the variance in the mean community respiration could be attributed to the between seasonal variability whiles the remaining 68 % represent within seasonal variability. It differed significantly between stratified and mixing periods (Tukey HSD, p = 0.206, df = 2, 13), but not between mixing and restratifying periods (Tukey HSD, p = 0.405, df = 2, 9) or stratified and restratifying periods (Tukey HSD, p = 0.315, df = 2, 14).

4.2.2.2 Phytoplankton community species composition and biomass

Temporally, the phytoplankton biomass was dominated by the Cyanophyceae almost year round and together with the Dinophyceae and the Chlorophyceae constitutes the bulk of the biomass (Fig 4.11). These 3 groups constituted 94 % respectively of the biomass in both the 1st (2004-2005) and 2nd (2005-2006) years respectively (Fig 4.13A & B). The other groups (Bacillariophyceae, Cryptophyceae, Euglenophyceae, and Chrysophyceae) together constitute the remaining 6 % of the biomass in each year (Fig

4.13A & B). The Bacillariophyceae and the Cryptophyceae were observed to be relatively prominent in the phytoplankton biomass in the mixing periods throughout the study period as in the horizontal study (Fig 4.11).

A total of 75 phytoplankton species in seven major groups were identified. The qualitative composition of the algal flora (Appendix 2A) and their occurrence (Appendix 2B & C) indicate that the over all sequence of dominance of the species richness during the entire temporal study is in the order; Chlorophyceae > Cyanobacteria > Bacillariophyceae > Cryptophyceae = Chrysophyceae = Euglenophyceae. The Chlorophyceae with the highest number of taxa (28) represented 37.3 % of total taxa with *Tetraedron* Kuetzing as the genus with the highest number of species among the group (3 species). The Cyanophyceae with the 2^{nd} highest number of taxa (23) represented 30.7 % of total taxa with *Chroococcus* Naegeli as the genus with the highest number of species among the group (3). The Baccillaryophyceae (9 species) and Dinophyceae (6 species) represented 12 % and 8 % of total taxa respectively. The Cryptophyceae, Chrysophyceae and the Euglenophyceae had 3 species each and together constituted 12 % of the total species richness.

In the 1st year (2004-2005), 70 species were observed of which 25 belonged to the Chlorophyceae (representing 35.7 % of total taxa,) 22 were Cyanophyceae (representing 31.4 %), 6 were Dinophyceae (representing 8.6 %), 8 were Bacillariophyceae (representing 11.4 %), and the Cryptophyceae, Euglenophyceae and Chrysophyceae had 3 species each respectively and together represented about 12.9 % of total taxa (Fig 4.14A). Common species i.e species that were frequently encountered in the phytoplankton throughout the sampling period included *Cosmarium leave, C. moniliforme, Tetraedron minimum, T. triangulare, Monoraphidium spiculiforme, M.* *irregulare* (Chlorophyceae), Anabaenopsis tanganyikae, Aphanizomenon spp, Cylindrospermopsis helicoidea, C. rasciborskii, Pseudoanabaena catenata, Microcystis rosea, M. subtillissima, Merismopedia cf punctata, Synechocystis aquatilis, Chroococcus disperses, C. minimus (Cyanophyceae); Peridinium elpatiewskyi (Dinophyceae), Cryptomonas erosa, C. marsonii (Cryptophyceae), and Nitzschia recta (Baccilariophyceae; Appendix 2B).

In the 2nd year (2005-2006), a total of 67 species occurred, 26 of which belonged to the Chlorophyceae (representing 38.8 %), 19 Cyanophyceae (representing 28.4 %), 7 Bacillariophyceae (representing 10.4 %), 6 Dinophyceae (representing 9 %), and 3 each of Cryptophyceae, Euglenophyceae and Chrysophyceae together representing about 13.5 % of total taxa during this period (Fig 4.14B). Common species were the same as was observed in the 1st year with the exception that some species, notably *Closterium acuatum* (Chlorophyceae); *Glenodinium* spp, *Gymnodinium* cf *uberimuum* and *Peridinopsis* spp (Dinophyceae), occurred frequently as well (Appendix 2C).

In both years, the Chlorophyceae were the richest group in terms of number of species. The 1^{st} year (2004-2005) was, however richer in species composition than the 2^{nd} year-2005-2006 (Appendix 2B & C). The highest species richness always occurred during the restratifying period for both years. In the 1^{st} year (2004-2005), the highest species richness for any one particular period was 46 and occurred in September whiles in the 2^{nd} year (2005-2006) it was 50 and occurred in October. Species richness however seems to be equally distributed in the stratified and mixing periods in both years.

4.2.3 Relationship between physico-chemical and biological parameters

Phytoplankton biomass and Z_{mix} had a significant negative relationship (p < 0.01, $r^2 = 10.34$ %, n = 51, simple linear regression; Fig 4.15A) whiles chlorophyll *a* and Z_{mix} had a positive relationship which was not however significant (p > 0.05, $r^2 = 1.45$ %, n = 31, simple linear regression; Fig 4.15B).

Phytoplankton biomass and Z_{eu} had a significant negative relationship (p< 0.01, $r^2 = 6.32$ %, n = 51, simple linear regression; Fig 4.16A). Chlorophyll *a* also had a significant negative relationship with Z_{eu} but with a relatively higher coefficient of determination (p < 0.01, $r^2 = 25.33$ %, n = 31, simple linear regression; Fig 4.16B).

No definite relationship was found between phytoplankton biomass and $Z_{mix}:Z_{eu}$ (p> 0.05, $r^2 = 0.009$ %, n = 51, simple linear regression; Fig 4.17A) but chlorophyll *a* had a strong positive relationship $Z_{mix}:Z_{eu}$ (p< 0.01, $r^2 = 54.5$ %, n = 31, simple linear regression; Fig 4.17B).

Again, no definite relationship was found between phytoplankton biomass and total phosphorus concentrations (p > 0.05, $r^2 = 1.13$ %, n = 51, simple linear regression; Fig 4.18A) but the relationship between chlorophyll *a* concentrations and total phosphorus concentration was positive and significant (p < 0.01, $r^2 = 8.02$ %, n = 31, simple linear regression; Fig 4.18B).

Phytoplankton biomass and chlorophyll *a* concentration had a positive and significant relationship but with a low coefficient of determination (p < 0.01, $r^2 = 8.3$ %, n = 31, simple linear regression; Fig 4.19).

Table 4.2 Means and	coefficient	of variance	for physic	co-chemical	limnological
	countratin	or variance	ior physic	co chemical	miniorosicui

Mea	n	Coeffic variar	Coefficient of variance (%)		Maximum:minimum ratio	
n = 26	n = 25					
2004-2005	2005-2006	2004-2005	2005-2006	2004-2005	2004-2006	
1.75	1.56	55.80	32.50	3.25	3.25	
6.63	4.73	55.80	32.50	10.30	3.90	
0.80	0.86	69.10	30.05	10.25	2.96	
9.90	9.95	63.94	70.40	15.00	3.40	
io 1.94	2.10	86.70	35.60	21.7	3.60	
2.21^{\dagger}	1.91+	24.00	30.71	5.30	2.80	
			1	1		
	Mea n = 26 2004-2005 1.75 6.63 0.80 9.90 to 1.94 2.21 [†]	Mean $n = 26$ $n = 25$ 2004-2005 2005-2006 1.75 1.56 6.63 4.73 0.80 0.86 9.90 9.95 io 1.94 2.10 2.21 [†] 1.91 ⁺	Mean Coeffic variar $n = 26$ $n = 25$ 2004-2005 2005-2006 2004-2005 1.75 1.56 55.80 6.63 4.73 55.80 0.80 0.86 69.10 9.90 9.95 63.94 io 1.94 2.10 86.70 2.21 ⁺ 1.91 ⁺ 24.00	Mean Coefficient of variance (%) $n = 26$ $n = 25$ 2004-2005 2005-2006 2004-2005 2005-2006 1.75 1.56 55.80 32.50 6.63 4.73 55.80 32.50 0.80 0.86 69.10 30.05 9.90 9.95 63.94 70.40 io 1.94 2.10 86.70 35.60 2.21 ⁺ 1.91 ⁺ 24.00 30.71	MeanCoefficient of variance (%)Maximum: ratio $n = 26$ $n = 25$ $2004-2005$ $2005-2006$ $2004-2005$ $2005-2006$ $2004-2005$ 1.75 1.56 55.80 32.50 3.25 6.63 4.73 55.80 32.50 10.30 0.80 0.86 69.10 30.05 10.25 9.90 9.95 63.94 70.40 15.00 10 1.94 2.10 86.70 35.60 21.7 2.21^{\dagger} 1.91^{+} 24.00 30.71 5.30	

variables of Lake Bosomtwe (Ghana) from 2004 to 2006

Table 4.3 Means and coefficient of variances for biological parameters of Lake Bosomtwe (Ghana) from 2004 to 2006.

Parameter	Mean		Coefficient of variance (%)		Maximum:minimum ratio	
	n = 26	n = 25		1 .59	/	
	2004-2005	2005-2006	2004-2005	2005-2006	2004-2005	2004-2006
$\mathbf{P}_{\mathbf{B}} \;(\mathrm{mg}\;\mathrm{m}^{-3})$	1570.01	2262.30	78.87	28.42	15.11	2.81
Chl a (µg L ⁻¹) 7.10*	10.90"	36.13	48.56	8.60	9.26

" \longrightarrow N=21 * \longrightarrow N=10



SP=Stratified periods, MP=Mixing periods, RP= Restratifying periods

Fig 4.7 Temporal variation of mixing depth (Z_{mix}) and euphotic depth (Z_{eu}) of Lake Bosomtwe (Ghana) from November 2004 to October 2006.





Fig. 4.8 Seasonal variation of Z_{eu} (A) and Z_{mix} (B) of Lake Bosomtwe (Ghana) during the 1st (2004-2005) and 2nd (2005-2006) years for three seasons.



SP=Stratified periods, MP=Mixing periods, RP= Restratifying periods

Fig 4.9 Temporal variation of phytoplankton biomass, Chlorophyll *a* and total phosphorus concentrations of Lake Bosomtwe (Ghana) between November 2004 to October 2006.





Fig. 4.10 Seasonal variation of Z_{mix} : Z_{eu} (A) and Total phosphorus (B) of Lake Bosomtwe (Ghana) in the 1st (2004-2005) and 2nd (2005-2006) years respectively for three seasons.



SP=Stratified periods, **MP=Mixing** periods, **RP=** Restratifying periods

Fig 4.11 Temporal variation of phytoplankton biomass showing the contribution of the different groups of phytoplankton in

Lake Bosomtwe (Ghana) from November 2004 to October 2006.



Fig. 4.12 Mean phytoplankton wet weight biomass (A) and Chlorophyll a (B) of L. Bosomtwe (Ghana) in 1st (2004-2005) and 2nd (2005-2006) years during stratified, mixing and restratifying periods for three seasons.



Fig 4.13 % Contribution of phytoplankton groups to wet weight biomass of Lake Bosomtwe (Ghana) in 1st-2004-2005 (A) and 2nd-2005-2006 (B) years respectively.





Fig 4.14 % Contribution of phytoplankton groups to the total species richness of Lake Bosomtwe (Ghana) in 1^{st} -2004-2005 (A) and 2^{nd} -2005-2006 (B) years respectively.



Fig 4.15 Regression of phytoplankton biomass (A) and Chlorophyll a (B) versus Z_{mix} of Lake Bosomtwe (Ghana) from November 2004 to October 2006 (Simple regression).



Fig 4.16 Regression of phytoplankton biomass (A) and Chlorophyll a (B) versus Z_{eu} of Lake Bosomtwe (Ghana) from November 2004 to October 2006 (Simple regression).



Fig 4.17 Regression of phytoplankton biomass (A) and Chlorophyll a (B) versus $Z_{mix}:Z_{eu}$ of Lake Bosomtwe (Ghana) from November 2004 to October 2006 (Simple regression).



Fig 4.18 Regression of phytoplankton biomass (A) and Chlorophyll *a* (B) versus total phosphorus concentration of Lake Bosomtwe (Ghana) from November 2004 to October 2006 (Simple regression).



Fig 4.19 Regression of Chlorophyll *a* versus phytoplankton biomass of Lake Bosomtwe (Ghana) from November 2004 to October 2006 (Simple regression).



4.3 Phytoplankton primary productivity

4.3.1 Temporal trends and variability in the primary productivity

Temporal trends in the gross productivity (P_G), community respiration (R_C) and net productivity (P_N) showed that generally as the gross productivity increased, community respiration also increased whiles net productivity decreased (Fig 4.20). Mean areal gross P_G ranged from a minimum of 1.22 during the restratifying period in October (2005) to a maximum of 7.68 gCm⁻²d⁻¹ during the stratified period in April (2006) respectively with a mean of 4.73 gCm⁻²d⁻¹ while mean areal R_C in the Z_{eu} (i.e. the euphotic depth) was 4.34 gCm⁻²d⁻¹ representing 90 % of the P_G during the period (n = 25; Table 4.4). This resulted in a P_G:R_C ratio of 1.10 implying net positive autotrophy within the Z_{eu} of the lake with the proportion of P_G available for assimilation (P_N:P_G) constituting just 10 % (Table 4.4). Mean growth rate during the period was respectively 0.13 d⁻¹ (n = 21) while mean phytoplankton carbon biomass was 1.92 gCm⁻² (Table 4.4). The Z_{mix} was net heterotrophic with P_G:R_C of 0.51 and a growth rate of 0.100 d⁻¹ (n = 9; Table 4.5).

The variability in the areal P_G was high (maximum:minimum ratio of over 6-fold and a CV of 33.1 %, n = 25) but the variability in the areal R_C and the phytoplankton P_N in the Z_{eu} were over twice and 18 times that of the P_G (Table 4.4) indicating a considerably high degree of intra-annual variability in the P_G . It also indicates very high intra-annual variability in the R_C and the assimilable photosynthate or P_N respectively. The variability in the growth rate in the Z_{eu} was equally high (CV of 62.0 %, n = 21) compared to the P_G and P_B (Table 4.5).

4.3.2 Seasonal trends in the primary productivity

Seasonally, mean P_G differed significantly among seasons (One-Way ANOVA, F (2, 22) = 4.638, p<0.01) being highest during the mixing period (5.75 gCm⁻²d⁻¹, n = 6) and lowest in the restratifying period (3.59 gCm⁻²d⁻¹, n = 8; Fig 4.21A). Only 29.7 % of the variance in the mean P_G can be attributed to the between seasonal variability whiles the remaining 70.3 % represent within seasonal variability. Mean P_G differed significantly only between the mixing period and the restratifying period (Tukey HSD, p = 0.021, df = 2, 12) but not between the stratified period and mixing periods (Tukey HSD, p = 0.518, df = 2, 15) and between the stratified and restratifying period (Tukey HSD, p = 0.095, df = 2, 17).

Community respiration (R_C) in the Z_{eu} also differed significantly among seasons (One-Way ANOVA, F (2, 22) = 4.704, p<0.01) and was highest in the stratified period (5.80 gCm⁻²d⁻¹, n = 11) and lowest in the restratifying period (2.30 gCm⁻²d⁻¹, n = 8; Fig 4.21B). Only 30 % of the variance in the mean community respiration can be attributed to the between seasonal variability whiles the remaining 70 % represent within seasonal variability. Mean community respiration differed significantly only between the stratified and the restratifying periods (Tukey HSD, p = 0.015, df = 2, 17) but not between the stratified and mixing periods (Tukey HSD, p = 0.263, df = 2, 12).

The assimilable photosynthate (ratio of $P_N:P_G$) in the Z_{eu} also differed significantly among seasons (One-Way ANOVA, F(2, 22) = 4.147, *p*<0.01) and was highest in the restratifying period (0.35, n = 8) and lowest (negative) in the stratified period (-0.17, n = 11; Fig 4.22A). Only 23.4 % of the variance in the mean assimilable

photosynthate can be attributed to the between seasonal variability whiles the remaining 76.6 % represent within seasonal variability. Mean assimilable photosynthate differed significantly only between the stratified and the restratifying periods (Tukey HSD, p = 0.030, df = 2, 17) but not between the stratified and mixing periods (Tukey HSD, p = 0.177, df = 2, 15) and between the mixing and restratifying periods (Tukey HSD, p = 0.808, df = 2, 12).

Mean growth rate in the Z_{eu} was highest in the restratifying period (0.14 d⁻¹, n = 8) and lowest in the mixing period (0.12 d⁻¹, n = 6; Fig 4.22B). However, it did not differ significantly between seasons (One-Way ANOVA, F (2, 18) = 0.086, p>0.05) and only close to 1 % of the variance in the mean growth rate can be attributed to variability between the seasons whiles the remaining 99 % represent variability within the seasons.

4.3.3 Relationships with physico-chemical variables

P_G had a significant positive relationship with both Z_{mix} (p < 0.01, $r^2 = 9.7$ %, n = 25) and Z_{eu} (p < 0.01, $r^2 = 6.6$ %, n= 25), simple linear regression; Fig 4.23A & B).

No definite relationship between P_G and the Z_{mix} : Z_{eu} ratio was found (p > 0.05, $r^2 = 0.12$ %, n = 25, simple linear regression) except that the P_G seem to concentrate below a ratio of 5 (Fig 4.24A). There was also no definite relationship between P_G and total phosphorus concentration (p > 0.05, $r^2 = 0.001$ %, n = 25, simple linear regression; Fig 4.24B).

A significant negative relationship between the wet weight biomass (P_B) and P_G was found (p<0.01, r² = 26.5 %, n = 25, simple linear regression; Fig 4.25A) but chlorophyll *a* and P_G were significantly positively related (p < 0.01, $r^2 = 5.2$ %, n = 25, simple linear regression; Fig 4.25B).

 R_C and P_G were significantly positively related (p < 0.01, $r^2 = 30.6$ %, n = 25; Fig 4.26A) whiles P_N does not seem to have any definite relationship with P_G (p>0.05, $r^2 = 0.008$ %, n = 25, simple linear regression; Fig 4.25B).

Also, growth rate is significantly positively related to P_G (p < 0.01, $r^2 = 26.5$ %, n = 21, simple linear regression; Fig; Fig 4.27).



Parameter	Mean	Standard deviation	Coefficient of variance (%)	Max:min	
Zeu (m)	4.10	0.91	22.40	2.40	
Zmix (m)	9.30	3.47	37.40	4.25	
Zmix:Zeu ratio	2.3	0.68	29.80	2.90	
TP (μ mol L ⁻¹) [†]	1.84	0.49	26.43	2.80	

Table 4.4 Means, standard deviations, coefficient of variances and maximum tominimum ratios for physico-chemical parameters

 $^{\dagger} \longrightarrow n = 20$

 Table 4.5 Means, standard deviations, coefficient of variances and maximum to

 minimum ratios for biological parameters.

Parameter	Mean (n =25)	Coefficient of variance (%)	Max:min
Z _{eu} estimates		100	
$P_{G}(gC m^{-2}d^{-1})$	4.73	33.10	6.30
P_N in Zeu (gC m ⁻² d ⁻¹)	0.38	333	-
R_C in Zeu (gC m ⁻² d ⁻¹)	4.34	64.00	17.60
P _B in Zmix (g m ⁻³)	2.26	38.20	3.60
Chlorophyll <i>a</i> (μ g L ⁻¹) in Zmix	10.61	53.90	5.30
Growth rate in Zeu (day ⁻¹)	0.13*	62.00	-
P _N :P _G in Zeu	0.10	S alon	-
R _C :P _G in Zeu	0.90	49.70	-
Z _{mix} estimates			
$P_{\rm N}$ in Zmix (gC m ⁻² d ⁻¹)	-4.52	-	-
$R_C in Zmix (gC m^{-2}d^{-1})$	9.24	63.50	-
Growth rate in Zmix (day ⁻¹)	0.10+	71.90	-
P _N :P _G in Zmix	-0.92	-	-
R _C :P _G Zmix	1.92	43.20	-
	+		

* **—** n = 21

 \rightarrow n = 9



Fig 4.20 Temporal variation of gross productivity, community respiration and net productivity of Lake Bosomtwe (Ghana) from September 2005 to August 2006.



Fig 4.21 Seasonal variation of the Areal gross primary productivity (A) and Community respiration (B) of Lake Bosomtwe (Ghana) for three seasons.



Fig 4.22 Seasonal variation of the $P_N:P_G$ ratio (A) and growth rate (B) in Z_{mix} of Lake Bosomtwe (Ghana) from September (2005) to August (2006) for three seasons.


Fig 4.23 Regression of gross productivity versus Z_{mix} (A) and Z_{eu} (B) of Lake Bosomtwe (Ghana) from September (2005) to August (2006).



Fig 4.24 Regression of gross productivity versus Z_{mix} : Z_{eu} (A) and Total phosphorus (B) of Lake Bosomtwe (Ghana) from September (2005) to August (2006).



Fig 4.25 Regression of wet weight biomass versus gross productivity (A) and Chlorophyll *a* versus gross productivity (B) of Lake Bosomtwe (Ghana) from September (2005) to August (2006).



Fig 4.26 Regression of community respiration versus gross productivity (A) and net productivity versus gross productivity (B) of Lake Bosomtwe (Ghana) from September (2005) to August (2006).



Fig 4.27 Regression of growth rates in the Z_{eu} versus gross productivity of Lake

Bosomtwe (Ghana) from September (2005) to August (2006).



CHAPTER FIVE

DISCUSSIONS

5.1 Horizontal variability

5.1.1 Physicochemical parameters

The range in the horizontal Secchi Disc (SD) transparency of Lake Bosomtwe (1.1 to 1.6 m; values up to 2.6 m) recorded during temporal studies in a stratified period at the central station during this study are in agreement with that of Karikari & Bosque-Hamilton's (2004). According to Reynolds (2006), it falls in the category of turbid lakes. Documented records of SD depths span a wide range from 0.2 to 77 m (Berman *et al.*, 1985) and are adequate to separate clear (SD depth \geq 10 m) waters from turbid ones (SD \leq 3 m; Reynolds, 2006). The variability of the SD depth for both seasons lake-wide is low (below a CV of 10 %). The observed increase in the SD transparencies during the stratified compared to the mixing period may be attributed to reduced nutrient input into the lake and probable increased zooplankton grazing of the phytoplankton (Tilzer, 1988). Also, the lower SD transparencies observed in inshore areas compared to the offshore station may be a result of the shallower depths (Table 4.1) that probably makes frequent contact with the sediments possible and thus increase the concentration of suspended particles that then leads to a lower water transparency.

The lake-wide range in temperature (27.6 to 30.4 °C) put it in the category of tropical lakes which are generally considered to be more productive than most temperate lakes (Hutchinson, 1967). Karikari & Bosque-Hamilton (2004) observed a similar range between 28.1 to 30.3 °C from several inshore stations. One of the factors that have been used to explain higher productivities of tropical lakes is the constant high temperatures which are believed to speed up primary productivity (Beadle, 1981; Kalff, 2002). But according to Beadle (1981), this higher temperature

that stimulates higher productivity in tropical lakes also stimulates all other processes in the metabolic cycle including respiration. Thus although gross productivities in the lake may be high, the net productivity may not necessarily be high which in turn may adversely affect the growth rate and therefore the biomass the phytoplankton are able to accumulate (Hecky & Fee, 1981). The variability of temperature lake-wide is very low (CVs of less than 1 %) implying uniformity of surface temperature of the lake.

Dissolved oxygen (%) in surface waters of the lake ranged from 49.82 % (about 3.8 mg L^{-1}) to 80.37 % (about 6.1 mg L^{-1}). This is within the range measured for several inshore areas of the lake by Karikari & Bosque-Hamilton (2004) which varied between 3.7 mg L^{-1} to 8.8 mg L^{-1} . Even for non-salmonid fishes, this range may imply some considerable impairment from early life to adult stages of their development (APHA, 1998). Fish are known to require at least 5 mg L⁻¹ of oxygen and below 3 mg L^{-1} , many of them cannot survive (Sverdrup & Armsbrust, 2008). However, the cichlids which dominate the fish species of the lake are known to be more tolerant of hypoxic conditions in lakes and streams and this tolerance is believed to contribute to the richness of habitats they occupy (Melnychuk & Chapman, 2002). This observation may explain in part the low fish species diversity and productivity in Lake Bosomtwe that consists perhaps exclusively of cichlids (Poste et al., 2008). The intense fishing pressure and anthropogenic encroachment of stream paths may also be contributing to this observation. Generally, the CVs of dissolved oxygen were low but the CV of the stratified period was higher than that of the stratified period. This may be due to the likely uneven distribution of the phytoplankton in the stratified compared to the mixing period.

Even though cold water is known to hold more oxygen than warm ones (Wetzel & Likens, 1979), higher mean dissolved oxygen concentrations occurred in

99

the stratified season when surface waters were warmer compared to the mixing season. This may be partly attributed to the higher light availability and mean biomass of phytoplankton observed during the stratified period when the light conditions within the water column were more favourable for photosynthetic complementation of the dissolved oxygen in surface waters (Reynolds, 2006). The occurrence of highest dissolved oxygen at an inshore station during the stratified period may be due to the high biomasses of phytoplankton observed at such places probably as a result of better nutrient availability compared to the offshore areas (Heaney, 1976). Another reason may be the shallow nature of inshore areas making them susceptible to wind stirring and therefore creating more surface area for oxygen diffusion.

Conductivities measured by Karikari & Bosque-Hamilton (2004) at several inshore stations and at the middle station that ranged from 1180 to 1256 μ S cm⁻¹ are in agreement with the lake-wide measurements during this study (1106.4 to 1312.88 μ S cm⁻¹) though the range is slightly higher in this study. The variability was low for both seasons (less than 4 % in each season; Fig 4.4). According to Goltermann (1975), the electrical conductivity of a water body is roughly proportional to the concentrations of its dissolved major ions and varies widely from about 10 to 10,000 μ S cm⁻¹. Among freshwaters however, the range is usually between 10 to 1000 μ S cm⁻¹ but may exceed 1000 (Chapman, 1992). Lake Bosomtwe is believed to have a low conductivity for a close basin lake of over a million years (even though its conductivity is over 13 times higher than oligotrophic lakes Superior and Tahoe-Michaud, 1991). This is because closed-basin lakes tend to accumulate solutes over time (Turner *et al.*, 1996b) since evaporation, the major source of water loss from the lake tends to concentrate the dissolved salts over time. However, the low catchment

to lake area ratio may also explain in part the relatively low conductivity of the lake (Michaud, 1991). Studies of inland freshwaters indicate that water bodies supporting good mixed fisheries have conductivities of between 150 to 500 μ S cm⁻¹ (APHA, 1998). The high conductivity of lake Bosomtwe may therefore also give some clue to the low species diversity of fish species in the lake as water bodies outside this range may indicate the unsuitability of it for certain species of fishes (APHA, 1998). The generally higher conductivities during the stratified period may be attributed to the higher temperatures and evaporation rates compared to the mixing period (Puchniak *et al.*, 2009; Michaud, 1991). The higher evaporation rates tend to reduce the lake water levels and concentrate dissolved solutes in a lesser volume of lake water. The conductivities appear to be horizontally homogenous as there was no clear inshore-offshore relationship.

5.1.2 Community species composition and biomass

Kalff (2002) have observed that in any normal study of a water body between 70 to 200 species of phytoplankton may be found and long term studies in temperate lakes can reveal as much as over 400 species. However in the tropics this number is expected to be low even in the long term. Despite this, several studies in some tropical lakes have revealed that species richness can range from as low as less than 10 in some saline lakes such as Elmenteita to as high as over 900 in some oligotrophic ones such as Tanganyika (Kalff & Watson, 1986; Cocquyt *et al.*, 1993). Thus, even though the 56 species found during this study is low, it is fairly within the range of total species richness found for several tropical lakes in Africa (Kalff & Watson, 1986; Kebede & Belay, 1994). One reason for this low species richness may be due to the fact that the sampling was restricted to only 2 periods in an annual cycle and also the limitation of the sampling to one depth.

The dominance of the total taxa by the Chlorophyceae is also a common feature in several tropical lakes (Kalff & Watson, 1986; Kebede & Belay, 1994). However, the Cyanophyceae species dominated most of the stations during the stratified and the mixing seasons and the higher percentage of the chlorophyte taxa is only real when the total numbers of species of all seasons are put together. The reason for the dominance of the total species richness in tropical lakes by the Chlorophyceae has been attributed to their tolerance of the high light intensities found in the surface waters of tropical lakes but they share this characteristic with the Cyanophyceae and Dinophyceae (Paerl, 1996; Sterner, 1989).

The lake-wide mean phytoplankton biomasses observed in the stratified and mixing periods are also within the range observed in several tropical and other lakes in temperate climates during the summer from the most oligotrophic i.e. about 100 mg m⁻³) to the most eutrophic i.e. about 100,000 mg m⁻³ (Kalff & Knoechel, 1978). This range may be exceeded in some lakes. For instance, in a Kenyan reservoir, Kotut *et al* (1998) observed as much as 3,360,850 mg m⁻³ of phytoplankton biomass which is over 33 times the maximum value within this range. Also the mean biomass of Lake Bosomtwe's phytoplankton compared to some closed basin lakes in East Africa show that it is low. In these lakes phytoplankton biomass were found to range from 6000 to 43000 mg m⁻³ (Kalff & Watson, 1986). However, its biomass is similar to that of other tropical lakes such as Lanao (1600 mg m⁻³) and Kivu (2100 mg m⁻³; Lewis, 1978; Sarmento *et al.*, 2006).

The higher mean biomass in the stratified period compared to the mixing period may be related to the nature of the groups that dominate the biomass namely,

102

the Cyanophyceae and the Dinophyceae which contributed over 80 % to the stratified period biomass and 64 % to the mixing period biomass (Fig 4.6B & C). These 2 groups are favoured in lakes with prolonged stratification like Lake Bosomtwe (Puchniak et al., 2009) which most times lead to reduced nutrient availability (Paerl, 1996) even though the Cyanophyceae are also known to have considerable biomasses in nutrient rich waters (Jensen et al., 1994). In nutrient deficient environments, the ability of these 2 groups to move between the light and nutrient fields to acquire essential nutrients needed for their metabolic activities enable them to out-compete other phytoplankton groups (Lewis, 1978; Paerl, 1996). For instance, Cyanophyceae and Dinophyceae are known to reveal dramatic vertical migrations speeds that range from 2 to over 140 m day⁻¹ in stratified waters (Reynolds & Walsby, 1975). Also, some Cyanophyceae such as the heterocyst-bearing filamentous forms which are abundant in the lake, in addition to their ability to regulate their position in the water column, are also able to fix nitrogen giving them a further advantage in stratified waters where bioavailable nitrogen (nitrates, nitrites and ammonia) are lost through denitrification to N_2 (g) at the oxic-anoxic interface of the water column (Seitzinger, 1988). On the other hand, the Dinophyceae are mixotrophic and are able to resort to phagotrophic feeding such as bactivory when nutrients or light become limiting (Graham & Wilcox, 2000). While the Cryptophyceae also possess the advantage of motility and phagotrophy, the selective preference of grazing zooplankton for the them because of their superior food qualities such us being unicellular, wall-less, readily ingested and digested, their lack of toxins and containing several essential fatty acids (Carpenter et al., 1987; Paerl, 1996; Graham & Wilcox, 2000), seem to keep their biomass down in Lake Bosomtwe during the horizontal study.

The high percentage contribution of the Euglenophyceae to the biomass in the mixing season is notable. This was due to their higher biomasses in the inshore stations during this period. The Euglenophyceae are usually abundant in shallow eutrophic lakes and thrive in waters enriched with organic matter (Hutchinson, 1967) where they often co-dominate with the Chlorophyceae (Kalff, 2002) but are known to make negligible contribution to the phytoplankton biomass of relatively deep stratifying lakes (Jensen *et al.*, 1994) such as Lake Bosomtwe as confirmed in this study. Also, in Lake Bosomtwe, genera like *Euglena* Ehrenberg, *Trachelomonas* Ehrenberg and *Phacus* Dujardin, indicative of organic pollution (Palmer, 1969; 1980), occur in inshore areas of Apewu and Dompah and may indicate higher anthropogenic activities compared to Asisiriwa which is uninhabited and where these species are not found. According to de Oliveira and Calheiros (2000), the Euglenophyceae are mostly littoral forms and are swept into pelagial zones during storms. The concentration of this group in the inshore areas of Lake Bosomtwe therefore gives some credence to this assertion.

The higher percentage of the Baccillariophyceae and the Cryptophyceae to the biomass in the mixing compared to the stratified period is a familiar phenomenon in several lakes (Lewis, 1978; Kalff & Watson, 1986). For the Baccillariophyceae, this may be attributed to the probable higher percentage of silica concentrations during mixing periods compared to stratified periods (Ferguson & Harper, 1982; Nixdorf, 1994) and also the greater turbulence of the water column that they need in order to stay suspended in the water column (Kalff *et al.*, 1975) since they, unlike the buoyancy regulating Cyanophyceae and the flagellated Dinophyceae and Cryptophyceae, cannot regulate their position in the water column. Also their silica cell walls make them even heavier, and therefore put them at a disadvantage in

stratified lakes (Ferguson & Harper, 1982; Nixdorf, 1994) such as Lake Bosomtwe (Puchniak *et al.*, 2009). Willen (1991) & Reynolds (1972) also indicate that the Baccillariophyceae are good competitors at low light conditions and are therefore favoured during mixing periods when most other phytoplankton are limited by low light water climates. The higher representation of pennate Baccillariophyceae compared to the centric ones in the lake may be due to their morphology which helps reduce sinking (Graham & Wilcox, 2000; Morabito *et al.*, 2007). They are also better competitors for silica at low silica concentrations (Tilman *et al.*, 1976) since silica levels may be low in the lake because of the high temperatures (and strong thermal stratification) and has an alkaline nature (basic pH) which tends to pull the available silica into the deep anoxic layer (Willen, 1991; Puchniak *et al.*, 2009).

For the Cryptophyceae, the higher percentage contribution to the biomass in the mixing period relative to the stratified period observed in Lake Bosomtwe may be attributed to the probable low zooplankton grazing during mixing (Lewis, 1978; Carpenter *et al.*, 1987; Kalff, 2002). During mixing periods, the high turbulence of the lake waters dilute the biomass and also restrict zooplankton grazing pressure on the more edible phytoplankton like the Cryptophyceae.

Chrysophyceae which formed just 2 % of the taxa and 2 % respectively of the biomass of both stratified and mixing seasons are usually associated with oligotrophic lakes (Hecky & Kling, 1981; Kalff & Watson, 1986; Sandgren, 1988; Jensen *et al.*, 1994) and cold waters (Taylor *et al.*, 1979). Also at pH levels found in Lake Bosomtwe, most of the carbon is likely to be in the bicarbonate form which the Chrysophyceae are unable to use and they also lack any known carbon concentrating mechanism (Puchniak *et al.*, 2009; Reynolds, 2006). Moreover, the Chrysophyceae are also known to prefer waters with specific conductivities less than 50 μ S cm⁻¹

(Sandgren, 1988). Conductivities in Lake Bosomtwe surface waters averages between over 1256 μ Sm⁻¹ (Karikari & Bosque-Hamilton, 2004) and 1294.8 μ S cm⁻¹. These observations in the conductivities of the lake are over 25 fold greater than the supposed preference of the Chrysophyceae and may be potentially affecting them negatively both in taxa and biomass contribution in the lake. Furthermore, the Chrysophyceae are known to prefer low phosphorus levels and total phosphorus levels greater than 20 μ g L⁻¹ is believed to be toxic to them. The mean total phosphorus concentrations observed in Lake Bosomtwe appear quite high and is characteristic of eutrophic lakes (Karikari & Bosque-Hamilton, 2004) and may be partly responsible for the low representation of the Chrysophyceae in the lake.

Lake-wide variabilities of the biomass in both the stratified and mixing periods of over 30 % are high (Melack, 1979) for a small lake like Bosomtwe but according to Welch, (1952), a well established fact concerning the horizontal distribution of phytoplankton is its irregularity or lack of uniformity when any area of fair size is considered (Reynolds, 2006). Welch (1952) and George & Heaney (1978) divide the factors that affect horizontal distribution of phytoplankton into those that produce local changes in the rate of population increase or decrease (e.g. grazing, nutrient and temperature differences) and those bringing about spatial redistribution of the population (e.g. wind induced water movements, currents and undertow currents, indirect results of diurnal migration of certain phytoplankters) and a combination of these factors may be responsible for these high variabilities. The higher variability in the lake-wide mean biomass of the phytoplankton of Lake Bosomtwe in the stratified season may in part be attributed to probable higher grazing pressure as a result of the probable selective grazing of the more edible, quality phytoplankton (Carpenter *et al.*, 1987). Zooplankton biomass are known to be high

during stratified periods of lakes due to reduce turbulence which enable them more scope to use their higher motility advantage compared to the phytoplankton, to move to areas where the phytoplankton are concentrated and graze on them (Reynolds, 2006). The limitation of sampling to just one depth at all stations may also have introduced additional variability in the biomass estimates since it is possible to miss some species or group of species that may be concentrated at certain depths that were not sampled especially in the stratified period. This is even more likely since the Cyanophyceae and the Dinophyceae (i.e. the 2 major components of the biomass in the lake) as well as the Cryptophyceae are capable of regulating their position in the water column (Lewis, 1978). Also nutrients may be scarcer especially during the stratified period (Reynolds, 2006) leading to lower biomasses in offshore compared to inshore areas as was observed for Lake Bosomtwe and introducing more patchiness in the distribution of the phytoplankton biomass.

5.2 Temporal variability

5.2.1 Phytoplankton community composition and biomass

The total number of 75 species of phytoplankton found in the lake during the temporal study is within the range observed in a considerable number of tropical and temperate lakes (Kalff & Watson, 1986; Reynolds, 2006). It also confirms that confining sampling to few dates even spatially can lead to dramatic underestimates of the total number of species present in a particular water body (Kalff, 2002). For instance, during the horizontal studies, only a total of only 56 species representing close to 75 % that during the temporal study were recorded. Kalff (2002) have observed that in any normal study of a water body between 70 to 200 species of phytoplankton may be found and long term studies in temperate lakes can reveal as

much as over 400 species. However in the tropics this number is expected to be low even in the long term. Despite this, several studies in some tropical lakes have revealed that species richness can range from as low as less than 10 in some saline lakes such as Elmenteita to as high as over 900 in some oligotrophic ones such as Tanganyika (Kalff & Watson, 1986; Cocquyt *et al* 1993). Thus, the 75 species found during this study is fairly within the range found for several tropical lakes in Africa (Kalff & Watson, 1986; Kebede & Belay, 1994).

Also, the dominance of the species richness in the order Chlorophyceae² Cyanophyceae confirms the lakewide observation which is typical of most tropical lakes, whiles the other phytoplankton groups are known to contribute differing number of taxa to the community species composition of tropical lakes (Hecky *et al.*, 1978; Lewis, 1978; Lewis & Riehl, 1982; Kalff & Watson, 1986; Kebede & Belay, 1994). The Chlorophyceae are thought to be tolerant of the high light intensities in the surface waters of tropical lakes though they share this characteristic with the Cyanophyceae and the Dinophyceae (Falkoswki & Raven, 1997). The higher number of taxa observed in the restratifying periods may be due to a combination of improved nutrient availability compared to the stratified period and improving light climate compared to the mixing seasons (Reynolds, 2006). These conditions (i.e. improved light and nutrient conditions) also reduce inter-specific competition for nutrients and light allowing more species of phytoplankton to coexist and develop (Hutchinson, 1961).

The mean phytoplankton wet weight biomass and chlorophyll *a* concentrations of both years (1570.00 mg m⁻³ and 7.1 μ g L⁻¹ respectively in the 1st year -2004-2005 and 2262.30 mg m⁻³ and 10.9 μ g L⁻¹ respectively in the 2nd year-2005-2006) are within the range observed in temperate lakes during summer from the

most oligotrophic to the most eutrophic (Kalff & Knoechel, 1978). It is also similar to that of some tropical lakes like Lake Kivu in East Africa which is dominated by Cyanophyceae and Chlorophyceae with biomasses of up to 2100 mg m⁻³ in surface samples (Hecky & Kling, 1987) and Lake Lanao with total species richness of 70 and dominated by Chlrophyceae with mean biomass of 1600 mg m⁻³ (Lewis, 1978). It is however low compared to most saline lakes in Africa (Kalff & Watson, 1986). For instance, saline lakes such as Nakuru and Elmenteita have biomasses that are over 10 to close to 20 times higher than the mean biomass of Lake Bosomtwe but have relatively low species richness (Kalff & Watson, 1986). The dominance of the biomass by the Cyanophyceae has been observed in several other tropical lakes like Oloidien, Nakuru, Elmenteita (Kalff & Watson, 1986) and George (Ganf, 1974) and again confirms the observation in the horizontal study. This may be the result of the longer stratification periods as a result of the sheltered nature of the lake, their ability to fix nitrogen and regulate position within the water column and the high total phosphorus concentrations observed in the lake (Puchniak et al., 2009, Paerl, 1996; Chorus & Bartram, 1999, Karikari & Bosque-Hamilton, 2004). For instance, vertical migration speeds of Cynophyceae can range from 50 to 140 m day⁻¹ (Reynolds, 2006) and high phosphorus concentrations have been implicated world-wide in the development of algal blooms (Chorus & Bartram, 1999). In Lake Bosomtwe total phosphorus concentrations are in the range of eutrophic to saline lakes (Reynolds, 2006). However, in many other tropical lakes, Chlorophyceae have been shown to dominate the biomass (Kalff & Watson, 1986; Hecky et al., 1978; Lewis, 1978; Ballot et al., 2005; Sarmento et al., 2006).

Both biovolume-based biomass and chlorophyll *a* concentrations have been historically used as estimates of standing crops in phytoplankton research (Malone,

109

1980; Desortiva, 1981; Canfield et al., 1985), and in Lake Bosomtwe even though they are positively related, the relationship between the two is not strong. The phytoplankton biomass explained just over 8 % of the variation in the chlorophyll a concentrations. A comparison of this to some American and European lakes reveal that the chlorophyll a and biomass of phytoplankton are strongly related (coefficient of determination ranged from 79 % to 98 %) compared to what was observed for Lake Bosomtwe (Kalff, 2002; Kirk, 1994; Reynolds, 1987). This may be explained in relation to the observed relationships between these two surrogates of phytoplankton standing crop and other physico-chemical parameters of the lake. For instance, while the phytoplankton biomass had a negative relationship with the Z_{mix} , chlorophyll a concentration was positively related to the Z_{mix} so that whiles peak chlorophyll a concentrations occur in mixing seasons, phytoplankton biomass peaked after mixing period during restratifying periods. Both were, however, consistently low in stratified periods. This phenomenon where chlorophyll a increases without a concomitant increase in the phytoplankton biomass has been observed in several lakes (Desortiva, 1981; Canfield et al., 1985) and has been attributed to dominance of the biomass by larger algal forms which have higher percentage of their biomass in mucilage, cell wall, and other non-chlorophyllous components (Canfield et al., 1985). In Lake Bosomtwe, such large forms such as the filamentous Aphanizomenon spp Morren, Cylindrospermopsis spp Geitler, Microcystis spp Kuetzing and several dinoflagellates (Peridinium spp Eddy, Gymnodinium spp Kofoid & Swezy, etc) with several nonchlorophyllous components are a major part of phytoplankton biomass. Smaller cells are known to have higher relative chlorophyll a content than larger ones (Malone, 1980). Also, chlorophyll a content has been observed to increase when light is limiting (Meeks, 1974; Falkowski & Owens, 1980; Osborne & Raven, 1986;

Desortiva, 1981). In Lake Bosomtwe higher chlorophyll *a* concentrations were observed during the mixing seasons when light was most likely limiting as a result of higher Z_{mix} : Z_{eu} ratios (Lewis, 1978). The relatively stronger coefficient of determination between phytoplankton biomass and the Z_{mix} compared to that of chlorophyll *a* concentration may partly be explained by the nature of the dominant phytoplankton groups namely, Cyanophyceae and the Dinophyceae which are known to be intolerant of mixing conditions and grow best in stratified waters (Paerl, 1996).

The increase in chlorophyll *a* concentrations from the stratified to the mixing period with little change in the community biomass (differences in mean community biomass of stratified and mixing period were not significant in both years; 1-way ANOVA) results in high chlorophyll *a* to biomass ratios in mixing seasons of both years. This observation is consistent with other observations in some lakes and is attributed to the reduced light availability and higher nutrient availabilities during such periods (Fennel & Boss, 2000). Changes in the chlorophyll *a* to biomass ratios could be a consequence of changing community composition (Reynolds, 2006). But in Lake Bosomtwe, there was little change in taxonomic composition during the study period. Therefore, the changes in this ratio are likely to be the result of ontogenetic adaptation to light and nutrient conditions (Meeks, 1974; Falkowski & Owens, 1980; Osborne & Raven, 1986; Desortiva, 1981). The higher ratios of the Z_{mix}:Z_{eu} in the mixing periods indicated nutrient sufficiency but also unfavourable light climate.

Unlike Z_{mix} however, Z_{eu} is negatively related to both the phytoplankton biomass and chlorophyll *a* concentrations. This may partly be due to the fact that higher Z_{eu} occured during prolonged stratified periods when nutrient concentrations were low and light intensities were higher compared to other periods. The phytoplankton may be adapting to such conditions by increasing the production of

non-chlorophyllous components with high energetic cost such as mucilage, cell walls as well as the production of toxins to reduce inter-specific competition (Canfield et al., 1985). Also during such periods, phytoplanktons have been observed to increase production of carotenoid accessory pigments that do not transfer excitation energy to chlorophyll a and thus acting as photo-protective pigments (Paerl, 1996; Paerl & Millie 1996; Zohary, 1989; Fogg, 1991; Ballot et al., 2005). All these processes may act to reduce the production of chlorophyll a and therefore photosynthesis and biomass as well as increase the R_C substantially as was observed during the stratified period. The dominance of the biomass by the Cyanohyceae and the Dinophyceae which are usually considered inedible during such periods and the lower percentage contribution by the other groups such as the Chlorophyceae (except the placoderm desmid Cosmarium laeve Naegeli) and Cryptophyceae which are considered superior zooplankton food may also suggest higher selective zooplankton grazing during such periods compared to other periods. Carpenter et al (1987) and others (Kumar & Rao, 1999; Smyada, 1997; Moore et al., 1994) corroborated this fact in experimental and field food web interactions where grazing pressure was found to be higher during stratified periods and lower in mixing seasons. Stratification enables zooplankton to move into areas where the phytoplankton are concentrated using their relatively higher motility and consequently reduce the phytoplankton biomass during such periods (Tilzer & Goldman, 1978). This explanation is especially plausible for Lake Bosomtwe since like the Dinophyceae, the Cryptophyceae can resort to phagotrophic feeding to compensate for low nutrient availabilities that they may experience during prolonged stratification since they are both mixotrophic (Wilcox & Graham, 2000) yet they have low biomasses during such periods. Chaoborus, the phantom midge may also be contributing to this grazing as they were abundant in the lake and are known to feed on moving prey (Wilcox & Graham, 2000). In one lake, Moore *et al* (1994) found that 70 % of their diet consisted of the dinophyte *Peridinium* which is incidentally prominent in the plankton of Lake Bosomtwe during stratified periods.

The lack of a clear statistical relationship between the phytoplankton biomass and the ratio Z_{mix}:Z_{eu} ratio and the concentration of the biomass below a Z_{mix}:Z_{eu} ratio of less than 5 except during the 1st year (2004-2005) when a deep mixing event that resulted in substantial fish kills (Puchniak et al., 2009) caused the ratio to increase close to 9 showing that the phytoplankton are trying to avoid light-limitation. This is because when this ratio is 5 or more, the phytoplankton will be spending over 80 % of their time in the aphotic zone and are likely to be light-limited even though nutrients may be available as is corroborated in this study by the low phytoplankton biomass during mixing periods. In fact, several authors have suggested a critical value of Z_{mix}:Z_{eu} ratio between 4 and 5 beyond which light limitation is expected to prevail (Strickland, 1965; Wood et al., 1978). In Lake Bosomtwe the concentration of most biomass at or below Z_{mix}:Z_{eu} ratio of 5 seem to give some credence to this assertion. At the same time however, chlorophyll a concentrations behaved differently and was strongly positively related to the Z_{mix}:Z_{eu} ratio (coefficient of determination of over 54 %; r = 0.73) implying that the phytoplankton are compensating or adapting ontogenetically to the increasing light-limitation by increasing their chlorophyll a concentrations (Meeks, 1974; Falkowski & Owens, 1980; Osborne & Raven, 1986; Desortiva, 1981).

The biomass of the phytoplankton did not seem to respond to increases in total phosphorus concentration in any definite way though chlorophyll a concentration had a weak positive relation with the total phosphorus explaining just 8 % of the variation in the chlorophyll a concentrations. This may imply that the total phosphorus

concentrations were probably adequate for phytoplankton throughout the study period. In fact the work of Karikari & Bosque-Hamilton (2004) has shown that nutrient concentrations especially phosphate and nitrate may not be limiting phytoplankton growth in Lake Bosomtwe as levels of orthophosphate and nitrate concentrations were far above the levels of P- or N-famine for phytoplankton (Reynolds, 2007). Levels of total phosphorus in this study confirm this as mean total phosphorus levels of the two years are in the range of eutrophic to saline lakes (Reynolds, 2006). However, nitrogen limitation is suggestive from the continuous presence and dominance of heterocyst-bearing Cyanophyceae like Aphanozomenon spp Morren, Anabaenopsis tanganyikae Miller, and Cylindrospermopsis helicoidea Geitler and C. rasciborskii Geitler (Appendix 1C & D). This is because heterocyst production is energetically very costly (requiring 12-15 ATPs per molecule of nitrogen fixed) and not likely to be produced if nitrogen is freely available (Postgate, 1984). However, some authors have observed no relationship between the production of heterocyst and N-limitation and have postulated that heterocysts production may rather indicate the absence of inorganic NH4-N not necessarily all inorganic nitrogen (Reynolds, 2006). Moreover, it can be argued that these nitrogen-fixing Cyanophyceae may be contributing to reduction in nitrogen limitation in the lake by making them available to other phytoplankton groups through release after fixation. According to Graham & Wilcox (2000), 40-60 % of fixed nitrogen by Cyanophyceae can be excreted from their cells into the open water, making it available to other phytoplankton groups.

Annual variabilities of the means expressed by the coefficient of variance indicate considerable variability for a tropical lake for both the wet weight biomass (CV of close to 79 % and over 28 % for the 1^{st} (2004-2005) and 2^{nd} (2005-2006)

years respectively) and chlorophyll *a* (CV of over 36 % and close to 49 % in the 1st and 2nd years respectively). These are characteristic of Melack's (1979) category 1 (CV $^{>}$ 25 %) in his assessment of variability of the phytoplankton of tropical lakes which is related to pronounced seasonal fluctuations associated with variations in rainfall, river discharges or vertical mixing. The similarly high CVs in the physico-chemical parameters monitored alongside phytoplankton during the study period suggest this is the case. Though both mean phytoplankton biomass and chlorophyll *a* concentrations differed significantly between the two years only the variability of the mean chlorophyll *a* concentration in an annual period may be significantly different, their variabilities may not.

Seasonal differences indicate different scenarios in the variability of the mean phytoplankton biomass. Whiles there was no significant difference in the means of the different seasons during the 1st year (2004-2005), seasonal differences were significant in the 2nd year (2005-2006) between the stratified period and the restratifying period but not between mixing and stratified periods confirming the observation in the horizontal study. The implication of this is that in the 1st year (2004-2005), seasonal and interseasonal differences formed 42.7 % of the variance whiles inter-seasonal differences formed 57.3 % of the variance. Thus in the 1st year (2004-2005) there was no real statistical evidence to suggest differences in the mean wet weight phytoplankton biomass between seasons. In the second year however, seasonal differences were far higher forming 69 % of the variance whiles inter-seasonal differences formed just 31

% of the variance and therefore there was a real statistical reason to suggest seasonal differences in the wet weight biomass.

5.2.2 Phytoplankton groups: Occurrence and biomass contribution

The dominance of the phytoplankton biomass of Lake Bosomtwe by the Cyanophyceae and the persistent occurrence of species such as *Aphanizomenon* sp, Cylindrospermopsis rasciborskii Geitler, C. helicoidea Geitler, Anabaenopsis tanganyikae Miller, Microcystis rosea Kuetzing and M. smithii Kuetzing which are typical tropical species (Huszar et al., 2000; Graham & Wilcox, 2000) in the lake all year round is particularly notable (Appendix 2B & C). These species are known to thrive in tropical lakes where there is considerable persistent stratification, high irradiances and high surface water temperatures 20 ^oC), as well as long water residence times (Paerl, 1996; Paerl & Millie, 1996; Sterner, 1989) which are also characteristic of Lake Bosomtwe (Turner et al., 1996a; Puchniak et al., 2009). Under such conditions their ability to fix nitrogen, store nutrients especially N and P, regulate buoyancy, sequester metals (Fe, Cu) by siderophore chelators, produce mucilage sheaths to counter desiccation, photoprotect by carotenoid accessory pigments are some of the factors attributed to their success as well as the production of toxins to reduce interspecific competition (Paerl, 1996; Paerl & Millie, 1996; Zohary, 1989; Fogg, 1991; Ballot et al., 2005). The seeming lack of nutrient limitation especially phosphorus in the lake (Karikari & Bosque-Hamilton, 2004) and the unpalatability of the Cyanophyceae to zooplanktons as well as their efficient carbon concentrating mechanisms give them a clear advantage over the other phytoplankton groups of Lake Bosomtwe (Reynolds, 2006).

The Dinophyceae which are the second group that makes the largest contribution to the biomass of Lake Bosomtwe may be this successful probably due to the longer stratification periods compared to the mixing periods of the lake in an annual cycle (Moore, 1989). This may result in nutrient depletion and therefore potentially mixotrophic groups especially, the Dinophyceae which are able to resort to bactivory or phagotrophy are favoured in such lakes (Olrik, 1998; Lewis, 1978). In Lake Bosomtwe, the Dinophyceae have higher biomasses during stratified and restratifying periods (Fig 4.11). During such periods, motile dinophytes like Peridinium Ehrenberg and Gymnodinium Kofoid & Swezy regulate their position in the water column and succeed under probable nutrient stressed conditions by moving between the light and the nutrient fields to acquire the essential light and nutrients for their growth and maintenance (Huszar et al., 2000; Gervais et al., 2003; Fogg, 1991). Swimming speeds for the Dinophyceae can range from 2 to 20 m day⁻¹ (Reynolds, 2006). Also, the larger energetic cost of capturing and ingesting motile relatively large dinophytes by zooplankton may also explain in part their substantial biomass in the lake (Kumar & Rao, 1999; Smayda, 1997) even though they may suffer loses from predation by the phantom midge (Chaoborus sp) which is common in the lake since they feed on moving prey (Moore et al., 1994). Under the prevailing environmental conditions therefore, the Cyanophyceae and the Dinophyceae are the best suited and therefore dominate the biomass of phytoplankton in the lake.

The biomass of the Chlorophyceae thrived better during the restratifying periods probably due to the improved nutrient and light conditions needed to stimulate growth and maintenance except in the case of the placoderm desmid *Cosmarium laeve* Naegeli which is prominent in the plankton even during stratified periods probably due to their low digestibility to zooplankton (Cossel, 1997). Lewis

(1987) has observed a similar trend for the Chlorophyceae biomass in tropical Lake Lanao. Another factor favouring their increased biomass during such periods may be reduced competition with the improved nutrient conditions.

Bacillariophyceae thrived better during the mixing and restratifying periods and their lowest biomasses occurred during the stratified period consistent with observations in several lakes (Lewis, 1978; Sterner, 1989; Paerl, 1996). Bacillariophyceae are known to be better competitors at low light intensities and also form a considerable portion of the biomass of phytoplankton in lakes where there is substantial contact between the epilimnetic water and lake sediment or where there is complete mixing since most of them depend on resuspension in the water column during mixing periods (Levin, 1974; Huisman et al., 2004; Chetelate & Pick, 2006; Willen, 1991). Lake Bosomtwe is however meromictic (Puchniak et al., 2009) and is stratified for most part of the year and so species that sink out of the epilimnion have little chance to get resuspended. Also only pennate diatoms were present most of the time since their morphology helps reduce sinking rates (Graham & Wilcox, 2000; Morabito et al., 2007) and are also better competitors for silica at low concentrations (Tilman *et al.*, 1976) since silica levels may be low in the lake because of the high temperatures (and strong thermal stratification) and alkalinity (basic pH) which tend to pull the available silica into the deep anoxic layer (Willen, 1991). The lower contribution of the Bacillariophyceae to the biomass may therefore be attributed to the potentially low silica concentrations, low wind intensity needed for mixing (because the lake is sheltered) as well as the small catchment to surface area.

The low representation in taxa and contribution of the Cryptophyceae and the Chrysophyceae to the biomass, may be due in part to the relatively low transparency, the productive nature and also the high surface water temperatures of the lake since these groups are usually associated with oligotrophic lakes (Hecky & Kling, 1981; Kalff & Watson, 1986; Sandgren, 1988) and cold waters (Taylor *et al.*, 1979). The superior food quality of cryptophytes to most zooplankton (Guillard, 1975), mixotrophic dinophytes as well as ciliates (Stemberger & Gilbert, 1985; Edmonson, 1969; Sarnelle, 1993) may also explain in part their low biomasses in the lake. Their higher biomass in the mixing compared to the stratified period may also be attributed to decrease zooplankton grazing rates during such periods (Reynolds, 2006).

The Chrysophyceae prefer waters with specific conductivities less than 50 μ Sm⁻¹ (Sandgren, 1988). Conductivities in Lake Bosomtwe surface waters averaged over 1256 μ Sm⁻¹ (Karikari & Bosque-Hamilton, 2004) which was over 25 fold greater potentially affecting them negatively both in taxa and biomass contribution. Also, most chrysophytes are unable to use HCO₃ at all as a carbon source and they also lack any known carbon concentrating mechanism (Kirk, 1994; Graham & Wilcox, 2000). But in the high pH waters of Lake Bosomtwe, most carbon is in the form of HCO₃ and may partly be limiting their growth. Furthermore, Reynolds (2006) suggests that total phosphorus levels greater than 20 µg L⁻¹ may be toxic to several chrysophytes. In Lake Bosomtwe, total phosphorus levels are several times higher than this value and are in the range of eutrophic to saline lakes. But chrysophytes like *Ochromonas* Ehrenberg found in the Lake are potentially mixotrophic (Olrik, 1998; Salonen & Jokinengs, 1988) and may be supporting autotrophy with other modes of nutrient acquisition.

The Euglenophyceae are usually abundant in eutrophic lakes and thrive in waters enriched with organic matter (Hutchinson, 1967). However in Lake Bosomtwe even though genera like *Euglena* Ehrenberg, *Trachelomonas* Ehrenberg and *Phacus* Dujardin indicative of organic pollution (Palmer, 1969; 1980) occur, they make very

little contribution to the percentage species richness and biomass of the phytoplankton of the lake in an annual cycle. Within the catchment of the lake, however, considerable anthropogenic changes to the vegetation and landscape are occurring but the low catchment area to lake surface area seem to mask the effect of likely increased nutrient loading into the lake. Also, they are unable to use other dissolved inorganic nitrogen sources apart from NH4-N (Reynolds, 2006). But in stratifying waters such as Lake Bosomtwe, rapid draw down and nitrification of NH4-N leads to its scarcity and thus potentially affecting them negatively. One probable attestation to the lack or low levels of NH4-N in the surface waters of Lake Bosomtwe is the continous presence of heterocysts in filamentous Cyanophyceae which is believed to signal incipient nitrogen limitation as a result of low levels of NH4-N (Reynolds, 2006).

The phytoplankton biomass and chlorophyll *a* dynamics in the end seem to be shaped by the dynamics of the physical conditions and probably zooplankton grazing in the water column compared to chemical conditions of the lake and it seems that the dominant phytoplankton groups i.e. Cyanophyceae and Dinophyceae are suited in so many ways to thrive in the lake compared to the other groups. Talling (1986) in a general account of the seasonal occurrence of phytoplankton in African lakes concluded that the factors of dominant importance are the hydrological or hydrographic or a mixture of the two water input-output and water column characteristics. The nature of Lake Bosomtwe's hydrography seems to drive the variations in the phytoplankton biomass.

The variability in the biomass and chlorophyll a are high for a tropical lake (Melack, 1979) and there are considerable seasonal and inter-annual differences in these two biomass surrogate of phytoplankton that seem to be driven by considerable

120

variations in the physical characteristics of the lake. Chlorophyll *a* does not seem to be a good surrogate of the phytoplankton standing crop since it is poorly related to the biomass.

For Lake Bosomtwe, it is concluded that the seasonal variation of the phytoplankton community species richness and biomass is evident and is dependent upon the stratification-mixing cycle. Also the dominance of the biomass by the Cyanophceae was favoured by the thermally stratified conditions especially, but they were not displaced by other groups during the mixing period. The wet weight biomass is low compared to some similar closed-basin lakes but the TP and the community composition are typical of eutrophic or saline lakes.

5.3 Phytoplankton primary productivity

5.3.1 Gross and net productivities, community respiration, and growth rates

The mean areal gross primary productivity (P_G) of Lake Bosomtwe of 4.73 gC m⁻²d⁻¹ with a range of 1.22 to 7.68 gCm⁻²d⁻¹ is well within the range observed in most tropical African lakes (Table 2.1). By temperate lake standards it may be considered hypertrophic since values have been found to range from 0.012 gC m⁻²d⁻¹ to 3.6 gC m⁻²d⁻¹ from the most oligotrophic to hypertrophic lakes temperate lakes (Goldman, 1968; Odour & Schagerl, 2007). It is close to 8 times more productive than the world average for streams and lakes (Whitaker & Likens, 1975) and over 4 times that of the oligotrophic Lake Tanganyika in Africa (Hecky & Fee, 1981; Beadle, 1981). It is however close to 7 times less productive than the most productive lake on record (Robarts, 1984). It is also more productive than similar closed basin saline lakes in East Africa namely, Elmenteita, Nakuru and Bogoria (Odour & Schagerl, 2007). Tropical saline lakes are recognized as the world's most productive ecosystems

(Talling *et al.*, 1973; Melack & Kilham, 1974). Several authors list high productivity per unit standing crop, high sustained standing crop per unit area, maximum transparency per unit of production, the combination of efficient nutrient cycling as a result of periodic intra-seasonal deep mixing and a restoration of a thin mixed layer, higher mean water temperatures and greater stability of solar irradiance as being related to the high productivity of tropical lakes (Lewis 1974, 1976; Talling, 1987; Melack, 1976, 1979; Melack & Kilham, 1974). Most of these conditions also characterize Lake Bosomtwe with high mean water temperatures (Turner *et al.*, 1996a; Puchniak *et al.*, 2009) as a reflection of its tropical status as well as stable supply of solar irradiance also characteristic of tropical lakes and an observed intraseasonal deep mixing in August and January (Beadle, 1981; Puchniak *et al.*, 2009).

A comparison of Lake Bosomtwe to some well studied tropical lakes show that its biomass is low and this is commensurate with the low growth rates of the phytoplankton and the high community respiration in the lake. In fact, the mean assimilable photosynthate in an annual cycle within the Z_{eu} was just 10 % of the gross productivity implying very high respiration rates. The gross productivity to community respiration ratio in the Z_{eu} is just slightly net autotrophic (1.10) but is heterotrophic in the Z_{mix} . Though algal respiration rates are known to vary between 5 to 15 % of the gross at light optimum (Ryther, 1954; Steelmann-Nielsen & Hansen, 1975; Talling, 1998; Reynolds, 1984), in some tropical lakes, community respiration has been observed to vary between 35 to 67 % of the gross productivity (Hecky, 1984). Even in axenic cultures, Bunt (1965), recorded values of respiration between 20 to 100 % of the gross productivity. In addition, Ganf (1972, 1974), found respiration in Lake George to be as high as 92 % of the gross productivity. In Lake Bosomtwe community respiration forms 90 % of the gross productivity and if this

high respiration rates are attributable to the phytoplankton alone, they may not be able to accumulate the observed biomass since they will be using almost all their production in respiration. Certainly this respiration is not due to the phytoplankton alone since bottle methods measure the respiration of other organisms that are entrained with the phytoplankton in the bottles during incubations including heterotrophic bacteria, zooplankton and other planktonic invertebrates (Odum & Wilson, 1962; Ganf & Blazka, 1974; Wissmer et al., 1981; Dokulil et al., 1983; Talling, 1984; Reynolds, 2006). Other reasons for the high respiration rates may be attributable to the generally higher temperatures of the lake water typical of tropical lakes that are known to stimulate most metabolic processes including respiration and thus reducing the net productivity (Beadle, 1981). Again, the respiratory rates of the phytoplankton groups that dominate the biomass of the lake namely, Cyanobacteria and Dinophyceae have been observed to be high (Bindloss, 1974; Tilzer, 1989). Moreover, photoperiod truncations whether real during night periods or effective when phytoplankton spend a lot of time in the aphotic zone relative to the Z_{eu}, also increases respiration rates substantially relative to the gross rates potentially reducing the net productivity (Reynolds, 2006). For instance, in Lake Bosomtwe phytoplankton spent between 56.9 % during stratified period to 81.1 % during mixing period (average of 71.9 %) in the aphotic compared to the Z_{eu} during the period. The average value is close to the 80 % normally required to lead to light inhibition (Strickland, 1965; Wood et al., 1978; Naselli-Flores et al., 2007) and is also potentially contributing to the observed high respiratory rates in the lake.

But even with all these additional sources of respiration, 90 % is still high compared to most other tropical productive lakes with similar conditions (Hecky, 1984). It is possible that this community respiration over much of the year is also

being supplemented by fixed carbon originating from outside the mixed layer possibly metalimnetic non-phytoplankton respiration which is being mixed in through the thermocline especially during deep mixing periods. Possibly the bacteria plate of a deep chlorophyll maximum (DCM) that has been observed in the lake (Puchniak *et al.*, 2009) throughout much of the year and consisting of purple and green sulphur bacteria that use anoxygenic photosynthesis may also be responsible for much of the observed respiration losses especially during the mixing seasons. Allocthonous sources from the catchment may also make some contributions during rainy seasons.

Areal rates of P_G in the lake varied over 6-fold with a CV of over 33 % indicating considerable intra-annual variability. Much of this is attributable to variability within the seasons with a small % attributed to variability between the seasons. This observation in the CV means that like the biomass, variability of the gross productivity of Lake Bosomtwe falls in pattern 1 of Melack's classification of tropical lakes which is typical of middle and high latitude lakes and implies that it exhibits pronounced seasonal fluctuation that is usually coupled to oscillations in hydrological and hydrographical conditions (Melack, 1979; Talling, 1969; Lewis, 1974). As is depicted in Table 4.3, the CVs of the physico-chemical variables taken alongside P_G measurements were also similarly high and seem to drive most of the variability in the P_G. The higher variabilities within seasons compared to between seasons seem to lead to considerable scatter along the lines of best fit and to lower coefficient of determination between P_G and several variables. But the relatively stronger relationship between the P_{G} and the physical factors notably Z_{mix} and Z_{eu} and the lack of any definite relationship between P_G and total phosphorus seem to suggest that physical factors exert greater effect in the regulation of the P_G than chemical factors. Among environmental abiotic factors involved in P_G control,

physical factors are usually thought to play the key role in productive or eutrophic and hypertrophic ecosystems (Harris, 1980; Robarts, 1984) whiles chemical factors are usually not thought of as strongly influencing the seasonality of the P_G (Cobelas et al., 1992). The present investigation may seem to give some credence to this claim though the continual presence and dominance of heterocyst-bearing cyanobacteria seems to suggest nitrogen limitation (Postgate, 1984). Therefore extensive investigation of the P_G and the various key nutrients, not only of total phosphorus is needed to access the nutrient limitations. But again given that the dominant phytoplankton of Lake Bosomtwe are the Cyanophceae and the Dinophyceae this assertion is highly plausible for Lake Bosomtwe since both groups are capable of moving between the nutrient and light fields especially in high gradients of these factors under calm water conditions to utilize these essential resources. For instance, the Cyanophyceae are capable of nitrogen fixation and buoyancy regulation (Paerl, 1996) and have very high affinity and uptake rates for phosphorus (Reynolds, 2006) and the Dinophyceae are motile and mixotrophic and though with low affinity for P, can access P and N from phagotrophic feeding (Graham & Wilcox, 2000; Lehman, 1976; Mann, 1995; Reynolds, 2006; Riemann et al., 1995; Geider & MacIntyre, 2002). This may imply that lower external concentrations of nutrients especially total phosphorus and nitrogen in the lake may not necessarily derail the phytoplankton growth and production.

5.3.2 Seasonality of the phytoplankton productivity

The positive though weak relation between gross productivity and Z_{mix} implies that the highest P_G occurred in the mixing period when the average mixed depth was highest and lowest P_G occurred in the restratifying and stratified periods

when average mixed depths were lowest. This may be partly attributed to the high chlorophyll a concentrations produced during the mixing season most likely as a result of the high effective photoperiod truncation (highest Z_{mix}:Z_{eu} ratio) leading to high light limitations during this period (Strickland, 1965; Wood et al., 1978; Naselli-Flores et al., 2007). The phytoplankton were observed to be adapting to this light limitation by increasing chlorophyll a concentrations since little change in community composition occured between the stratified and mixing periods (Falkowski & Raven, 1997; Meeks, 1974; Falkowski & Owens, 1980; Osborne & Raven, 1986; Desortiva, 1981; Fennel & Boss, 2000; Reynolds, 2006). Steelman-Nielsen & Hansen (1959) concluded that during mixing periods, the entire phytoplankton assemblage is exposed to higher light levels than during thermal stratification. This coupled with high nutrient availability leads to high productivities. For instance in Lake Bosmtwe during mixing periods total phosphorus concentrations and chlorophyll *a* oncentrations keep increasing compared to the stratified period. These two resources may be optimized to bring about the observed highest P_G during the mixing period. However, the high community respiration observed during this period led to low net productivity, low assimilable photosynthate and low growth rate compared to the restratifying period. Though P_G was lowest during the restratifying period, community respiration was lowest compared to either the mixing or stratified period and this led to higher net productivity, high percentage assimilable photosynthate and high growth rates. The highest levels of total phosphorus concentrations coupled with the highest growth rates during the period enabled the phytoplankton to build up their biomass to the maximum.

The favourable light climate during the stratified period compared to other periods seemed to promote higher productivity which did not differ significantly from

126

that in the mixing period. However, the total phosphorus and chlorophyll a concentrations were low compared to other periods. Despites this, total phosphorus may not necessarily be limiting the productivity in the lake as is observed by the lack of a definite relation between the two due to the considerable scatter in the line of best fit. In fact Karikari & Bosque-Hamilton (2004) observed phosphate concentrations in excess of phytoplankton requirements in the lake (Reynolds, 2007). However, the community respiration observed during the stratified period was higher than the gross productivity and led to a negative net productivity and lowest biomass during this period though growth rates were comparable to that of the mixing season. The low biomass may however be partly attributed to the higher selective zooplankton grazing pressure during stratified periods (Carpenter et al., 1987). This is supported by the low cryptophyte biomass during this period. This is because the cryptophytes are mixotrophic and can survive and increase their biomass if nutrients become limiting in stratified periods by resorting to bactivory (Graham & Wilcox, 2000). However, their high quality as zooplankton food probably explains in part their low biomasses. The high maintenance requirements during this period may explain in part the high respiration rates. For example, the low Chlorophyll a concentration in the surface waters during this period may be attributed to the diversion of resources to the production of non-chlorophyllous components such as mucilages, heterocysts, toxins etc for adaptation to the low nutrient, high light intensity environment with high energetic costs (Canfield et al., 1985). Heterocyst production for instance is very energetically costly requiring 12-15 ATPs per molecule of nitrogen fixed and are therefore not likely to be produced if nitrogen is freely available (Postgate, 1984). The high community respiration may also be partly explained by the strong presence and dominance of mixotrophic dinophytes such as Gymnodinium spp Kofoid &

Swezy and *Peridinium elpatweikyi* Ehrenberg during this period. This is because dinophytes acting as autotrophs may undergo rapid transition to heterotrophy especially during this period when some nutrient may be limiting. As heterotrophs they contribute only to the respiration and not to photosynthesis. This will result in an increase in the community respiration and a decrease in the net productivity since instantaneous measures such as the oxygen method used in this study will not detect shifts from autotrophy to heterotrophy (Graham & Wilcox, 2000). Increase in protective pigments like carotenoids which do not transfer excitation energy to chlorophyll *a* and subsequently act to screen the cells from the excess light are known to be produced during such periods. A combination of these factors may be responsible for the greater community respiration than the productivity during this period.

In the end the phytoplankton productivity seems to be controlled more by the physical environmental conditions in the water column than by chemical factors as evidenced by the higher coefficients of determinations especially since growth rates do not differ significantly between seasons. Biological factors such as grazing through selective feeding may also be playing a part in shaping the dynamics of the phytoplankton productivity.
CHAPTER SIX

CONCLUSIONS AND RECOMMENDATIONS

6.1 CONCLUSIONS

6.1.1 Community composition, biomass and chlorophyll a

- 1. The total number of phytoplankton species found in Lake Bosomtwe during this study from November 2004 to October 2006 varied between 56 during spatial and 75 during the temporal studies respectively and is within the range of total number of species found in most tropical lakes. Species composition of the phytoplankton taxa is also typically tropical in nature.
- 2. The Chlorophyceae dominated the phytoplankton community species richness during the study period. This is also typical of most tropical lakes.
- 3. Higher species richness and community biomass seem to be promoted by increased nutrients, low inter-specific competition and better light climate during restratifying periods.
- 4. Horizontal and temporal observations show that more species are likely to be found when the sampling interval is decreased to say weekly sampling.
- 5. There were no definite inshore-offshore trends in the total species richness in both the mixing and stratified periods during spatial study.
- 6. The mean biomass of the phytoplankton is also within the range observed in a considerable number of tropical lakes.
- 7. The dominance of the biomass by the Cyanophyceae both horizontally and temporally in Lake Bosomtwe is also similar to several tropical lakes.
- Contrary to the general believe of reduced seasonality in tropical regions, the variability of the biomass and chlorophyll *a* in of phytoplankton in Lake Bosomtwe is high both horizontally and temporally.

- 9. There were no definite inshore-offshore trends in the community biomass in both the mixing and stratified periods during horizontal surveys.
- 10. Significant inter-annual and seasonal variabilities of the phytoplankton biomass occurred during the temporal studies.
- 11. The biomass and Chlorophyll *a* concentration though positively related had a weak relationship and indicated that Chlorophyll *a* may not be a good indicator of phytoplankton biomass in Lake Bosomtwe. Because there is little change in community composition in the lake, changes in chlorophyll *a* concentrations is an adaptation by the same community to varying conditions at different times of the year or season.
- 12. Physical factors such as mixing depth and the euphotic zone seem to play the major role in the dynamics of the phytoplankton.
- 13. But selective zooplankton grazing especially of the Cryptophyceae and parasitic infections by chytrids (*Hyaloraphidium* spp) may also be involved to some extent. Chytrids are known to particularly infect cyanobacteria, dinophytes, chlorophytes, chrysophytes and diatoms. The Cyanobacteria and the Dinophyceae dominate Lake Bosomtwe biomass.
- 14. Nitrogen-limitation is also suggestive because of the abundance and persistent occurrence of nitrogen fixing cyanophytes throughout the study period.

6.1.2 Gross primary productivity, community respiration and growth rates

- The gross productivity of Lake Bosomtwe is high compared to similar close basin saline lakes in some tropical lakes in Africa.
- 2. However, the unusually high community respiration representing 90 % of the gross productivity as well as the low growth rates found in the lake compared

to some other tropical lakes makes the net productivity extremely small. This may indicate higher physiological loss rates. Also bottle methods estimate more than the respiration of the phytoplankton making the respiration higher than the actual value.

- 3. Phytoplankton productivity like the biomass seems to be controlled more by the physical characteristics of the water column than any other factor.
- 4. The variability of the productivity is also high just like biomass.

In the end contrary to the general believe of muted seasonality or lack of seasonality in tropical regions, phytoplankton wet weight biomass and productivity of Lake Bosomtwe was observed to be quite pronounced both spatially and temporally.



6.2 RECOMMENDATIONS

- Future research in the community composition and biomass should sample at reduced temporal and spatial scales as this may reveal more species and give a better spatio-temporal resolution in the community composition and biomass than presented in this thesis.
- 2. The more sensitive carbon-14 method of primary productivity should also be adopted in subsequent research in this field since it estimates more directly the net productivity so that a better estimate of the growth rates not only in the euphotic zone but also in the mixed layer which is the productive zone to measure net productivities and growth rates can be gotten.
- 3. The unusually high community respiration brings to question whether the contribution to carbon in the lake by the observed microbial plate that is present in the lake for a greater part of the year should not be fully investigated since it may account for some part of the respiration during mixing periods.
- 4. The role of the microbial food web in the dynamics of the food web should also be investigated to give a more complete picture of the trophic structure of the lake.
- 5. The role of fungi and other parasites of phytoplankton should also be given some attention to help understand the dynamics of the phytoplankton of the lake better.

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Appendix 1A Physico-chemical and biological parameters of Lake Bosomtwe (Ghana) during mixing season (August) of 2006

Parameter/station		ABO	NO-APE	EWU TR	ANSECT	[ASISIRIWA-DOMPAH TRANSECT									
Distance from shore	200 m	1 km	2 km	4 km	6 km	7 km	7.8 km	200 m	1 km	2 km	4 km	6 km	7 km	7.8 km		
Maximum depth (m)	11.30	25.50	>50	>50	>50	24	11.5	6.7	47.3	>50	>50	29.7	11.7	1.8		
Secchi disc depth (m)	1.40	1.40	1.6	1.4	1.4	1.4	1.4	1.2	1.1	1.2	1.4	1.4	1.3	1.2		
Conductivity (μ S cm ⁻¹)	1283.63	1285.16	1284.35	1284.27	1307.82	1283.46	1285.31	1289.82	1219.67	1289.70	1288.67	1285.41	1289.41	1106.40		
Dissolved oxygen (%))	54.60	54.98	47.19	55.75	58.36	59.47	52.37	49.82	59.47	64.62	72.35	53.01	57.41	62.41		
Temperature (°C)	27.84	27.77	27.55	27.81	27.90	28.10	28.10	28.10	28.10	28.00	28.13	27.88	27.88	27.80		
Biomass (mg m ⁻³)	6250.66	4418.52	1989.56	6034.66	6568.5	3756 <mark>.68</mark>	5386.68	2840.68	3664.10	4667.50	4667.50	5666.38	2619.46	4691.48		

Appendix 1B

Physico-chemical and biological parameters of Lake Bosomtwe (Ghana) during mixing season (November and December) of 2006

Parameter/station		ABC	NO-APE	EWU TR.	ANSECT	Γ	ATT		ASIS	IRIWA-I	DOMPAH	I TRANS	SECT	
Distance from shore	200 m	1 km	2 km	4 km	6 km	7 km	7.8 km	200 m	1 km	2 km	4 km	6 km	7 km 🤺	7.8 km
Maximum depth (m)	11.30	25.50	>50	>50	>50	24	11.5	6.7	47.3	>50	>50	29.7	11.7	1.8
Secchi disc depth (m)	1.50	1.60	1.80	1.80	1.50	1.50	1.50	1.50	1.60	1.50	1.60	1.60	1.50	1.50
Conductivity (μ S cm ⁻¹)	1297.33	1297.60	1298.93	1218.33	-	-		1312.88	1307.00	1307.46	1307.46	1305.88	-	-
Dissolved oxygen (%))	80.37	80.90	82.93	86.10	22	-	- 5	51.72	50.96	53.58	53.58	55.36	-	-
Temperature (°C)	30.37	30.34	30.23	30.20	Z W	JSAN	F NO	30.10	30.14	29.73	29.73	29.81	-	-
Biomass (mg m ⁻³)	5149.94	5016.20	4849.88	3910.36	6451.16	4656.54	7214.02	1462.22	5838.18	5608.76	5608.76	2779.16	10335.22	1573.50

Appendix 1C Species lists of Lake Bosomtwe during spatial survey in August, November, and December 2006

CHLOROPHYCEAE

Arthrodesmus convergens Ehrenberg Chlamydomonas spp Snow 1903 Chlorella spp Beyerinck 1890 Closterium acuatum Nitzsch 1817 Coelastrum astroideum Naegeli 1849 Cosmarium leave Rabenhorst Cosmarium moniliforme Corda 1834 Crucigenia tetrapedia Morren 1830 Monoraphidium contortum Naegeli Monoraphidium spiculiforme Naegeli Oocystis submarina Naegeli 1855 Ooocystis lacustris Naegeli 1855 Pyramidomonas tetrarhynchus Schmar. Selenastrum spp Reinsch 1867 Tetraedron minimum var granulata Kuetzing 1845 Tetraedron minimum Kuetzing 1845 Tetraedron trigonum Kuetzing 1845 Treubaria triapendiculata Bernard 1908

BACILLARIOPHYCEAE

Aulacoseira spp Hustedt Cymbella spp (Hempr.) Kirch Fragillaria africana Desm., Nitszchia recta W. Smith Navicula phyllepta Bristol, 1919 Surriella spp Ehrenberg Synedra ulna Hustedt

DINOPHYCEAE

Glenodinium spp Stein 1883 Gymnodinium spp Kofoid &Swezy 1921 Gyrodinium spp Kofoid &Swezy 1921 Peridinium elpatiewskyi Ehrenberg 1832 Peridinium inconspicum Eddy 1930 Peridinopsis spp Eddy 1930

CYANOBACTERIA

Anabaenopsis tanganyikae Miller 1923 Aphanizomenon spp Morren 1838 Aphanotheca spp Naegeli 1849 Aphanocapsa grevillii Naegeli 1849 Chroococcus dispersus Naegeli 1849 Chroococcus minimum Naegeli 1849 Chroococcus turgidus Naegeli 1849 Coelomoron tropicalis Geitler Coelosphaerium spp Naegeli 1849 Cylindrospermopsis helicoidea Geitler Cylindrospermopsis rasciborskii Geitler Lemmemaniella palida Geitler Merismopedia punctata Meyen 1839 Microcystis rosea Kuetzing 1833 Microcystis subtillissima Kuetzing 1833 Psudoanabaena catenata Geitler Synechocystis aquatilis Naegeli

EUGLENOPHYCEAE

Phacus orbicularis Dujardin 1841 Trachelomonas scarab Ehrenberg 1835

CRYPTOPHYCEAE

Cryptomonas erosa Ehrenberg 1838 Cryptomonas marsonii Ehrenberg 1838 Ochromonas spp Ehrenberg 1838 Rhodomonas lacustris Pascher

CHRYSOPHYCEAE

Synura spp Pascher, 1916

Station	Approximate	e distance Latitude	Longitude	Depth (m)
1	200 m	6°31'595"N	1°25'650''W	11.4
2	1 km	6°31'595"N	1°25'365''W	25.5
3	2 km	6°30'810"N	1°23'821"W	>50
4	4 km	6°30'609''N	1°24'671"W	>50
5	6 km	6°28'852''N	1°24'407''W	>50
6	7 km	6°28'961"N	1°25'908''W	24
7	7.8 km	6°28'620"N	1°26'185''W	11.5

Sampling sites duringhorizontal studies Appendix 1D ABONO-APEWU TRANSECT

Sampling sites duringhorizontal studies Appendix 1E ASISIRIWA-DOMPA TRANSECT

Station	Approximate dist	ance Latitude	Longitude	Depth (m)
1	200 m	6°31'853"N	1°23'564"W	6.7
2	1 km	6°31'293"N	1°23'713''W	47.3
3	2 km	6°30'810''N	1°23'821''W	>50
4	4 km	6°30'609"N	1°24'671''W	>50
5	6 km	6°28'852"N	1°24'407''W	29.7
6	7 km	6°28'476"N	1°24'59 <mark>6''W</mark>	11.4
7	7.8 km	6°28'432''N	1°24'668''W	1.8
	AP3 P	2 5	BAD	

Appendix 2A Species List of Lake Bosomtwe sampled from November 2004 to October 2006

CHLOROPHYCEAE

Actinastrum hantzschii Lagerheim 1882 Ankistrodesmus falcatus Corda 1838 Tetrastrum elegans Chodat 1895 Scenedesmus polyglobus Meyen 1829 Closteriopsis longissima Lemmermann 1899 Mesotaenium spp Turner Fa., Dictyosphaerium spp Naegeli Golenkinia radiata Chodat 1894 Pandorina spp Bory 1824 Franceia spp Lemmermann 1894 Arthrodesmus convergens Ehrenberg Chlamydomonas spp Snow 1903 Chlorella spp Beyerinck 1890 Closterium acuatum Nitzsch 1817 Coelastrum astroideum Naegeli 1849 Cosmarium leave Rabenhorst Cosmarium moniliforme Corda 1834 Crucigenia tetrapedia Morren 1830 Monoraphidium contortum Naegeli Monoraphidium spiculiforme Naegeli Oocystis submarina Naegeli 1855 Ooocystis lacustris Naegeli 1855 Pyramidomonas tetrarhynchus Schmar. Selenastrum spp Reinsch 1867 Tetraedron minimum var granulata Kuetzing 1845 Tetraedron minimum Kuetzing 1845 Tetraedron trigonum Kuetzing 1845 Treubaria triapendiculata Bernard 1908

BACILLARIOPHYCEAE

Aulacoseira spp Hustedt Cymbella spp (Hempr.) Kirch Fragillaria africana Desm., Nitszchia recta W. Smith Navicula phyllepta Bristol, 1919 Surriella spp Ehrenberg Synedra ulna Hustedt Cocconeis phyllepta Ehrenberg Cyclotella stelligera Kuetzing Fragilalaria construens Desm.,

DINOPHYCEAE

Glenodinium spp Stein 1883 Gymnodinium spp Kofoid &Swezy 1921 Gyrodinium spp Kofoid &Swezy 1921 Peridinium elpatiewskyi Ehrenberg 1832 Peridinium inconspicum Eddy 1930 Peridinopsis spp Eddy 1930

CYANOBACTERIA

Anabaenopsis tanganyikae Miller 1923 Aphanizomenon spp Morren 1838 Aphanotheca spp Naegeli 1849 Aphanocapsa grevillii Naegeli 1849 Chroococcus dispersus Naegeli 1849 Chroococcus minimum Naegeli 1849 Chroococcus turgidus Naegeli 1849 Coelomoron tropicalis Geitler Coelosphaerium spp Naegeli 1849 Cylindrospermopsis helicoidea Geitler Cylindrospermopsis rasciborskii Geitler Lemmemaniella palida Geitler Merismopedia punctata Meyen 1839 Microcystis rosea Kuetzing 1833 Microcystis subtillissima Kuetzing 1833 Psudoanabaena catenata Geitler Synechocystis aquatilis Naegeli Romeria spp Geitler *Limnothrix spp* Geitler Gloeotichia echinulata Agardh 1842 Planktolynbya subtillissima Geitler Botryococcus braunii Kuetzing 1849 Gloeocapsa pupestris Naegeli

EUGLENOPHYCEAE

Phacus orbicularis Dujardin 1841 Trachelomonas scarab Ehrenberg 1835 Euglena texta Ehrenberg 1838

СКУРТОРНУСЕАЕ

Cryptomonas erosa Ehrenberg 1838 Cryptomonas marsonii Ehrenberg 1838 Ochromonas spp Ehrenberg 1838 Rhodomonas lacustris Pascher

CHRYSOPHYCEAE

Synura spp Pascher, 1916 Mallomonas caudata Iwanoff

DUSU)111L W	еш	une	Ι.	year								
CLASS		Ν	D	J	F	Μ	A	Μ	J	J	Α	S	0
CHLOROPHYCEAE													
Actinastrum hanzschii		х	х	х	Х	х	х		х	Х	х	х	х
Ankistrodesmus falcatus		Х	х	х	Х	х	х	х	х	Х	х		х
Arthrodesmus convergens		Х	х	х	Х	х	х	х	х	Х	х	х	х
Tetrastrum elegans		Х	х	х	Х	х	х	х	х	Х	х	х	х
Selenastrum spp		х			Х	х	х	х	х	Х	х	х	
Closteriopsis longissima		х	х	х	Х	х	х	х	х	Х	х	х	х
Closterium acuatum													х
Coelastrum astroideum													х
Cosmarium leave	21	\checkmark			V								\checkmark
Cosmarium moniliforme		\checkmark			\checkmark								\checkmark
Mesotaenium spp		х		х	\checkmark	\checkmark		х	х	Х	х		\checkmark
Scenedesmus polyglobus					\checkmark	\checkmark			\checkmark	Х	\checkmark		\checkmark
Pyramidomonas tetrarhynchus		х	х	\checkmark	Х	х	х	х	х	Х	х	х	х
Chlamydomonas spp		х	x	\checkmark	\checkmark				\checkmark		\checkmark		\checkmark
Chlorella spp				\checkmark	\checkmark				\checkmark		\checkmark		\checkmark
Crucigenia tetrapedia		х	х	\checkmark					\checkmark		\checkmark		\checkmark
Dictyosphaerium spp		х	х	х	X	х	х	х	х	Х	х		\checkmark
Golenkinia radiate		х	х	х	Х	х	х	х	х	Х			\checkmark
Monoraphidium contortum				\checkmark	\checkmark				\checkmark		\checkmark		\checkmark
Monoraphidium spiculiforme				\checkmark	\checkmark				\checkmark		\checkmark		\checkmark
Oocystis lacustris		х	х	х	\checkmark			х	х	Х	х		х
Oocystis submarina	1			\checkmark	\checkmark	\checkmark		\checkmark	\checkmark		\checkmark		\checkmark
Pandorina spp	<u> </u>			\checkmark	\checkmark			Х	х		\checkmark		\checkmark
Francia spp		х	х	х	Х	х	х	х	х	Х	х	х	х
Tetraeedron minimum	\leq	\checkmark		\checkmark	\checkmark			\checkmark	\checkmark				\checkmark
Tetrahedron minimum var granulate	3	\checkmark		\checkmark	\checkmark	х	х	х	х				\checkmark
Tetraedron trigone	2			\checkmark	\checkmark	\checkmark			\checkmark		\checkmark		\checkmark
Ttreubaria triapendiculata	The	х	х	\checkmark	Х	х	х	\checkmark	\checkmark	\checkmark	\checkmark		\checkmark
	La	v	v	v	x	v	v	v	v	x	v	v	v
Aulacoseira spp		A V	A V	A V	X	A V	A V	A V			л v	л v	л v
Fragilalaria construens	~	A V	A V	A V	N N	л	N	N	v	v	N	۸ ا	л v
Fragilaria Africana	-	л v	л v	A V	x	v	v	v	v	N	Ň	Ň	N N
Nitzschia clostarium		N	N	A V	X	л v	A V	A V	N	v	v	v	v
Nitzschia recta		N	N	N	N	N	N	N	N	$\frac{\Lambda}{}$	N	۸ ا	N N
Surriella spn		v	v	v	x	v	v	v	v	x	v	v	v
Synedra ulna	· · · ·	л v	л v	A V	X	A V	A V	л v	л v	X	л v	л v	л v
Cocconeis phyllenta	-	A V	A V	A V	X	A V	A V	N N	N	$\frac{\Lambda}{}$	л v	۸ ا	N N
Cyclotella stelligera	2.5	A V	A V	A V	X	A V	A V	N	v	v	л v	N	v
Cyclolella stelligera		A V	A V	A V	A V	A V	A V	v	A V	л V	A V	v	A V
FUCI ENODHVCEAE		A v	A V	A V	X X	A V	A V	A V	A V	л V	A V	A V	A V
EUGLENOFHICEAE Fuglong toxta		A V	N N	A V	$\frac{\Lambda}{}$	A N	x v	N N	N N	$\frac{\Lambda}{}$	N N	N N	N N
Euglena lexia Phagus orbigularis		A V	N	N N	Ň	N	v	N	N	v	v	N	N
Frachelomonas scarab		X V	v	v	v	v	2	N	N	л У	x v	v	v
Trachelomonas scarad		х	х	λ	Λ	х	N	N	N	Λ	N	х	х
CHRYSOPHYCEAE			,				,				,		
Mallomonas caudate		Х		Х	Х	х		х	х	Х	\checkmark	х	х
Ochromonas creanata		Х	X	X,	X	X	x	X	Х	Х	х	x	х
Synura ulna		Х				\checkmark		\checkmark	х	Х	Х		Х

Appendix 2B. The monthly occurrence of phytoplankton species in Lake Bosomtwe in the 1st year

CYANOPHYCEAE	Ŋ	D	J	F	M	A	M	J	J	A	S	0
Anabaenopsis tanganyikae								N				V
Aphanizomenon spp	N	N	V	N,	N	N	V	N	V	V	V	V
Cylindrospermopsis helicoidea								N				
Cylindrospermopsis rasciborskii												
Gloeotichia echinulata	x			X	X		Х	X	Х	х	х	Х
Pseudoanabaena catenata												
Microcystis rosea												
Microcystis smithii												
Botryococcus braunii	х	х	х	Х	х	Х	х	Х	Х	х	х	Х
Planktolynbya subtillissima	\checkmark						\checkmark		\checkmark			
Limnothrix spp	х	х		Х	х	х	\checkmark	х	Х	х	х	х
Merismopedia punctata	\checkmark											
Lemmemaniella palida	х	Х		Х	Х	Х	х			х	х	
Coelosphaerium spp	x	\checkmark		Х		х	х	х			х	
Aphanocapsa grevillii				\checkmark								
Aphanotheca spp	х	х	x	X	х	х	х	х	Х	х	х	х
Coelomoron tropicalis				Х					Х	х	х	
Romeria spp	х	x	х	Х	х	х	х	х			х	х
Svnechocvstis aquatilis			\checkmark									
Chroococcus disperses		V										V
Chroococcus turgidus	х	x	V	X	х	х		х	X	X		V
Chroococcus minimus			V									V
Gloeocapsa pupestris	х	X		Х					Χ	х		х
	16											
DINOPHYCEAE	1	1	1	1	1							
Gymnodinium cf uberimuum	N	V	N	N	N	X	X	X	X	x	X	X
Glenodinium spp	х	х	V	N	V	V	V	V	V	\mathcal{N}	\mathcal{N}	γ
Gyrodinium spp	X	X	X	X	X	X	V	N	X	х	X	X
Peridinium elpatiewskyi	\checkmark	\checkmark	V	V		V	V	N	V	х		
Peridinium inconspicum	х	х	X	X	Х					х	х	Х
Peridinopsis spp	Х	Х	V	Х	Х	Х	х	Х	Х	х	х	Х
СВУРТОРНУСЕАЕ	10											
Cryptomonas erosa	\checkmark											
Cryptomonas marsonii	V	V	V	V	V	V	V	Ń	Ń	Ń	Ń	Ń
Rhodomonas lacustris	x	Ň	Ň	x	Ń	V	Ń	Ń	x	x	Ň	x
	-	-	<				-	5	••			
Legend:												

<u>Legend</u>: $\sqrt{}$ means species is present x means species is absent

CLASS	Ν	D	J	F	Μ	Α	Μ	J	J	Α	S	0
CHLOROPHYCEAE												
Actinastrum hanzschii	х	х	х	Х	х	х	х	Х	Х	х	х	х
Ankistrodesmus falcatus	х		х		х	х	х	Х	Х	х	х	х
Arthrodesmus convergens	х	х	х	X	х	\checkmark	\checkmark			х	х	
Tetrastrum elegans	х		х	Х	\checkmark	х	\checkmark				х	
Selenastrum spp		х			\checkmark	\checkmark	\checkmark					
Closteriopsis longissima		х	х	Х	х	х	х	Х		х	х	х
Closterium acuatum			х									\checkmark
Coelastrum astroideum			Х							х	х	\checkmark
Cosmarium leave							\checkmark					\checkmark
Cosmarium moniliforme	\checkmark		\checkmark	\checkmark	\checkmark	\checkmark	\checkmark					\checkmark
Mesotaenium spp			х	Χ	х	\checkmark	х	Х			х	х
Scenedesmus polyglobus		х	х	Χ	х	х	Х	Х	Х	х	х	х
Pyramidomonas tetrarhynchus	х	х	Х	Х	Х	х	Х	Х	Х	х	х	х
Chlamydomonas spp		V			\checkmark	\checkmark	х	Х	Х			\checkmark
Chlorella spp			\checkmark		\checkmark	\checkmark	\checkmark					\checkmark
Crucigenia tetrapedia					\checkmark	\checkmark	\checkmark			х	х	\checkmark
Dictyosphaerium spp	х	х	x	Х	х	х	х	Х	Х	х	х	х
Golenkinia radiate		х	х	Χ	Х	х	\checkmark	Х		х	х	\checkmark
Monoraphidium contortum			х	Х	х	х		Х		х	х	х
Monoraphidium spiculiforme				Х	Х	х						\checkmark
Oocystis lacustris	х	х	х		х		х	Х			х	\checkmark
Oocystis submarina						\checkmark						\checkmark
Pandorina spp		х	X	\checkmark	х	Х	Х	X	Х	х	х	х
Francia spp	х		х		х	х		X		х	х	\checkmark
Tetraeedron minimum			\checkmark				\checkmark					\checkmark
Tetrahedron minimum var granulate			\checkmark					Х			х	\checkmark
Tetraedron trigone				\checkmark	\checkmark	\checkmark						\checkmark
Ttreubaria triapendiculata				\checkmark	\checkmark	\checkmark	\checkmark					
	1											
BACILLARYOPHYCAEA												
Aulacoseira spp	Х	x	Х	Х	Х	Х	Х	Х	Х	х	Х	х
Fragilalaria construens	Х		X	Х	X	X	X	X	X	X	Х	х
Fragilaria Africana	х	х	\checkmark	Х			\checkmark	V			Х	х
Nitzschia closterium	Х	х	x	X	X	X	X	X	Х	x	X	x
Nitzschia recta	Х	Х			V	V	V		V			\checkmark
Surriella spp	Х	Х	Х	X	\checkmark	V	V				Х	x
Synedra ulna	Х	x	X	X	x	V			Х	х	Х	
Cocconeis phyllepta	Х						Х	Х	Х	x	Х	\checkmark
Cyclotella stelligera	х	Х	Х	Х	х	Х	Х	Х	Х		Х	х
EUCI ENODUVCEAE												
EUGLENULTI CEAE	2	2	v	2	v	2	v	2	v	v	2	v
Engletiu textu Phagus orbigularis		N	N N	1	N V	v	N V	v	л V	∧ √	N	N N
Trachelomonas scarab	v	N	N	N	v v	∧ √	v v	$\frac{\Lambda}{}$	л Х	N	N N	N
racheiomonus scarao	Λ	N	N	N	л	N	л	N	Λ	v	N	N
CHRYSOPHYCEAE												
Mallomonas caudate	х	х	х	Х	x	х	х	Х			х	Х
Ochromonas creanata	х	х	Х	Х	\checkmark	х	х	X			х	X
Synura ulna	х	х	х	Х	х	х	х	\checkmark	Х	х	х	

Appendix 2C. The monthly occurrence of phytoplankton species in Lake Bosomtwe in the 2^{nd} year

CYANOPHYCEAE Anabaenopsis tanganyikae	N √	D √	J √	F √	\mathbf{M}	A √	M √	J √	J √	A √	S √	O √
Aphanizomenon spp	N		N	V	N	N	V	N	N	N	N	N
Cylindrospermopsis helicoidea	V	N	N	N	N	N	V	N	N	N	N	N
Cylindrospermopsis rasciborskii	N	N	N	N	γ	N	γ	N	N	γ	N	γ
Gloeotichia echinulata	x	X	X	X	X	N	X	X	X	X	X	X
Pseudoanabaena catenata	N	N	N	N	N	N	N	N	N	N	N	N
Microcystis rosea	N	N	N	N	N	N	N	N	N	N	N	N
Microcystis smithii	N	γ	γ	N	γ	γ	N	N	N	γ	γ	γ
Botryococcus braunii	x	x	x	X	X	X	N	N	N	X	X	X
Planktolynbya subtillissima	N	Ν	γ	N	γ	γ	γ	N	N	γ	γ	γ
Limnothrix spp	x	X	X	X	X	X	X	X	X	X	X	X
Merismopedia punctata	N	N	N	N	N	N	N	N	N	N	N	N
Lemmemaniella palida	N	N	X	X	х	ν	γ	N	N	N	N	N
Coelosphaerium spp	х	γ	N	N	х	Х	Х	۷ V	۷ N	γ	х	γ
Aphanocapsa grevillii	X	X	x	X	X	Х	Х	X	X	х	х	X
Aphanotheca spp	N	N	N	N	N	Х	Х	X	N N	x	х	N
Coelomoron tropicalis	ν	N	N	N	N	Х	Х	۷ V	X	γ	х	γ
Romeria spp	X	X	X	X	N	X	X	X	X	x	x	X
Synechocystis aquatilis	N	N	N	N	N	N	N	N	N	N	N	N
Chroococcus disperses	N	N	V	N	N	N	γ	N	V	γ	γ	γ
Chroococcus turgidus	X	X	X	X	X	X	X	X	X	X	X	X
Chroococcus minimus	V	N	V	N	N	N	γ	N	V	γ	γ	γ
Gloeocapsa pupestris	х	х	х	Х	Х	Х	Х	Х	Х	х	х	Х
DINOPHYCEAE	19				,		,	,		,	,	,
Gymnodinium cf uberimuum	x	x	V	V	V	X	V	V	V	V	V	V
Glenodinium spp	V	V	V		V	V	V	\checkmark		V	N	V
Gyrodinium spp	V	V	V	X	X	V	V	X	X	V	V	V
Peridinium elpatiewskyi	V		V		\checkmark	V	V					V
Peridinium inconspicum	V	х	V	X	Х	V	X	X	X	x	x	V
Peridinopsis spp	\checkmark	х		\checkmark	х		\checkmark					
СПУРТОРНУСЕАЕ	10											
Cryptomonas erosa	\checkmark		\checkmark		\checkmark		\checkmark			\checkmark		
Cryptomonas marsonii	\checkmark				V		\checkmark			\checkmark		
Rhodomonas lacustris	Х	X	X	Х	х	х	х	X	Х	X	\checkmark	X
Legend:												
√ means species is present												

 $\frac{\text{Legend:}}{\sqrt{\text{means species is present}}}$ x means species is absent

Phytoplankton species	Length (µ)	Width (µ)	Count	Factor	Biovolume (μm ³ L ⁻¹)	Cells L ⁻¹	Biomass (mg L ⁻¹)
Chlorella spp	4	4	120	29838	120664872	3580560	120.67
Microcystis spp	3	3	1800	29838	763733448	53708400	763.73

Appendix 2D: Sample phytoplankton biomass estimation sheet

Formula for calculating biovolume of individual phytoplankton:

Biovolume (µg/L) = Geometric shape)*(Factor) *(number of counts)

For example for a spherical cell like *Chlorella* biovolume is generated from the volume of a sphere –

 $V = (\pi/6)^* d^2$

Factor refers to the dimensions of the Counting chamber and the microscope at x400.

For a *Chlorella* cell of dimension 4 (μm) X 4 (μm)

$$V = 3.16*4^{3}/6$$

$$V = 33.7 \ \mu m^{3}$$

Biovolume (\mu g L⁻¹) = V* Counts*factor
Biovolume (\mu g L⁻¹) = 33.7*120*29838

Biomass (mg m⁻³) = $120664872*10^{-6}$ (10^{-6} converts to mg/m³)

Geometric shapes are based on Rott (1981).

The Northern Eclipse programme (University of Waterloo, Ontario, Canada) was used to generate all biomasses of individual phytoplanktons.

	2004-2005													
	November	November	Decemebr	December	January	January	January	Febraury	Februar	ry March	March	April	April	
P _B	1252.10	335.30	634.00	481.40	311.40	624.70	976.30	788.10	873.00	558.40	689.30	565.00	1137.00	
Chl a	-	-	7.50	-		> 1 $ > 1$	J.	D-1	-	-	-	9.94	6.90	
Z _{mix}	2.00	5.00	8.00	9.00	12.00	19.00	9.00	9.00	7.00	9.00	9.00	5.00	8.00	
Z _{eu}	4.72	4.72	6.70	9.65	7.55	7.55	2.60	2.91	3.73	4.72	5.31	5.96	7.55	
	May	May	June	June	June	July	July	August	August S	September	September	• October	October	
P _B	2843.80	3508.00	2475.70	893.90	2017.30	2676.30	535.30	1504.60	1386.60	1747.00	3756.80	3544.90	4704.50	
Chl a	-	8.20	6.72	1.80	5.15	7.30	7.53	10.41	-	-	-	-	-	
Z _{mix}	6.00	7.00	7.00	11.00	8.00	16.00	16.00	23.00	30.00	9.00	4.00	4.00	5.00	
Z _{eu}	7.55	10.96	16.86	10.98	10.98	9.65	9.65	9.65	3.30	3.30	2.60	1.64	1.64	

Appendix 2E: Phytoplankton wet weight biomass (mg m⁻³), chlorophyll *a* (μ g L⁻¹), mean mixing depth (Z_{mix} in meters) and euphotic depth (Z_{eu} in meters) for Lake Bosomtwe (2004-2006).

				(24	2005-2	.006						
	November	November	Decemebr	December	January	January	Febraur	y Februai	ry March	March	April	April	May
P _B	3827.40	2378.20	1748.30	2311.70	2945.50	2655.10	2405.80	2126.50	1847.20	2707.70	1669.00	1727.10	1858.50
Chl a	-	-	-	- 3	14.90	7.03	5.13	9.20	10.43	8.90	7.40	7.15	9.92
Z _{mix}	5.00	7.00	7.00	19.00	9.00	6.00	8.00	9.00	7.00	7.00	9.00	10.00	12.00
\mathbf{Z}_{eu}	3.30	3.30	3.73	3.73	3.30	4.20	4.20	3.73	4.72	4.72	4.72	7.55	7.55
	May	June	June	July	July	July	August	August	September	September	October	October	
P _B	1893.10	1762.70	1418.70	1583.80	1654.50	1362.60	2749.80	2242.10	2579.40	2465.40	3241.80	3394.60)
Chl a	7.22	10.05	6.42	7.10	11.51	9.70	21.60	27.10	15.80	13.54	9.99	9.10	
Z _{mix}	12.00	10.00	10.00	15.00	17.00	15.00	12.50	12.50	10.00	5.00	5.00	8.00	
\mathbf{Z}_{eu}	5.96	5.96	7.55	7.55	4.72	5.96	4.72	2.90	3.30	2.55	4.20	4.20	

Appendix 2F: Mean total phosphorus (µmol L⁻¹) in the mixing depth (Z_{mix}) for Lake Bosomtwe (2004-2006). (i)

					2	004-2005	5 (first y	ear)					
Month	Nov	Nov	Dec	Dec	Jan	Jan	Jan	Feb	Feb	Mar	Mar	Apr	Apr
TP	-	-	2.41	2.12	2.34	3.12	2.36	2.80	2.74	1.95	2.66	2.35	2.38
Month	May	May	Jun	Jun	Jun	Jul	Jul	Aug	Aug	Sept	Sept	Octo	Oct
TP	-	2.69	2.57	0.61	1.94	1.80	1.73	2.00	-	2.16	-	1.98	1.71
	(ii) 2005-2006 (second year)												
Month	Nov	Nov	Dec	Dec	Jan	Jan	Feb	Feb	Mar	Mar	Apr	Apr	
TP	-	1.87	1.26	1.76	1.66	3.53	1.79	1.71	1.60	1.44	1.48	1.75	
Month	May	May	Jun	Jun	Jul	Jul	Jul	Aug	Aug	Sept	Sept	Octo	Oct
TP	-	1.57	1.73	1.80	1.48			2.52	2.10	2.35	3.23	-	1.58



Regression Parameters	<i>p</i> -value	r	\mathbf{r}^2	Relationship equation
P _B vs Z _{MIX}	0.0214	0.332	0.1034	y=2573.5777-68.0228x
Chl <i>a</i> vs Z_{MIX}	0.5194	0120	0.0145	y=8.2277+0.1417x
P _B vs Z _{EU}	0.0752	0.251	0.0632	y=2410.5384-87.9369x
Chl <i>a</i> vs Z_{EU}	0.0039	0.503	0.2533	y=14.7721-0.7765x
P _B vs Z _{MIX} :Z _{EU}	0.9466	0.003	9.26*10 ⁻⁶	y=1893.7782+7.7050x
Chl <i>a</i> vs Z_{MIX} ; Z_{EU}	< 0.0001	0.738	0.5450	y=2.1348+41787
P _B vs TP	0.5075	0.106	0.0113	y=2239.1474-7591x
Chl a vs TP	0.1524	0.288	0.0802	y=4.6967+2.4615x
P _B vs Chl a	0.1162	0.288	0.0829	y=6.1741+0.0017x

Appendix 2G: Table of relationship Between P_B and some physicochemical and biological parameters of L. Bosomtwe (2004-2005)

Appendix 2H Depth distribution of phytoplankton biomass (mg m⁻³) during November 2004 to October 2005 in Lake Bosomtwe (Ghana)

Date/	Depth (m)									
time	0	1	2	5	8	10	12.5	15	20	30
Nov	1622.02	1107.68	1026.46	2465.9	444.84	140.10	208.14	129.27	140.44	-
Nov	224.02	339.06	585.04	193.126	140.17	548.92	621.6	43.12	22.42	-
Dec	1253.37	633.64	670.4 <mark>5</mark>	341.88	270.5	206.46	152.1	271.9	164.8	123.1
Dec	613.66	1084.50	355.86	192.9	437.0	204.38	262.96	186.82	147.32	84.74
Jan	368.72	208.18	464.84	227.12	343.94	401.96	164.92	61.32	47.8	33.64
Jan	987.92	761.4	405.7	580.26	559.44	226.46	1075.7	619.68	405.98	232.68
Jan	1618.06	1250.86	1908.7	460.62	3 <mark>94</mark> .3	225.24	608.78	1031.32	614.68	343.16
Feb	863.84	577.73	1361.39	689.1	448.52	737.26	298.36	184.58	142.02	67.28
Feb	487.36	1436.12	1200.12	939.6	301.4	197.46	288.34	145.76	92.6	67.94
Mar	819.3	977.36	268.54	230.64	401.78	652.58	462.50	218.58	471.82	151.34
Mar	524.20	778.84	626.22	918.14	633.06	655.14	197.28	412.34	171.44	52.00
Apr	365.48	689. <u>38</u>	695.12	509.72	330.92	483.24	683.3	308.82	94.86	97.74
Apr	772.16	11 <u>35.5</u> 6	1494.86	1028.22	1254.1	850.74	473.32	357.7	612.40	206.14
May	2974.1	3393.8	2532.2	2475.1	1515.4	2515.1	288.78	813.64	422.76	223.78
May	3856.4	3019.8	3467.8	4613	2582.1	2063.18	2117.84	989.12	342.76	133
Jun	2688.1	2368.3	1922.6	2183.2	<mark>321</mark> 5.9	2158.3	738.84	1433.86	1391.18	685.8
Jun	537.62	473.66	384.53	436.65	643.1	431.66	147.768	286.772	278.236	137.16
Jun	1700.0	3114.1	2307.9	1919.2	1045.1	1913.62	856.5	2272.8	288.12	199.6
Jul	4249.3	3118.4	3547.5	1663.5	3029.94	2254.68	2534.64	1012	2093.62	169.5
Jul	849.87	623.68	709.51	332.71	605.98	450.93	506.928	202.4	418.72	33.9
Aug	1375.5	1817.4	2035.3	1997.9	1337.74	1447.4	1378.6	1219.68	932.14	563.5
Aug	1195.8	2317.6	721.46	1568.1	1447.28	1060.54	2070.44	1709.3	896.22	879.38
Sep	1450.1	1854.7	1959.6	3062.9	1386.1	768.7	582.72	516.94	747.06	400.74
Sep	3967.2	3679.4	4054	3326.5	2089.12	2200.96	2448.08	1155.5	1134.64	200.9
Oct	3725.0	3216.3	4984.9	2253.4	956.9	1045.4	921.18	882.16	746.74	200.7
Oct	3310.38	6375.2	5150.88	3981.66	1232.68	707.4	1036.48	548.6	584.4	200.5

Date	Depth (m)									
/time	0	1	2	5	8	10	12.5	15	20	30
Nov	3150.04	3294.9	4160.02	4704.8	954.56	608.38	478.76	115.56	141.14	142.92
Nov	1676.94	1646.62	4203.36	3021.8	1342.14	638.2	336.18	349.62	243.88	232.84
Dec	1366.32	2044.24	1818.48	2229.96	1282.74	755.66	388.52	639.16	175.62	143.98
Dec	4185.78	2891.66	1786.72	2353.98	1911.44	740.68	526.32	850.76	542.32	463.28
Jan	5281.54	3345.72	3229.56	2199.4	1559.14	2057.38	1400.98	1150	1198.14	959.42
Jan	2418.1	2756.8	3621.28	1824.16	2875.78	2014.06	2756.8	895	1233.38	578.92
Feb	3280.8	2747.74	2524.94	2596.72	878.7	843.48	899.68	580.76	519.52	362.72
Feb	1317.64	2967	2508.76	2634.28	2106.52	1224.62	1317.68	813.98	592.38	545.28
Mar	1864.96	2891.96	2089.96	1153.34	1236.14	1019.46	560.18	706.18	550.86	485.44
Mar	2438.7	5178.42	2231.02	2138.24	1551.88	587.44	778.52	647.32	523.04	392.18
Apr	1345.32	1517.14	3277.26	2163.38	470.78	1240.34	1045.18	571.32	179.86	405.7
Apr	2134.44	851.22	2379.06	2792.76	1664.3	541	1031.62	700.18	436.92	471.02
May	1649.68	4666.84	1836.16	1539.68	6 33.84	1720.42	963.18	169.26	395.76	311.84
May	3495.1	3433.52	882.46	2303. <mark>38</mark>	1222.06	1102.42	812.78	643.94	433.68	472.3
Jun	1056.02	2193.3	1033.92	2 <mark>603.1</mark>	2785.72	904.38	1042.86	836.72	372.22	296.12
Jun	740.76	408.98	1189.12	949.92	2978.94	2244.76	1676.64	791.4	910.08	176.14
Jul	3091.1	1219.94	972.4	2638.36	931.82	1139.42	1299.62	1378.1	289.02	495.82
Jul	2457.34	935.52	1251.52	2833.76	2083.48	1729.46	1402.76	542.12	238.6	263.64
Jul	2179.48	825.52	2175.16	1154.02	769.18	1500.78	1431.46	865.4	252.24	452.6
Aug	3308.36	3 <mark>152.2</mark>	2422.7	2446.28	3274.12	1326.76	3318.18	1620.28	377.7	819.34
Aug	2890.44	3334.74	2477.8	2024.9	2469.6	1643.62	853.32	846.2	628.56	524.42
Sep	2198.68	2666.84	3975.98	2165.76	2939.78	1529.36	1176.8	1293.04	637.8	429.52
Sep	4194.42	2691.84	2295.16	680.2	1566.92	905.92	729.9	937.68	733	365.78
Oct	4460.48	2812.22	2907.48	2787.2	2313.74	1506.04	1017	1609	923.96	130.66
Oct	1782.86	3575.42	2396.04	5362.72	3856.04	2133.72	912.6	889.48	418.94	366.66

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Appendix 2I Depth distribution of phytoplankton biomass (mg m⁻³) during November 2005 to October 2006 in Lake Bosomtwe (Ghana)





Appendix 2J Plates of some Phytoplankton species of Lake Bosomtwe (x 400)



- 1. Cryptomonas erosa 2. Phacus orbicularis 3. Cosmarium moniliforme
- 4. Gymnodinium spp 5. Peridinium elpaktweiskyi 6. Cosmarium laeve
- 7. Tetraedron minimum 8. Cosmarium laeve (dividing) 9, 10. Tetraedron trigone
- 11. Nitzschia spp18, 33. Cylidrospermopsis rasciborskii
- 19. Cylidrospermopsis helicoidea 20, 21. Anabaenopsis tanganyikae
- 22. Microcystis rosea 23. Merismopedia punctata 24. Synechocystis aquatilis
- 25. Pseudoanabaena catenata 26, 31. Aphanocapsa spp 27. Romeri spp
- 28, 29. Aphanizomenon spp showing distinct inter-calary heterocysts
- 31. Microcystis spp 32. Lemmermaniella palida

Appendix 3A

Limitations and assumptions of the oxygen bottle method for estimation of phytoplankton primary productivity.

- 1. The method uses isolated plankton samples to indicate response of natural samples and therefore population may diverge by growth, decay or animal grazing in total density and quality composition from the original population as well as increased bacteria numbers (Pratt & Berkson, 1959).
- 2. Microbial activity and chemical oxygen demand may cause loss of oxygen when incubation time exceeds a few hours. Chemical composition of enclosed bottles may be altered and modify rates of phytoplankton growth and photosynthesis (Gessner & Panier, 1958).
- 3. Differences in the respiration and productivity rates are likely to occur in the paired light and dark bottles.
- 4. Benthic productivity is ignored since these methods are generally applicable to planktonic systems.
- 5. Many undesirable features with this method become more pronounced with longer exposures. Evidence of decline in photosynthetic rates in exposures longer than 4-6 hours has been observed (Ichimura & Saijo, 1951; Vollenweider & Nauwerk, 1961).
- Maintenance of samples at fixed positions during incubation may not reflect the natural condition. Example natural water currents may be reduced or eliminated.
- Bottles may absorb and reflect considerable amount of light (Findenegg, 1966).

- 8. Not usually applicable to phytoplankton densities expressed by concentration of chlorophyll *a* lower than 1 mg/m^3 .
- 9. Presence of O_2 bubbles is a common source of experimental error introduced accidentally during filling of the BOD bottles, from temperature changes or oxygen super-saturation by photosynthesis. Complete filling, stoppering and handling of bottles, avoidance of strong temperature changes in the sample and reduction of exposure times were employed to reduce these biases.
- 10. Under normal conditions respiration in the light and dark bottles are not the same as the use of this method assumes.
- 11. Respiration measured using this method is not only that of phytoplankton. Other non-photosynthetic components of the plankton (bacteria and zooplankton and other non-green microorganisms) contribute to the respiration. Thus the method measures community respiration and is therefore not good for measurement of Net Primary Productivity (P_N).

Appendix 3B

Table of relationship Between P_G, R_C, P_N and some physicochemical and biological parameters of L. Bosomtwe (September, 2005- August, 2006)

Regression Parameters	<i>p</i> -value n = 25	r	r ² I	Relationship equation
P _G vs Z _{eu}	0.2157	0.275	0.0658	y=3,6850+0.2276x
P _G vs Z _{mix}	0.1300	0.311	0.0968	y=3.4165+0.1400 x
P _G vs Z _{mix} :Z _{eu}	0.8705	0.035	0.0012	y=4.8720-0.0720x
P _G vs TP	0.9879	0.004	1.3118* 10	0^{-5} y=4.8656-0.0125x
P _G vs P _B	0.0085	0.515	0.2648	y=3.6098+0.2852x
R _C vs P _G	0.0041	0.553	0.3061	y=0.3088+0.9867x
P _N vs P _G	0.9661	0.009	8.0246* 10	y=0.3088+0.0133x
P _{G VS} Chl a	0.3797	0.228	0.0158	y=6.1597+0.8929x
P _{G VS} growth rate	0.1146	0.355	0.1258	y=0.1810+0.0766x