Nutrient Status and Planktonic Nitrogen Fixation in Lake Victoria, Africa

by

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Abstract

Eutrophication of Lake Victoria is attributable to the burgeoning human population in its watershed. The lake is experiencing increasing anthropogenic P loads from expanding urban, agricultural and industrial development. Paleolimnological and nutrient status indicators indicate excess P on a system scale. Excessive P has stimulated phytoplankton biomass and promoted blooms of N-fixing cyanobacteria. High algal biomass provides organic matter that contributes to extensive oxygen depletion in hypolimnetic waters during the stratified period. Low oxygen concentrations cause a complex suite of direct and indirect impacts including loss of aquatic animals and changes in nutrient cycling. Anoxia may be contributing to fish kills upon upwelling in Lake Victoria, and also causes release of materials bound to the bottom sediments including P. This release of nutrients reinforces eutrophication during periods of deeper and stronger mixing when dissolved nutrients are redistributed in the water column.

Data from this study suggest two patterns controlling nutrient status and phytoplankton biomass production in the surface waters of Lake Victoria. The first is seasonal alteration of N and P limitation and underwater light. Circumstantial evidence indicates that thermal stratification led to better light conditions for increased phytoplankton biomass, and increased P and N deficiency. Higher light during stratification compensated for and lessened effects of N deficiency and hence maintained higher algal biomass. Destratification and deeper mixing led to low underwater irradiance and reduced algal biomass and nutrient limitation. Entrainment of nutrient-rich hypolimnetic waters with low algal biomass reduces the potential for nutrient limitation during periods of stronger and deep mixing. A second pattern controlling

nutrient status is a longitudinal pattern of increasing light limitation and decreasing nutrient limitation, especially P, from inshore to offshore. Generally, light was the principal factor limiting phytoplankton production offshore as the ratio I_{24}/I_k was often below one and indicating light deficiency.

Thermal stratification and destratification influenced cyanobacterial species composition. Relatively warmer and shallowly mixing epilimnion promoted elevated N-fixing cyanobacteria and heterocyst biomass production which in turn led to elevated rates of algal N-fixation and rapid N turnover during stratification. N-fixation was an important source of N in Lake Victoria that resulted in increased total N as well as higher particulate N:P ratios during the stratified period. N-fixation in Lake Victoria was predictable from heterocyst abundances and light attenuation. Heterocyst abundances can also be used to infer N-availability in Lake Victoria and as guide to water resource management in the lake.

Overall, Lake Victoria is an example of a large ecosystem in which the phytoplankton community is usually limited by light availability but seasonally limited by nutrient availability. The ability to identify factors limiting phytoplankton community is of considerable importance to water management practices of Lake Victoria. Since both P and N are limiting, their reduction is essential in the control of cyanobacterial blooms and eutrophication of Lake Victoria. Nutrient status also provides a simple and yet an important tool for monitoring water quality.

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Chapter 1: General introduction

A clear understanding of how physical. chemical and biological processes interact at ecosystem scale is imperative in the protection and sustainable utilization of aquatic resources (Vigano et al. 1999, Vallentyne 1999). An understanding of interrelationships among air, water, land and biota, including human beings, is required for the development of effective nutrient control strategies that would led to successful management of culturally eutrophic systems (Vallentyne 1999) such as Lake Victoria (Hecky 1993). Human activity in the watershed has been found to induce lake responses at various levels, including at population and ecosystem scale. Goldman et al. (1990) found that atmospheric deposition of material produced by fires stimulated productivity in large lakes. Recently, Carignan and Steedman (2000) reported on disruptions of biogeochemical cycles in temperate lakes following watershed deforestation and /or wildfire and Carignan et al. (2000) concluded that water quality and aquatic biota are strongly influenced by disturbances in the watershed.

Already, human activity including overfishing, deforestation, intense cultivation, animal husbandry and introduction of exotic fish species has been linked to the modification of Lake Victoria in the 1990s (Bugenyi and Balirwa 1989, Hecky and Bugenyi 1992, Ogutu-ohwayo 1990 a, b, 1992, Lowe-McConnel et al. 1992, Lipiatou et. 1996, Ogutu-Ohwayo et al. 1996). There is evidence that atmospheric loads of sulphur and nitrogen (N) have increased due to acid rain produced by biomass burning in the catchment (Simons 1989). Further, precipitation over the African Great Lakes, Malawi and Victoria (Bootsma 1993) is now more enriched with phosphorus (P) and N than the in early 1930s.

Research to answer key questions on how human activity and a suite of watershed disturbances have impacted water quality and biodiversity in Lake Victoria is underway in the three riparian states (Uganda. Kenya and Tanzania). By examining major physico-chemical and biological processes that vary and interact in complex patterns. critical factors that control nutrient availability and influence phytoplankton biomass and productivity in lakes can be determined (Goericke and Welschmeyer 1998. Guildford et al. 2000). The goal of this research was to contribute to the knowledge that would be useful in the reduction of cyanobacterial blooms and reversal of eutrophication in Lake Victoria. Specifically, I examined how nutrients (P &N) and light availability influence phytoplankton N-fixation and algal biomass development through time and space in Lake Victoria.

Lake Victoria. the world's second largest (68,800km^2) freshwater body after Lake Superior, has become more eutrophic due to nutrient enrichment from a variety of anthropogenic sources, including agricultural, urban and industrial runoff and atmospheric deposition (Hecky and Bugenyi 1992, Hecky 1993, Lipiatou et al. 1996). The long water residence time (140 years, Bootsma and Hecky 1993), and the long (3440 km) and highly indented shoreline that includes numerous bays exacerbate eutrophication effects in Lake Victoria. Human settlement in the numerous urban and rural centers along the shoreline enhances eutrophication in the inshore regions, where nutrient loads from municipal and agricultural effluents are high.

In Lake Victoria, eutrophication manifests as increased total P and N accompanied by severe silica depletion and proliferation of cyanobacteria (Hecky 1993, Kling et al. 2001). Eutrophication has undoubtedly resulted in increased phytoplankton biomass and primary productivity (Mugidde 1992. 1993) that supports fish yields that have risen 4 to 5-fold since the 1950s (Ogutu-Ohwayo 1996). Increased fish production is a blessing as more local people have turned to the lake for their livelihood and fish exports to international markets earn foreign exchange for the riparian states. However, increased eutrophication has had several negative consequences that include elevated algal biomasses and proliferation of the obnoxious water hyacinth that thrives in the shallow eutrophic bays receiving nutrient-rich influents from rural and urban watersheds.

Anoxia created by decomposition of huge algal biomasses and aggravated by stronger thermal stability (Hecky 1993, Hecky et al. 1994, 1996. Lehman et al 1998) is one of the detrimental impacts of eutrophication in Lake Victoria today. Low oxygen provides reducing conditions conducive to release of trace metals from their oxides, and P release from generic hydroxides and N loss to the atmosphere through denitrification (Seitzinger 1988). In addition to affecting nutrient concentrations, anoxia directly affects distribution of biotic organisms in Lake Victoria. The loss of approximately 50% of aerobic water volume in Lake Victoria since the 1960s (Hecky et al. 1994) reduces fish habitat, which can lower the potential fish production. Hypolimnetic anoxia is thought to have forced haplochromine and tilapiine fish species into the oxic surface waters where they experience heavy mortality by the introduced Nile perch (*Lates Niloticus*) (Ogutu-Ohwayo 1990a, Goldschmidt and Witte 1992, Lehman et al. 1998).

Whether introduction of the piscivorous Nile perch in the late 1950s and ensuing food-web changes have modified algal responses to nutrient enrichment through the "top-down" effects in Lake Victoria has become a question of interest (Basin 1992). Elsewhere, changes in fish community accompanied by changes in grazing pressure have been shown to lead to changes in phytoplankton biomass and species composition through cascading effects (Carpenter et al. 1985. Blomqvisit 2001). After introduction of *Lates niloticus*, several herbivorous haplochromines and tilapiine fish species disappeared, while populations of some fish species (*Rastrineobola argentea* and *Oreochromis niloticus)* that prey on zooplankton increased in Lake Victoria (Ndawula 1994). Loss of the phytoplanktivorous cichlids and increased abundance of zooplanktivorous fishes likely led to reduction in the grazing pressure that allowed a build up of excess algal standing crops in Lake Victoria. Ndawula (1994) found increased predation by fish upon zooplankton contributes to the dominance of small-bodied zooplankton (Lehman and Branstrator 1993, 1994. Lehman 1996, Branstrator et al. 1996) incapable of controlling biomass of the large heterocystous cyanobacteria that dominate in Lake Victoria today (Kling et al. 2001). A reduction in grazing can result in reduced nutrient cycling including accumulation of particulate organic nutrients (Lehman 1996)8. These changes would favor the observed increase in abundance of the detritivore *Caradina niloticus* (Lehman 1996).

Changes in the fish community in Lake Victoria could also be linked to changes in algal species composition since the 1960s (Evans 1962 a, b, Talling 1966, 1987, Kling et al. 2001). The dominance of cyanobacteria including toxic forms and blooms of large heterocystous filamentous cyanobacteria such as *Cylindrospermopsis*, could have led to reduction of available food for the native fish species. Besides, cyanobacteria are less digestible and provide poor quality food (Taylor et al. 1991) that may have contributed to the reduction or loss of planktivorous haplochromines and tilapiines that once flourished in Lake Victoria. It is, therefore, reasonable that that changes in the fishery may have resulted, in part, from dramatic shifts in phytoplankton species composition in Lake Victoria.

In nature, several factors including grazing, light and nutrient availability affect phytoplankton biomass, growth and species composition (Reynolds 1984, Levine and Lewis 1987, Agrawal 1998, De Nobel et al. 1998, Kahru et al. 2000). When physical and biological controls are negligible, macronutrient (P, N & C) concentrations control algal growth and species composition (Brown et al. 2000), as well as planktonic N_2-fixation (Schindler 1977, Horne and Communis 1987) in a variety of ecosystems. P and N are the two nutrients generally considered most likely to limit algal growth in aquatic ecosystems.

Nutrient limitation occurs when the availability of a given element is not close to the Redfield ratio of C: N: P = 105:16:1 (Redfield 1963). This is possible through nutrient loss by uptake by biota, sedimentation or loss to the atmosphere. Deviations from the average Redfield ratios can also be due to alterations in the effective supply of nutrients to the phytoplankton through allochthonous inputs to the lake and internal inputs such as N-fixation, release from the sediments and cycling from the heterotrophs (Levine and Schindler 1992). In general, P limitation of phytoplankton is expected when the effective supply N: P ratios are much higher than the average Redfield ratios of 16:1 (Hecky and Kilham 1988). In this study, particulate nutrient (P, N & C) ratios and P and N uptake rates (N and P-debt) were used to assess nutrient deficiency. Guidelines of Healey and Hendzel (1980) that have been developed and accepted as indicators of nutrient status in temperate freshwater lakes were used to help interpret phytoplankton nutrient status in Lake Victoria.

For a long time. P has been identified as the primary limiting nutrient in freshwater and N in marine ecosystems (Howarth et al. 1988a). However. it has now been recognized that both P and N can be limiting in freshwater ecosystems in tropical and temperate locations (Smith 1983, Guildford and Hecky 2000). Phosphorus had been demonstrated to be the primary nutrient controlling and limiting phytoplankton biomass and productivity in temperate lakes during the summer (Schindler 1977. 1990. Hecky and Kilham 1988, Mollot and Dillon 1991). Few studies available demonstrate P-limitation in tropical East African lakes (Melack, et al. 1982). Switching from P to N or co-limitation by both P and N does occur in some lakes (Morris and Lewis 1988. Miller et al. 1986, Guildford et al. 2000). In Lake Victoria, N-limitation was initially suggested by Talling and Talling (1965) and both N and P-limitation can be present (Hecky 1993. Lehman and Branstrator 1993, Lehman et al. 1998). The increased presence of heterocystous N-fixing cyanobacteria (Kling et al. 2001) indicates the high N-demand and gives clue to the importance of N-fixation in Lake Victoria. Any P supply to an aquatic ecosystem will increase the N-demand which, if not met by allochthonous N supply and/or N return from the sediments, may favor growth of N-fixing cyanobacteria (Schindler 1977, Hendzel et al. 1994. Howarth and Marino 1999). N-fixation as a source of N has received considerable attention as a natural process capable of reducing N shortages in lakes (Schindler 1977, Flett et al. 1980, Tilman et al. 1982, Howarth et al 1988a). Whether N-fixation will balance N to P and eliminate N-deficiency in Lake Victoria remains to be evaluated.

Low N availability relative to P, indicated by the low N: P ratios, has often been suggested as one of the important factors that control cyanobacteria biomass and subsequently rates of N-fixation in situ (Levine and Schindler 1992). Schindler (1977) hypothesized that low N: P ratios should result in N-limitation of phytoplankton growth, and should, therefore, be associated with blooms of N-fixing cyanobacteria in lakes and estuaries. This hypotheses has been supported by several experimental and observational studies around the world (Flett et al. 1980, Howarth et al. 1988a, Levine and Schindler 1992, Hendzel et al. 1994) which show that low N: P external loading ratios (generally N: P<11:1 atom: atom) exert a strong selective influence on algal species composition and lead to dominance of N-fixing cyanobacteria, while higher N: P loading ratios favor other algal types that are not capable of fixing atmospheric nitrogen. On analysis of data from 17 lakes throughout the world Smith (1983) found that low epilimnetic ratios of total N to total P determine the relative proportions and composition of individual cyanobacterial species. He concluded that cyanobacterial blooms occur at low N: P ratios (TN: TP <29:1) and were rare when TN: TP exceeded this value.

In some aquatic ecosystems, however, variations in N: P ratios do not always account for changes in cyanobacterial biomass and N-fixation (MacFarland and Toetz, 1988, Smith et al. 1995). Neither do the low N: P loading ratios always result in dominance of heterocystous cyanobacteria in lakes (Pick and Lean 1987, Howarth et al. 1988 b, Levine and Schindler 1992). Using data from temperate and tropical (including sub-tropical) lakes Smith (1990) found no evident significant relationship between N: P loading ratios and annual rates of N-fixation. In Lake Victoria, proliferation of cyanobacteria including heterocystous N-fixers and nuisance toxic blooms of *Cylindrospermopsis* and *Microcystis* (Ochumba and Kibaara 1989, Ochumba 1990, Kling et al. 2001) is consistent with increased P (Hecky and Bugenyi 1992, Lipiatou et al. 1996) that can lower the N: P ratios in the lake.

Although increased nutrient (P & N) enrichment and biotic community changes have been invoked to explain cyanobacteria dominance and algal taxonomic changes in Lake Victoria, the stronger thermal stability in the 1990s (Hecky 1993, Lehman et al. 1998) may also be a contributing factor. Cyanobacteria, in general, occur in warm waters and are positively correlated to temperature in temperate lakes (Pick and Lean 1987). In addition, increased thermal stability affects light and nutrient cycling and availability, which in turn affects biological productivity. Most nutrients in lakes reside in the hypolimnion and can be made available for biological processes in the epilimnion by vertical mixing. The frequency and extent of mixing governs nutrient and dissolved oxygen exchange between bottom and surface waters and as well as light availability in the water column.

In tropical African lakes, thermal stratification has been found to regulate exchange of dissolved oxygen and nutrients between the epilimnion and hypolimnion (Talling 1966, Hecky 2000). A stronger thermal stratification due to elevated temperatures can accelerate temperature dependent chemical reactions and microbial processes such as denitrification-nitrification (Seitzinger 1988), thus affecting nutrient cycling and availability. In both temperate and African tropical lakes anoxic hypolimnia allow return of P to surface waters during mixing, but can act as permanent sinks for N (Hecky et al. 1996, Hecky 2000). Continuous N loss to denitrification during persistent thermal stratification can lead to high N demand that favors growth of cyanobacteria including N-fixers, if light and other chemical variables such as micronutrients are adequate.

Thermal stratification can regulate algal biomass development and phototrophic N-fixation in the euphotic zone through alterations of the mixing layer depth (Reynolds 1984, Levine and Lewis 1987). In temperate and high-altitude lakes, the role of light availability in controlling phytoplankton standing crops is often viewed from a seasonal perspective (Levine and Lewis 1987, MacFarland and Toetz 1988). Because of its light dependence, N-fixation in temperate lakes can be quite variable with season (MacFarland and Toetz 1988). Lower winter irradiance, combined with deeper mixed layers precludes development of high standing algal crops. Besides, mixing can return ammonia and nitrate to the epilimnion, which inhibits N-fixation. Thus, warm monomictic and dimictic lakes in temperate regions tend to have low rates of N_2-fixation during lake mixing. In many lakes cyanobacteria biomass and N_2-fixation can be restricted to periods of lake stratification during the warm water period in the summer, when phytoplankton sufficient light for growth, but dissolved inorganic nitrogen is scarce. However, high algal biomass or turbidity in eutrophic environments can reduce light available to the algae (Smith 1986, Pick and Lean 1987) with subsequent reductions in N-fixation. This study examines whether the tropical Lake Victoria, which experiences continuous irradiance and warm temperatures dubbed as the "endless summer" (Kilham and Kilham 1989), follows the rules of warm monomictic and dimictic temperate lakes. In this study, nutrient status measurements, algal biomass and biological N_2-fixation of the de-stratified and stratified phases are compared to elucidate the importance of thermal stratification in Lake Victoria.

In temperate aquatic ecosystems, rates of N_2-fixation are strongly dependent on the biomass of cyanobacteria and on the density of the heterocysts (Levine and Lewis 1987, Horne and Goldman 1972, Findlay et al. 1994). Given that N-fixation occurs in the heterocyst of cyanobacteria (Adams and Duggans 1999) it is logical to look for the relationships between rates of N -fixation and heterocyst abundance and cyanobacteria biomass in Lake Victoria.

This study adds to existing data on nutrient status, algal biomass, thermal and dissolved oxygen stratification and the light environment in Lake Victoria. Emphasis was on estimation of planktonic N-fixation and the potential for light limitation in Lake Victoria as N-fixation seems important and yet remains an unknown component of the N input into Lake Victoria. Biological N-fixation is fundamental to an understanding of what constrains algal productivity and subsequently fish production in Lake Victoria today. Both nearshore and offshore stations were most sampled in 1998 to allow determination of seasonal dynamics of phytoplankton nutrient status, N-fixation, and algal biomass. Measurements from nearshore and offshore waters were compared through periods of stable thermal stratification and de-stratification in Lake Victoria. The three specific objectives of this study were to (1) Determinate whether P and/ or N limits the phytoplankton community of Lake Victoria. Under this objective, the test hypothesis **was: N-fixation and biomass production are restricted by P availability in inshore regions of Lake Victoria.** (2). Quantify planktonic N-fixation and determine the role of light availability in controlling rates of N -fixation. Under this objective, the test hypothesis was: **N-fixation and algal biomasses were restricted by light availability in the deep pelagic regions, but not in the shallow inshore bays.** (3) Derive a predictive model for N-fixation that relates N_2-fixation to heterocyst abundance and light. Under this objective, the test hypothesis was: **N-fixation can be modeled and predicted from heterocyst abundance and N-fixation response to light.**

Thesis Format

Each chapter in this thesis follows a research paper format with exceptions of the introduction (chapter 1) and conclusion (chapter 6). While chapter 4 on algal N-fixation is the central theme for this thesis, Chapter 2 on nutrient concentrations and thermal stratification is presented first, as these are important factors that may influence variations in algal abundance and species composition as well as N-fixation activity in Lake Victoria. Chapter 3 on particulate nutrient concentrations and nutrient status has been presented to explain why N-fixation occurs and how P and N availability affect rates of N-fixation in Lake Victoria. Chapter 5 addresses the relationship between N-fixation and cyanobacteria biomass and considers how N-fixation can be predicted using biological variables such as heterocyst and cyanobacteria biomass in Lake Victoria. It is important that N-fixation is reasonably predicted using biological variables because lakewide measurements of N-fixation are not possible given the size of Lake Victoria and biological N-fixation is the dominant input of fixed N to the lake. Chapter 6 provides a general conclusion on the importance of N-fixation in Lake Victoria and suggests possible effective management options for the resources of Lake Victoria.

Chapter 2: Nutrient concentrations and thermal stratification in Lake Victoria.

Abstract

Temperature and dissolved oxygen profiles in combination with Wedderburn numbers were used to determine the patterns of thermal stratification or destratification in Lake Victoria. Thermal stratification, as described by the increasing Wedderburn number ($W \geq 1.0$), occurred between September and March/April. Deeper and stronger mixing ($W \leq 1.0$) occurred around July and resulted in almost uniform distribution of dissolved oxygen and nutrients in the water column and increased surface soluble reactive phosphorus (SRP). Decreased epilimnetic dissolved inorganic nitrogen (DIN) and SRP occurred during the stratified period and coincided with increased algal biomasses. Strong stratification also led to impoverishment of DIN in bottom waters as microbial populations use nitrate as an electron acceptor in anaerobic dissimilatory metabolism.

Organic particulate N and P were the most abundant forms of N and P in surface inshore waters but not offshore. Particulate P and N contributed a lesser fraction (< 35%) of the total P and N stock in the offshore stations. SRP made up a dominant fraction (48-80%) of the TDP offshore and was approximately 30-60% of the TDP in inshore. Mineralization of organic nutrients resulted in accumulation of inorganic fractions in the hypolimnion, especially P, during the stratified period. Total N, chlorophyll-a and particulate nutrient concentrations were higher by factors of 2 to 5 inshore than offshore, but total P was similar inshore and offshore. The low TN:TP ratios (≤ 20) suggest that N was the potentially limiting nutrient of phytoplankton offshore except in September-

October. This study suggests that Lake Victoria was P-sufficient at an ecosystem scale given that molar TN:TP ratios were always $\leq$ 50.

Introduction

Nutrients, chemical elements essential for biological growth, have received much attention in temperate freshwaters, and the pace of their study has increased in the tropics over the last fifty years. Nutrients have often been invoked to explain seasonality in algal biomass and productivity (Talling 1966, 1969: Hecky and Kling 1987: Mugidde 1993: Hecky 1993: Patterson et. al 1998), and in species composition and succession (Schindler 1977, 1990; Hecky and Kling 1987; Kling et al. 2001) in both temperate and tropical freshwaters. Nutrient availability sets the general level of productivity in many aquatic ecosystems (Vollenweider 1968; Schindler 1977), and Hecky (1993) specifically invoked nutrient availability as likely to have led to emergence of cyanobacteria as the dominant algae in Lake Victoria.

In an effort to understand and subsequently manage the deteriorating ecosystem of Lake Victoria, inter-disciplinary research has been conducted since the beginning of the 1960s. Recent results indicate modifications in the water chemistry compared to historic records in Lake Victoria (Talling and Talling 1965, Talling 1966a; Hecky and Bugenyi 1992; Hecky 1993; Hecky et al. 1994, 1996, Lehman and Branstrator 1993, 1994; Lehman et al. 1998). Phosphorus concentrations doubled between the 1960s and 1990s, while sulfate and soluble reactive silica concentrations have decreased (Hecky 1993, Lehman et al. 1998). Silica concentrations have decreased ten-fold and are often < 1μM, suggesting severe silica depletion comparable to that observed during the eutrophication of the Laurentian Great Lakes (Schelske 1975. 1988). Further evidence of nutrient modification in Lake Victoria comes from paleolimnological records that indicate widespread and progressive enrichment of the lake's sediment with the essential nutrients P, N. and silica (Hecky et al. 1996. Verschuren et al. 1998). Both limnological data and paleolimnological evidence indicate that increased nutrient inputs. in particular N, started in the 1920s, followed by increased P input in the 1950s (Hecky 1993). Verschuren et al. 1998). Elevated algal biomasses and a two-fold increase in algal primary productivity (Mugidde 1992, 1993) provide further evidence of increased nutrient enrichment of Lake Victoria in the 1990s compared to the 1960s.

Nutrient dynamics in aquatic ecosystems can be altered by several factors that include anthropogenic activities (Hecky and Bugenyi 1992; Hecky 1993; Lipiatou et al. 1996), changes in trophic relationships (Carpenter et al. 1985) and local or global climate change (Lehman et al. 1998). Numerous studies have demonstrated that "top-down" control by top consumers can have a cascading effect on the ecosystem through changes in planktivorous fish, zooplankton, phytoplankton and nutrients (Carpenter et al. 1985, Howarth and Mario 1999). Consequently, changes in the nutrient concentrations in Lake Victoria may partly be in response to biotic changes that include introduction and establishment of the top predator, Nile Perch *(Lates niloticus)* and loss of native fish species since the 1960s (Ogutu-Ohwayo 1990). Fish and invertebrates (zooplankton & *Caridina*) populations in Lake Victoria may influence nutrient cycling within the water column through grazing, excretion and decomposition. High nutrient concentrations support elevated algal biomasses which, on sedimentation and decomposition, contribute to increased oxygen demand which partly accounts for pronounced hypolimnetic anoxia in the modern Lake Victoria compared to the 1960s (Hecky et al. 1994). Anoxia has direct effects on element cycling, in particular P and N cycling, and on the distribution of aerobic organisms.

Thermal stratification is one of the major physical factors responsible for seasonal changes in chemical properties and biological processes in aquatic freshwater ecosystems in the world (Talling and Lemoalle 1998). Changes in thermal stratification associated with changes in local meteorological conditions have often been invoked to explain nutrient availability and distribution in tropical lakes, especially on seasonal time scales (Talling and Talling 1965, Talling 1969, Beadle 1981, Talling and Lemoalle 1998). Thermal stratification has direct physical impact on the depth of the mixed layer, which in turn affects the vertical distribution of nutrients including oxygen (Talling and Lemoalle 1998, Talling 1965) and light availability in the water column (Hecky 1993). In lakes, the strength and frequency of mixing governs the movement of nutrients from deeper waters into the euphotic zone as well as the development of anoxia and the distribution of plankton and fishes.

Despite scarce records of temperature profiles for the 1970s and 1980s, recent published studies indicate that climatic trends have increased thermal stability of the lake in the 1990s compared to 1960s (Hecky 1993; Hecky et al 1994, Hecky et al. 1996; Lehman et al. 1998). Lehman et al. (1998) specifically suggests that increased thermal stability due to climate change may be a master variable contributing to the eutrophication in Lake Victoria. This might occur through thermal stratification's direct physical impact on the depth of the mixed layer, which in turn affects the vertical distribution of nutrients including oxygen (Talling & Lemoalle 1998) and light availability in the water column (Hecky 1993).

Earlier published studies of thermal stratification (Fish 1957, Talling 1966) indicated a mobile thermal stratification, which was later found to be more persistent (Newell 1960). This earlier research gave initial insight to temporal variations of nutrients (Talling 1966) and phytoplankton (Fish 1957, Evans 1962; Talling 1966) with thermal conditions in Lake Victoria. Since the 1960s, however, similar studies were rarely done in Lake Victoria until the early 1990s. Some information on variation of oxygen concentrations over seasons are now published (Hecky et al. 1994) but a more detailed account of the interrelationships of nutrient, thermal and oxygen variations over the annual cycle remains to be made. Given this information gap and the relevance of thermal conditions in understanding nutrient dynamics, as well as biological productivity in aquatic ecosystems, temperature, dissolved oxygen and nutrients were measured in Lake Victoria from 1994 to 1998. This five-year study (1994-1998) allowed observations of the weakening and strengthening of thermal stratification and subsequent changes in nutrient dynamics. The degree of thermal stratification was determined from temperature and dissolved oxygen profiles and Wedderburn numbers. Thermal stratification effects were assessed from measured dissolved and particulate nutrients. The overall goal of this study was to determine nutrient concentrations and describe thermal conditions of Lake Victoria in the 1990s. This study focused on the macronutrients phosphorus (P) and nitrogen (N) because N and to some extent P have been suggested to limit algal productivity and biomass production in Lake Victoria (Evans 1962 a, b; Talling and Talling 1965; Hecky 1993; Lehman & Branstrator 1993, 1994; Lehman et al. 1998). At the same time, both P and N seem important in driving current eutrophication processes in Lake Victoria.

Data of thermal stratification is presented first, because of its affects on vertical and horizontal nutrient distributions. Then data on nutrient concentrations and distribution follow.

Materials and Methods

Study areas

To examine variability among stations, nutrient measurements were made frequently at three inshore sites and one offshore site (Figure 1 a, b,). The inshore areas included: 1) Napoleon Gulf (maximum depth 20 m), a generally shallow well sheltered gulf located near Jinja town and near the River Nile outlet; 2) Pilkington Bay (maximum depth 11 meters), a relatively shallow and isolated bay on the north side of Buvuma island; 3) Buvuma Channel (maximum depth 22 meters), a relatively turbulent channel and Bugaia, the offshore station (maximum depth 65 m). Itome Bay (maximum depth 30 m) and the Far station (maximum depth 70 m) were sampled less frequently to enable a comparison with the corresponding inshore and offshore stations. To examine broad inshore and offshore trends sites XL1 to X10 (Figure 1 b) were sampled infrequently between 1994 and 1996. Using a commercial Ferry Wagon, surface waters samples from Portbell, Uganda, to Mwanza, Tanzania, were sampled in December, 1994, and October, 1995.

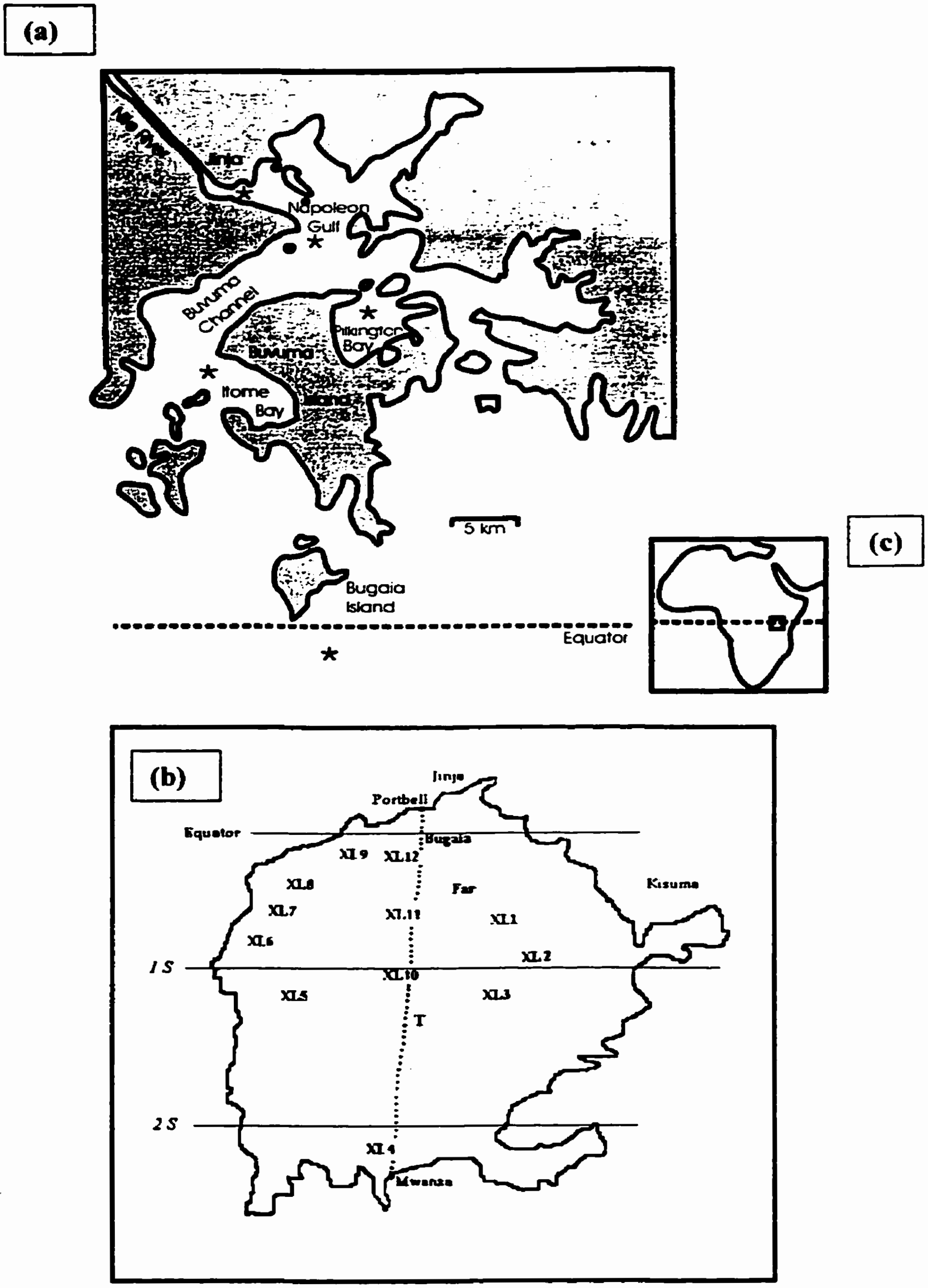


Figure 1. (a) Lake Victoria sampling stations (a) inshore, (b)offshore and cross-lake transect (T) from Portbell (Uganda) to Mwanza (Tanzania) and (c) map of Africa showing location of Lake Victoria.

Field sampling

In order to compare temporal events. measurements of nutrient concentrations. temperature and dissolved oxygen were done between 1994 and 1998. Measurements were done more frequently in 1994 to 1996 and most intensely in 1998. Inshore shallow regions (Napoleon Gulf, Pilkington Bay and Buvuma Channel) were sampled monthly in 1998. The deep offshore station (Bugaia) was sampled at least bi-monthly between 1994 to 1996. Bugaia was sampled monthly from July to December 1998 in an attempt to capture events during phases of thermal breakdown and re-establishment.

Temperature and dissolved oxygen

Vertical profiles of temperature and dissolved oxygen were measured during the day between 10 .00 and 14.00 hours in 1994-1998 using a submersible Hydrolab and/or a conductivity-temperature-depth profiling system (CTD, Sea-bird Electronics ®, SeaCat SBE 19) programmed to take measurements at one-second intervals. The CTD was calibrated annually by Sea-bird Electronics. The Winkler technique for determining dissolved oxygen was often used in conjunction with oxygen meters to assess their accuracy in measuring dissolved oxygen. At each site, water samples for nutrient concentration were drawn from discrete depths using a 3-L Van Dorn water sampler and dispensed into 1-L brown polyvinyl chloride bottles. In general, water samples for nutrient chemistry were taken from the surface to 60 m depth at 5 m to 10 m intervals in the offshore (Bugaia) water column, and from 2 m to 5 m intervals from the shallower inshore regions of Lake Victoria.

Water samples for dissolved nutrients were filtered through Whatman GF/F filters either in the field or in the laboratory. Water samples of 200-300 ml from offshore and of 50-100 ml from inshore were filtered onto Whatman GF/F filters and retained for particulate nutrients (P, C & N) and chlorophyll-a analyses. These filters were either desiccated over silica gel in the field or in an oven at 55 ° C for 24 hours and sealed in aluminum foil for storage. Samples for particulate P, C & N were shipped to the Freshwater Institute (FWI), Winnipeg, Canada, for analysis. The filtrate was analyzed for ammonium (NH_4^+), nitrite (NO_2^-), nitrate (NO_3^-), soluble reactive silica (Si), and soluble reactive phosphorus (SRP) within 2 hours or preserved with one molar hydrochloric acid and kept refrigerated for analysis within 48 hours. Unfiltered lake water samples were analyzed for total nitrogen and phosphorus concentrations.

Laboratory methods

Chemical and chlorophyll-a analysis

Chlorophyll-a filters were immersed in 10 mL of 95% methanol for approximately 20 hours at 4 ° C in the dark and absorbances of the extracts were measured spectrophotometrically at 665 nm and corrected for turbidity at 750 nm. Chloropyll-a concentrations were calculated as in Stainton et al. (1977), using the relationship:

$$\text{Chlorophyll-a } (\text{mg m}^{-3}) = \frac{(665_a - 750_a * v * 13.9 * 1000 * L}{V}$$

Where, 665_a and 750_a are absorbances at wavelengths 650 and 750 nm,

v = volume of extract, V = volume of water sample filtered, 13.9 is a constant using cold methanol. L = path length of the cuvette.

Dissolved inorganic nutrients (NH_4^-, NO_2^-, NO_3^-, Si, SRP) and chlorophyll-a (Chl-a) were determined spectrophotometrically following methods of Stainton et al. (1977). Ammonia was measured by the indophenol-blue method. Nitrate plus nitrite were determined using the cadmium method as described in Stainton et al. (1977). Briefly, the water sample was passed through a column packed with cadmium granules. Then the sample color was developed with a combined sulfanilamide and (1-naphthyl)-ethylenediamide dihydrochloride reagent and absorbance was read at 540 nm within 2 hours. Total dissolved nitrogen (TDN), total dissolved P (TDP) concentrations were determined following oxidation of the filtrate of 20-ml subsamples in alkaline and acidic persulfate, respectively, and through subsequent analysis of nitrate and phosphate as in Stainton et al. (1977). Dissolved organic P (DOP) and dissolved organic N (DON) were calculated as the difference between dissolved total and inorganic N and P. Samples for TDN, total P and particulate nutrients were shipped to Freshwater Institute (FWI), Winnipeg, Canada for analyses. Filters were stored in the dark, sealed in aluminum bags and shipped to FWI for analysis, because these analysis were not possible at FIRRI. Analyses of particulate samples were done following methods of Stainton et al.(1977).

A dimensionless Wedderburn numbers (W), a ratio of density stratification to wind forcing was used to describe the thermal stratification and was calculated as in Spigel and Imberger (1980) using the formula:

$W = g'h^2/(u^2 \cdot L_m)$

This formulae combines mixing depth h (in m), the reduced acceleration of gravity proportional to the density jump across the thermocline g' ($m\ s^{-2}$), shear velocity

u_* (m s^{-1}) and the lake length l_m (in m), with $g' = 2g (\rho_2-\rho_1)/(\rho_2+\rho_1)$, ρ_1 and ρ_2 = densities of epilimnion and hypolimnion respectively, $g = 9.8$ m s^{-2}, $u_*^2 = (\rho_{air}/\rho_{water}) CV$, ρ_{air} and ρ_{water} = densities of air and water in the mixed layer respectively, C = coefficient of drag and V = wind speed. Water density of the epilimnion and hypolimnion was calculated from temperature and salinity as in Chen, C.T and Millero (1977). Salinity was estimated from conductivity as in Wüest at la. 1996). Daily mean wind speed data was from the weather station at Jinja Peer. Water temperature data from Bugaia was used for the calculation of the densities of the epilimnion and hypolimnion. The hypoxia was defined as dissolved oxygen concentrations ≤ 4.0 mg L^{-1}, and the hypoxic-oxic interface as the depth at which dissolved oxygen concentrations were approximately 4.0 mg L^{-1}.

Results

Thermal conditions and dissolved oxygen concentrations in Lake Victoria

Surface water temperatures ranged from 24.4 °C to 28.1 °C and averaged 26.2 ± 0.9 °C in Lake Victoria. Differences between surface and bottom water temperatures were small and in the range 0.1 to 2.3 °C, average 1.2 ± 0.6 ° (Figures 2.1, 2.2 & Tables 2.0, 2.1). Maximum surface-bottom temperature differentials were in November-December in Napoleon Gulf (1.8-1.9 °C) and in September (2.2 °C) and March (2.3 °C) in Bugaia and coincided with increasing Wedderburn numbers (≥ 1.0) that indicate more stable thermal stratification.

Diurnal heating with temperature amplitudes of about 1 °C was often present in the upper surface waters of Lake Victoria (Figures 2.1 & 2.2 a-f). This diel stratification was superimposed upon a persistent annual stratification in both Napoleon Gulf and

Bugaia. Thermal stratification was more intense offshore (Bugaia) than inshore (Napoleon Gulf) as indicated by the distinctively curved depth-temperature profiles and stronger thermal discontinuities in the water column (Figures 2.1 & 2.2 a-f). At Bugaia, a persistent seasonal thermocline was observed between September and April. A shallow thermocline developed at 20 m in September, and progressively deepened throughout November, forming a distinctive secondary persistent thermocline at 40 m in December and an even deeper thermocline between 45 to 50 m in March 1998 (Figure 2.1). At the same time, Bugaia exhibited a well-developed oxycline between 30-40 m, which rendered 33-50 % of the deep-water column hypoxic from November to March in 1998.

Although thermal stratification usually occurs in sufficiently deep waters, the shallow sheltered Napoleon Gulf (Z_{max} = 20.0 m) located in a low wind stress area had moderate thermal stratification (Figure 2.1). Well-developed oxyclines occurred between 9 m to 20 m, which apportioned 40-60% of Napoleon's waters to deep-water hypoxia in 1998. With the exception of July, thermal stratification and hypoxia were persistent, suggesting lack of holomixis in Napoleon Gulf most of the year. Shallower Pilkington Bay (Z_{max} = 11.0 m) was different from other studied locations in that it experienced brief hypoxia that lasted 1-2 days only during extreme calm weather conditions. Pilkington Bay lacked persistent seasonal stratification and usually maintained relatively high dissolved oxygen concentrations (> 4.0 (mg L^{-1}) throughout the water column.

Table. 2.0. Temperatures and dissolved oxygen from inshore (Napoleon Gulf) Lake Victoria during 1998.

Month	Temperature (° C)		Dissolved oxygen (mg L^{-1})		Mixing depth
	Surface	Bottom	Surface	Bottom	Z_{mix} (m)
January	27.4	26.4	8.3	2.1	12.0
March	28.1	26.9	9.7	4.4	8.0
July	25.3	24.3	10.6	6.2	20.0
August	25.9	25.3	6.6	0.04	10.0
October	25.6	25.4	5.8	1.3	6.0
November	27.7	25.8	9.8	0.5	6.0
December	26.8	23.9	7.0	0.6	8.0

Table 2.1 Temperature and dissolved oxygen from offshore (Bugaia) Lake Victoria. during 1998.

Month	Temperature (°C)		Dissolved Oxygen ((mg L^{-1})		Mixing depth (m)
	Surface	Bottom	Surface	Bottom	
March	26.7	24.4	8.2	0.4	25.0
May	26.6	25.7	7.7	5.6	40.0
July	25.4	25.1	6.1	6.0	65.0
September	26.6	24.4	9.0	4.7	40.0
November	27.7	25.8	11.0	2.2	30.0
December	25.2	24.7	7.4	2.4	30.0

Within the period of this study (1994-1998), three major phases of thermal stratification were recognized in Lake Victoria. Early and then persistent thermal stratification occurred between September and December and between January-April respectively, as indicated by the increasing (≥ 1.0) Wedderburn numbers (Figure 2.2 g). Deep and stronger mixing occurred between June and August as indicated by the falling (≤ 1.0) Wedderburn numbers. Surface waters were coolest around July and the timing of this cool period remained relatively constant in 1994-1998. Stronger vertical mixing was also indicated by weak thermal gradients in July and re-oxygenation of deep waters in both Napoleon Gulf and Bugaia (Figures 2.1 a, 2.2 a, f).

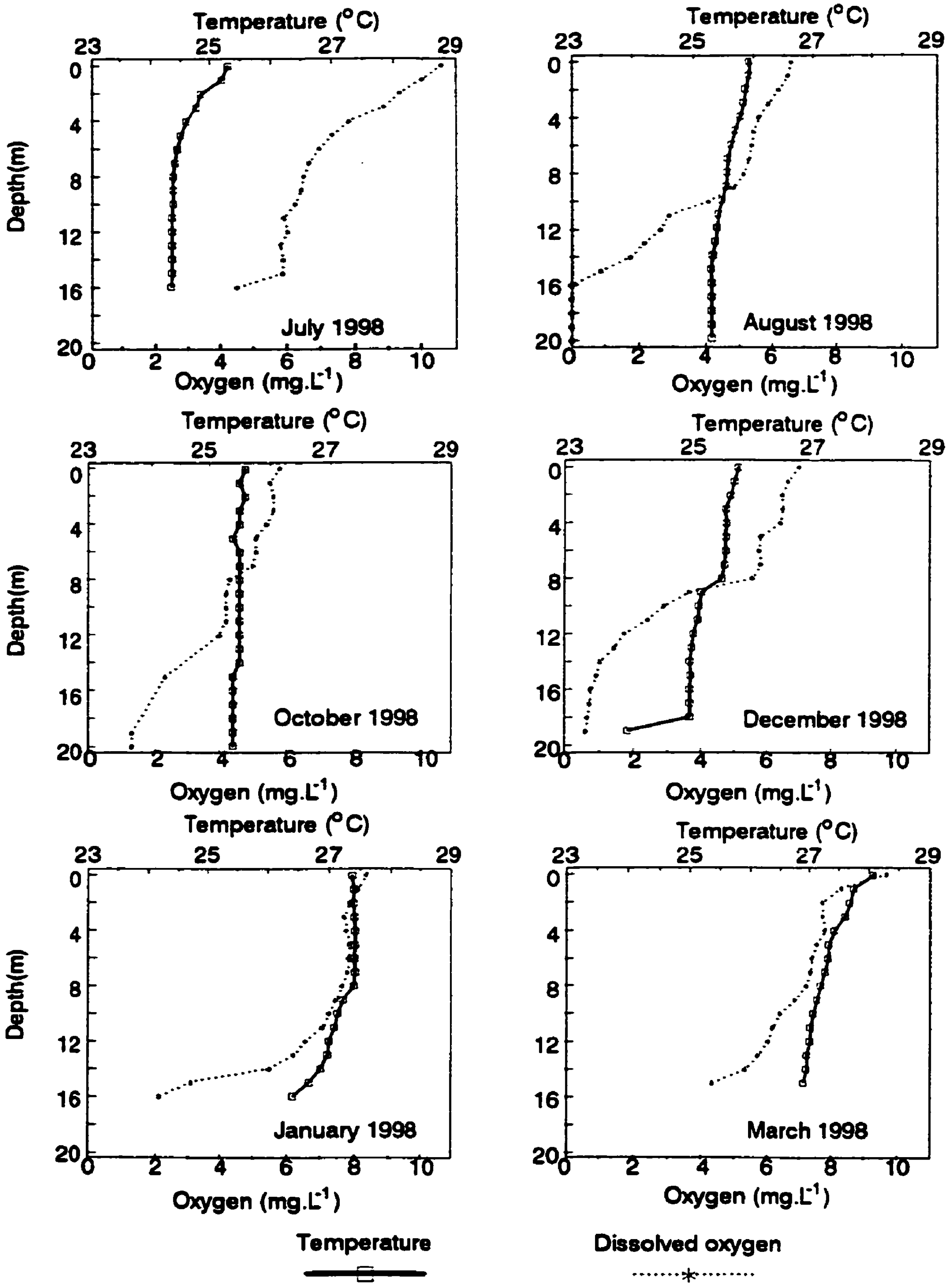


Figure. 2.1. Temperature and dissolved oxygen profiles from the inshore region (Napoleon Gulf) of Lake Victoria during 1998.

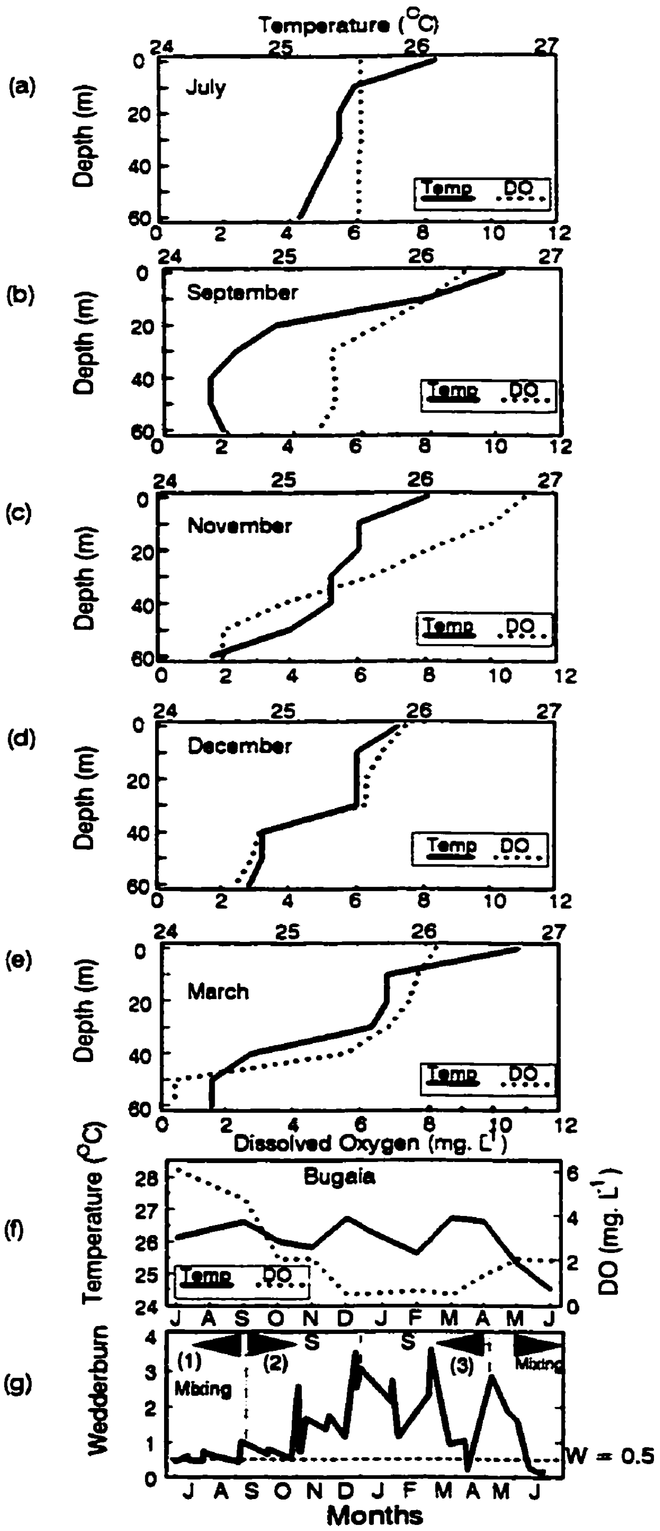


Figure. 2.2. (a) - (e) temperature (Temp) and dissolved oxygen (DO) profiles, (f) temporal variation of temp and hypolimnetic DO and (g) Wedderburn numbers from Bugaia. Dashed line, W, = 0.5, (2) = early thermal stratification & (3) = persistent stratification period.

After August. surface waters of Lake Victoria quickly and progressively warmed up from September to November. a period of shallow but stable stratification at both inshore and offshore sites (Tables 2.1 & 2.2. Figures 2.1 & 2.2). At the same time. the mixing depth decreased from 65 m to 30 m at Bugaia and from 20 m to 6 m at Napoleon Gulf and dissolved oxygen concentrations fell in concert to < 3.0 mg L^{-1} in the bottom waters (Figures 2.2 f. table 2.0, 2.1). Bottom waters of Napoleon Gulf were quickly and severely deoxygenated (< 0.1 mg L^{-1}) by August, but. a month later, had relatively high dissolved oxygen (4.7 mg L^{-1}). At Bugaia, surface temperatures fell slightly only at the surface in December, but did not result in deeper circulation as indicated by well developed thermoclines (Figure 2.2 d), bottom water anoxia (Table 2.1) and high Wedderburn numbers (Figure 2.2 g). A deepening of the mixing depth by 2 m occurred in Napoleon Gulf but a similar occurrence in offshore surface waters was not clearly evident.

Surface temperatures began to rise again between January and March causing more stable thermal stratification as indicated by maximum Wedderburn numbers (Tables 2.0, 2.1 & Figure 2.2 g). This intense thermal stratification was accompanied by further contraction of the mixed layer depth to 25 m at Bugaia. but Napoleon Gulf experienced a rise to 12 m and a fall to 8 m in the mixed depth during this time (Table 2.1). Further, bottom oxygen depletion to < 0.5 mg L^{-1} occurred at Bugaia (Table 2.0) but not in Napoleon Gulf. In the offshore regions of Lake Victoria (Bugaia), seasonal thermal stratification occurs over approximately 70-80% of the year, as it lasted from September to April/May. Napoleon Gulf, unlike Bugaia, was susceptible to short term changes in the thermal structure as evidenced by fluctuations in dissolved oxygen and mixed depth during the stratified period. Napoleon Gulf is likely to experience episodes of deeper partial mixing due to wind generated turbulence, given its relatively shallower depth and incursions of offshore waters due to set up under the dominant Southerly winds.

Vertical distribution of phosphorus and nitrogen in Lake Victoria

Particulate phosphorus (PP), dissolved P and total P varied over depth and time in Lake Victoria (Figure 2.3, 2.4). Generally, particulate phosphorus concentrations (PP) were much higher in the epilimnion than in the corresponding bottom waters, while dissolved P was higher in the hypolimnion (Figure 2.3). Dissolved inorganic P concentrations (SRP) were more easily measurable in offshore waters and were in the range 0.2 – 4.5 μM at Bugaia, Buvuma and Itome Bay (Figure 2.3, Table 2.2). Average SRP concentrations were 2 to 4-fold lower inshore at Pilkington Bay, Buvuma Channel and Napoleon Gulf than in offshore surface waters (Table 2.2). Vertical profiles of DOP and TDP were similar to those of SRP. Strong vertical gradients of total P and its dissolved components were encountered in Bugaia during December-March. Persistent thermal stratification enhanced the accumulation of hypolimnetic P in Bugaia (Figure 2.3). At the same time, surface water SRP concentrations decreased remarkably as strong thermal stratification became established from December to March (Figures 2.3 d, f & 2,2 g). Similarly, areal total P concentration in the whole water column (0-65 m) and in surface waters (0-20 m) decreased 2 to 4-fold during the stratified period (Table 2.3). Total P concentrations in the water column at Bugaia decreased by half between September and October and between December and March.

On the contrary, areal total P concentration increased 2-fold in the whole water column and 5-fold within the surface mixed waters during destratification (May- July) at Bugaia (Table 2.3). As the thermocline continued to deepen, areal P concentrations for the whole water column rose to the annual maximum concentrations of 565 μM P m^{-2} in September. However, above 20 m depth total P concentrations remained relatively constant between July and September. In July, particulate P, dissolved P and total P exhibited an almost homogenous vertical distribution (Figure 2.3a). SRP and DOP reached relatively high concentrations in surface waters in July to September indicating P return from bottom water and sediments. Despite increased SRP and DOP concentrations, minimum particulate P concentrations were measured in surface waters in July at Bugaia (Figure 2.3a).

Table 2.2. Average soluble reactive phosphorus (SRP), total dissolved phosphorus (TDP) and total phosphorus (TD) and their standard deviation from the inshore (0-5 m) and offshore (0-10 m) surface waters of Lake Victoria. Numbers in brackets indicate sample size.

Station	SRP(μM)	TDP(μM)	TP(μM)
Bugaia	2.0 ± 0.7 (25)	2.5 ± 1.1 (25)	3.1 ± 0.9 (13)
Far Station	1.1 ± 1.2 (14)	1.7 ± 1.2 (4)	2.6 ± 1.3 (2)
Itome Bay	1.5 ± 1.5 (14)	1.5 ± 1.2 (6)	2.3 ± 1.0 (6)
Buvuma Channel	0.8 ± 0.9 (13)	2.5 ± 0.1 (15)	3.1 ± 0.7 (7)
Napoleon Gulf	0.8 ± 1.3 (20)	1.4 ± 2.5 (14)	2.9 ± 2.1 (9)
Pilkington Bay	0.5 ± 0.8 (11)	1.4 ± 0.1 (13)	2.3 ± 0.9 (7)

Table 2.3. Areal total P concentrations (μM m^2) from offshore (Bugaia) Lake Victoria during 1998

Month	Water column(0-65 m)	Surface water(0-20 m)
March 1998,	156.6	35.5
May 1998	247.4	29.5
July, 1998	442.8	137.7
August, 1998	575.9	148.7
September, 1998	564.6	145.5
October, 1998	178.3	59.3
November, 1998	247.5	72.3
December, 1998	296.5	60.5

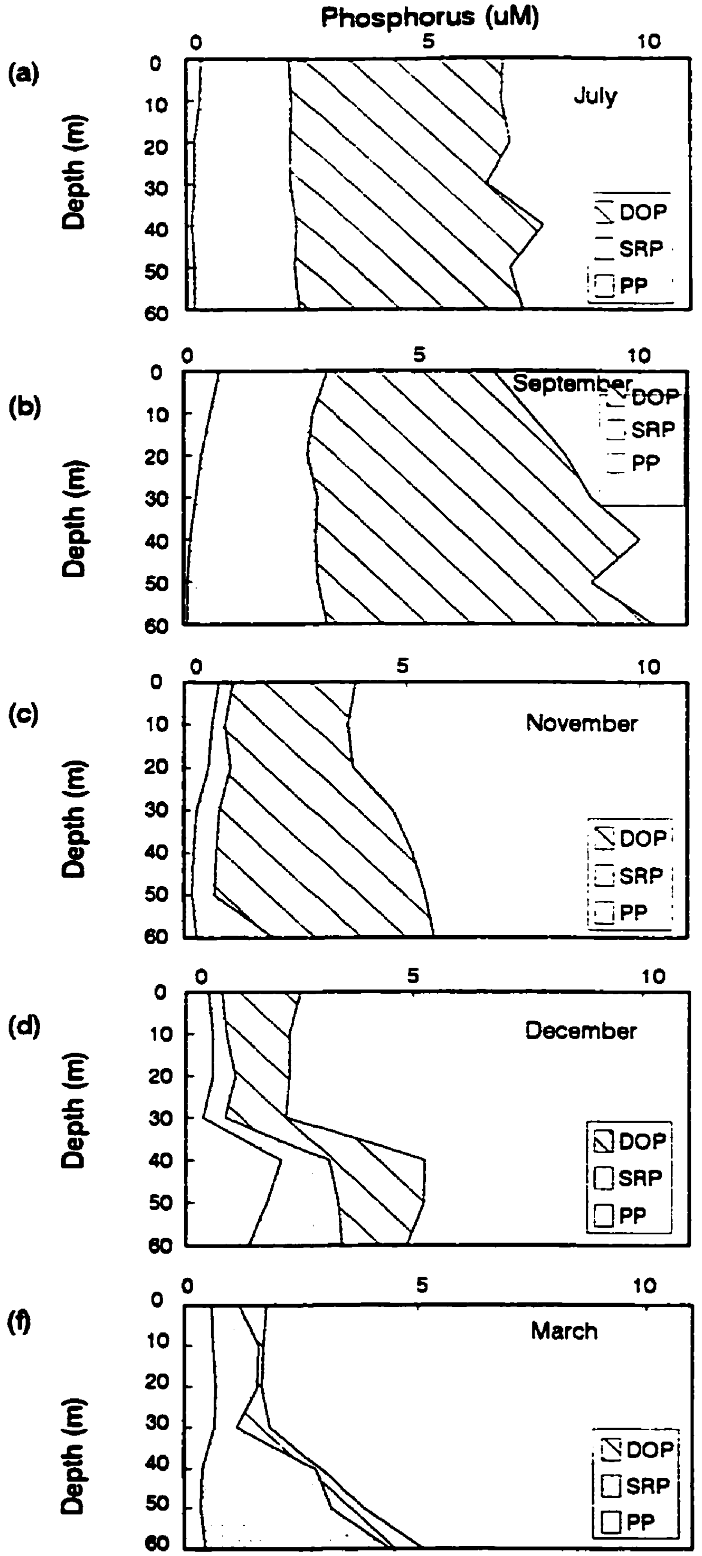


Figure. 2.3. Depth profiles of particulate P (PP), soluble reactive P (SRP) and dissolved organic P (DOP) from of offshore (Bugaia) Lake Victoria, during, 1998.

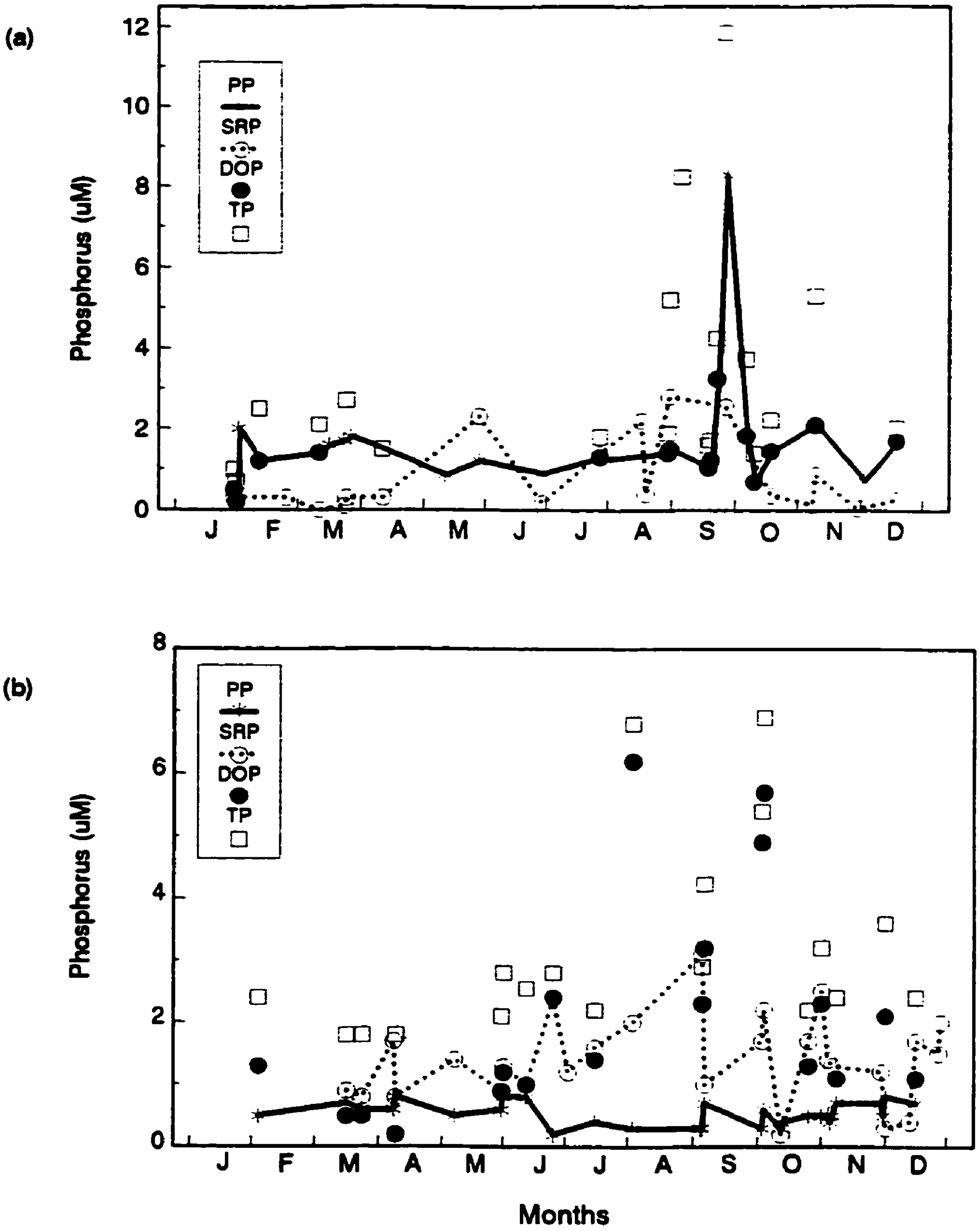


Figure. 2.4. Temporal variation of particulate P (PP), soluble reactive P (SRP), dissolved organic P(DOP) and total P (TP) from (a) inshore (Napoleon Gulf) and (b) offshore (Bugaia) surface waters, 1994-1998.

Vertical distribution of dissolved inorganic nitrogen in Lake Victoria

Figure 2.5 shows representative depth profiles of dissolved inorganic nitrogen (DIN) from Bugaia. Dissolved inorganic nitrogen varied over time and at all depths at Bugaia, although concentrations hardly exceeded 20 μM in the water column (Figures 2.5 & 2.6). Surface waters (0-10 m) were impoverished in DIN between September and March. The most prominent feature of the vertical distribution of dissolved N was the DIN maxima that occurred between 30 and 40 m depth in September-March (Figure 2.5 b-d). The DIN maximum was less prominent in July and occurred below 50 m in December (Figure 2.5 a-e). A decrease in DIN concentrations to as low as 2.0 μM was observed just above the ammonium nutricline beginning at 40 m depth in December.

Ammonium concentrations were generally $\leq$ 2.0 μM in the surface waters and tended to decrease slightly at 10 m depth (Figure 2.5 a, c, d), but increased below 30 m in December. Ammonium profiles show a distinct nutricline beginning at 40-m depth in December. Mid and bottom water ammonium maxima occurred below the oxycline between October and March in Bugaia. A deep-water (50-60 m) ammonium pool ($\geq$ 10 μM) occurred when dissolved oxygen concentrations fell to $\leq$ 1.0 mg L^{-1} in December. This hypolimnetic ammonium reservoir vanished or became very low ($\leq$ 2.0 μM) when dissolved oxygen concentration began to increase ($\geq$ 2.0 mg L^{-1}) in March and in June-July. Apparently, much of the ammonium regenerated in the hypolimnion in December hardly reached the surface layers as indicated by the falling DIN concentrations between the nitrate maximum and ammonium minimum (Figure 2.5 b, c, d).

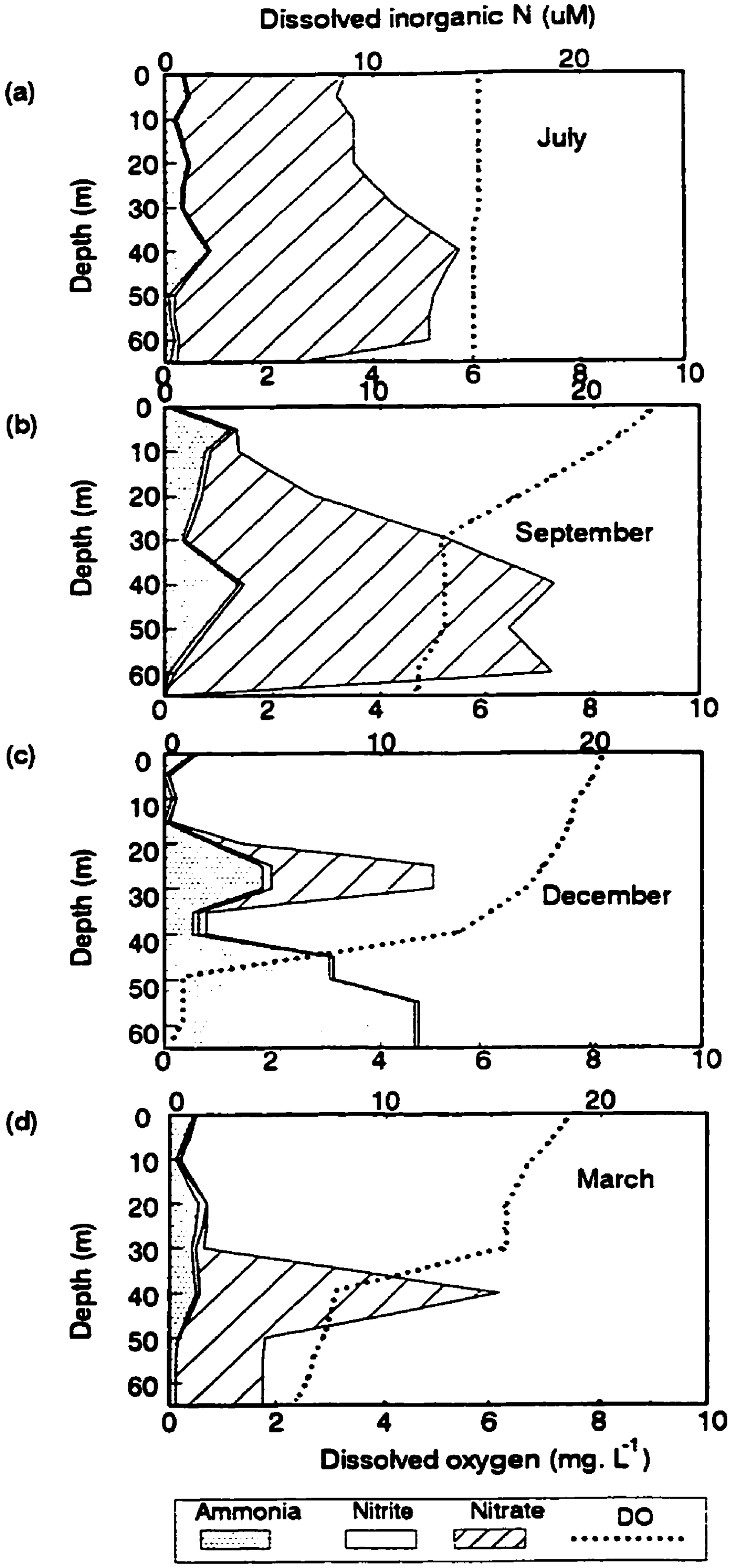


Figure. 2.5. Selected depth profiles of dissolved inorganic nitrogen (ammonia, nitrate, nitrite) and dissolved oxygen (DO) at Bugaia, during 1998.

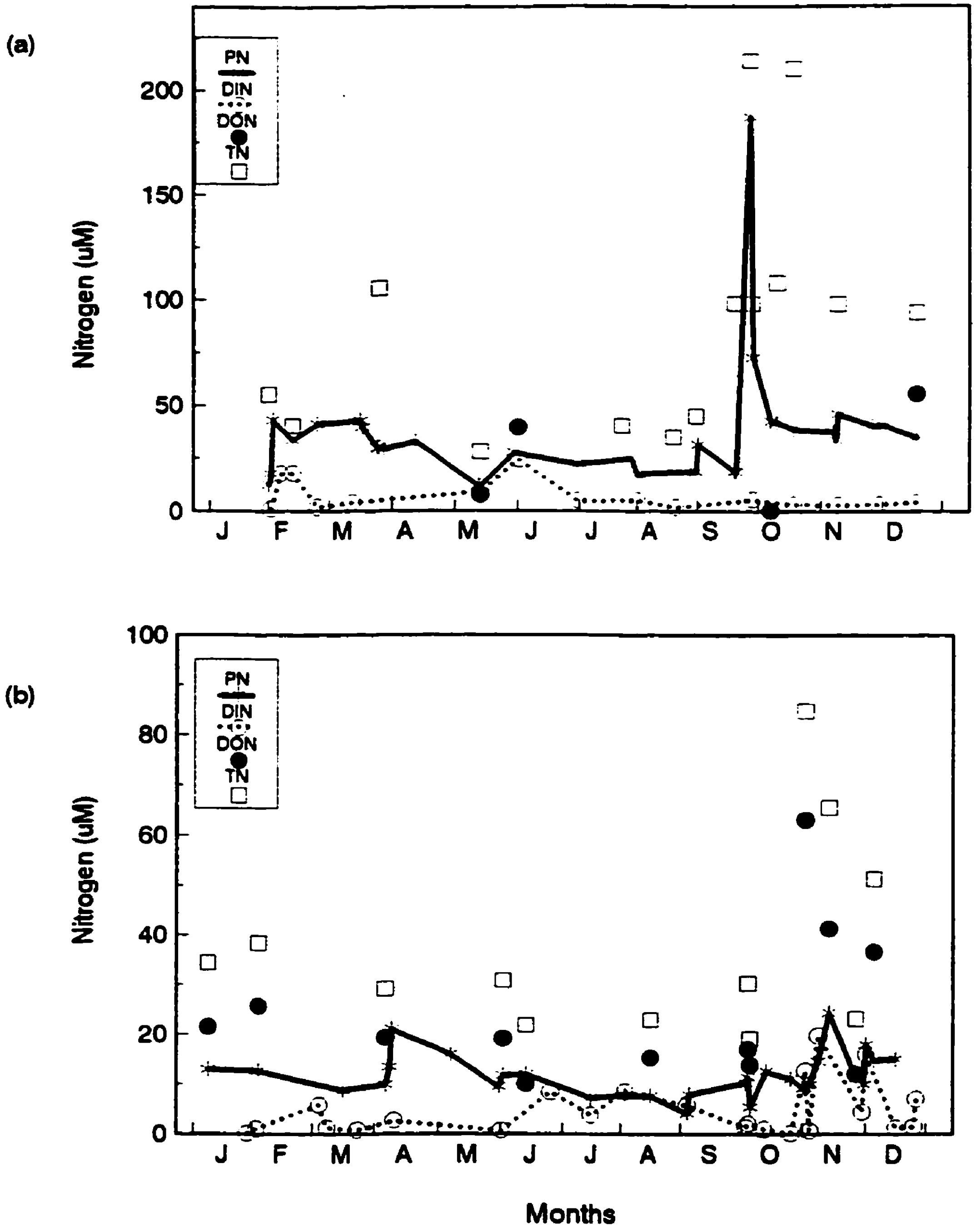


Figure. 2.6. Temporal variation of particulate N (PN), dissolved inorganic N(DIN), dissolved organic N(DON) and total N (TN) at (a) inshore (Napoleon Gulf) and (b) offshore (Bugaia) surface waters, 1994-1998.

Nitrate concentrations in surface waters (0-10 m) were generally low ($\leq$ 2.0μ) and bottom waters were equally impoverished in nitrate except in July-September and March. Deep vertical mixing allowed a build up of elevated nitrate concentrations (7.0-13.0 μM) throughout the oxic water column of Bugaia in June-July (Figure 2.5a), but surface water concentrations begun to decrease in September. The highest concentrations of nitrates (7-14 μM) were observed in mid-waters (20-40 m) as indicated by the depth-nitrate profiles in September, December and March at Bugaia. The mid-water nitrate maxima occurred just above the ammonia minima and were also above the oxic-anoxic interfaces where dissolved oxygen was $\geq$ 4.0 mg L^{-1}. With falling hypolimnetic dissolved oxygen concentrations ($\leq$ 2.0 mg L^{-1}) nitrate diminished to low concentrations (0-1.2 μM) and was undetectable below 50 m depth except in March. Total N increased to maximum concentrations between September and November in both inshore and offshore surface waters.

Spatio-temporal variability of nutrients in surface waters of Lake Victoria.

Total P concentrations were in the range 1.0 to 12.0 μM (Figure 2.3, 2.4 a, b). Average total P concentrations in surface waters generally had a narrower range of 2.3μM to 3.1 μM (Table 2.2) and were not significantly different among stations ($p > 0.05$). Bugaia and Buvuma Channel had similar but slightly higher total P concentrations compared to the Napoleon Gulf, Pilkington Bay and Itome Bay. However, SRP concentrations were significantly lower inshore than offshore. Inshore shallow waters in contrast had highest values of particulate P as well as other particulate nutrients and chlorophyll-a (Figure 2.6. 2.7. 2.8. Table 2.4).

Table 2.4. Average particulate phosphorus (PP). nitrogen (PN). carbon (PC) and their standard deviation from the inshore (0-5 m) and offshore (0-10 m) surface waters of Lake Victoria. Numbers in brackets indicate sample size.

Station	PP(μM)	PN(μM)	PC(μM)
Bugaia	0.5 ± 0.2 (24)	10.6 ± 4.4 (24)	79.1 ± 31.1 (33)
Far Station	0.7 ± 0.1 (8)	11.3 ± 2.0 (8)	109.7 ± 23.6 (8)
Itome Bay	1.0 ± 0.5 (19)	20.3 ± 10.9 (19)	138.8 ± 73.9 (19)
Buvuma Channel	1.0 ± 0.6 (33)	25.5 ± 20.8 (33)	178.4 ± 127.4 (33)
Pilkington Bay	1.4 ± 0.6 (38)	31.1 ± 14.9 (38)	230.6 ± 103.1 (38)
Napoleon Gulf	1.9 ± 1.7 (33)	42.8 ± 47.1 (33)	289.7 ± 283.0 (33)

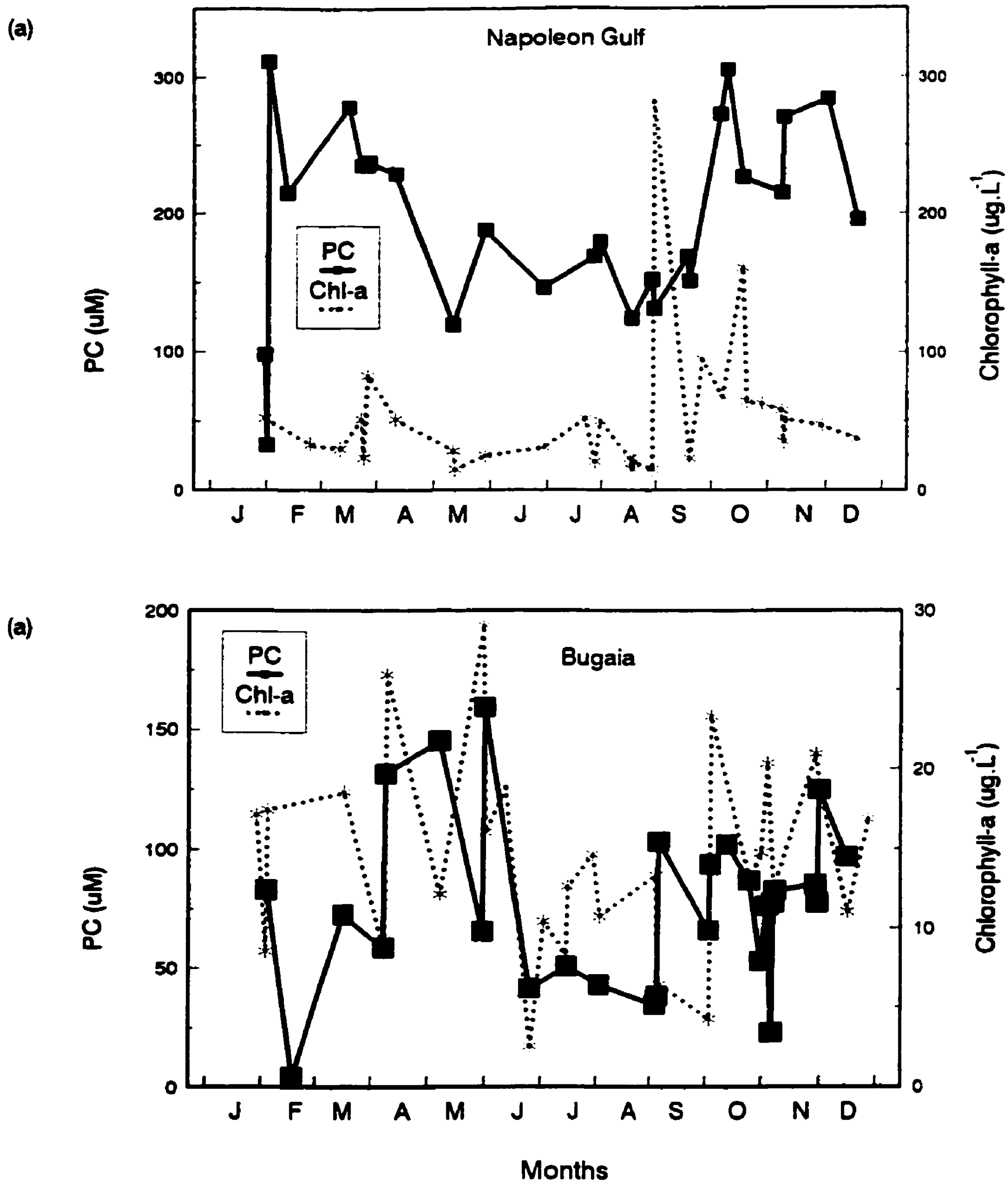


Figure. 2.7. Temporal variation of particulate C (PC) and chlorophyll-a from surface water of (a) Napoleon Gulf and (b) Bugaia, 1994-1998.

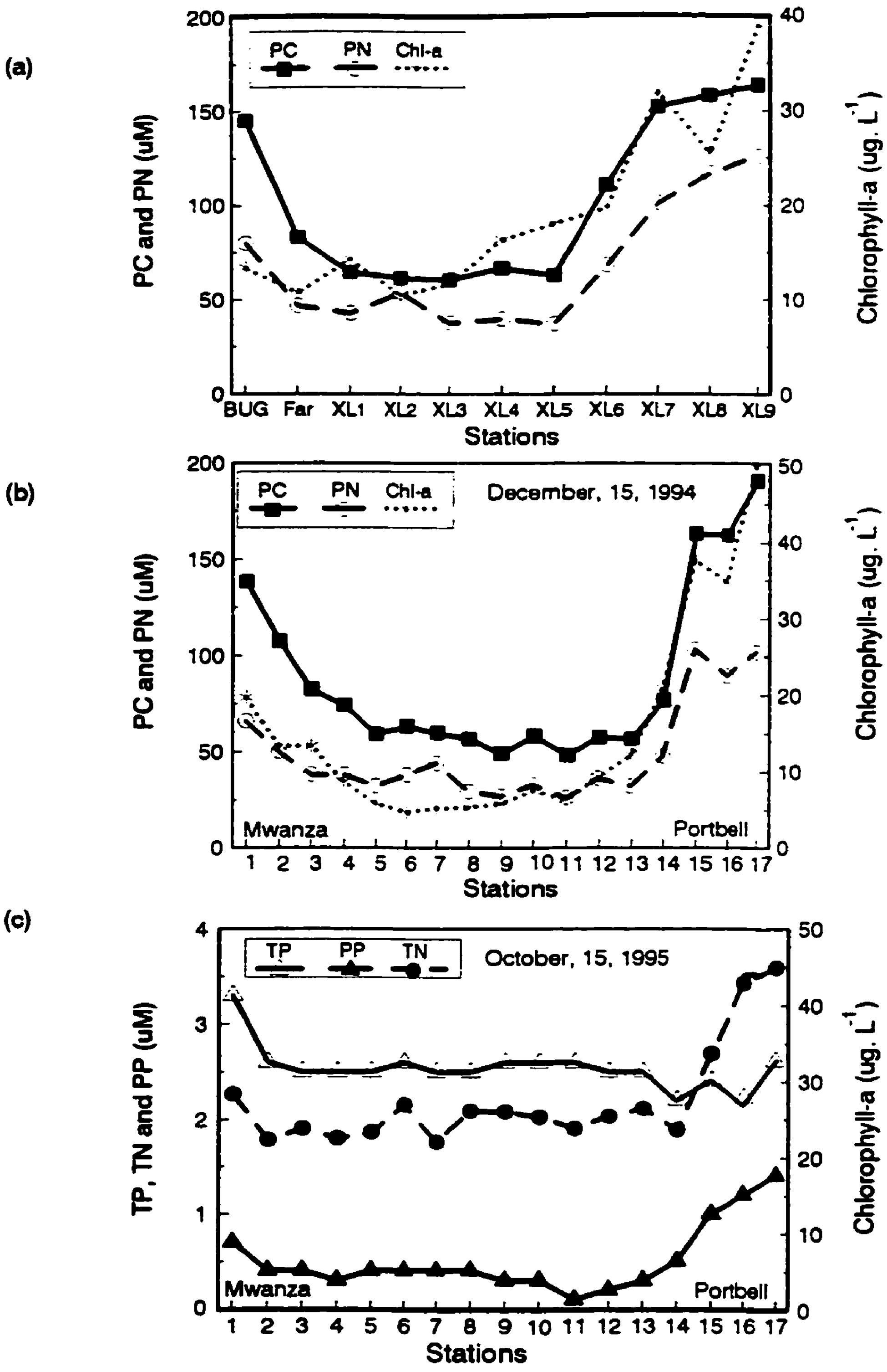


Figure. 2.8. (a) particulate carbon (PC) and nitrogen (PN) and chlorophyll-a concentrations (chl-a) from Bugaia and other offshore stations, (b) and (c) cross-lake transects from Portbell to Mwanza of particulate nutrients, chl-a, total N and P, in 1994-1995.

Seasonal dynamics illustrate similar trends in dissolved and total P in inshore and offshore surface waters of Lake Victoria (Figure 2.4 a. b). The greatest change in total P concentrations occurred between July and September corresponding to mixing and early stratification period (Figure 2.1 a & 2.2 a, g). At Bugaia. a major total P maximum (5-8 μM) occurred in July to September during de-stratification and early re-stratification respectively. Total P concentrations were halved (2-4 μM) during periods of prolonged intense stratification (December to April) in Lake Victoria (Figure 2.4 b).

Total nitrogen concentrations were in the range 19.0-231 μM in the surface waters of Lake Victoria (Figure 2.6 a & b). Average total N, total dissolved N and particulate N were 2x-3x higher nearshore than offshore (Table 2.5). Average total N was of similar magnitude in Napoleon Gulf and Pilkington Bay and was somewhat lower (19-23%) in Buvuma Channel. Napoleon Gulf had higher dissolved N concentrations than Pilkington Bay and Buvuma Channel (Table 2.5). Temporal variation in dissolved N, particulate N and total N were qualitatively similar (Figure. 2.6 a & b). Total N concentrations rose to maximum concentrations in September-November at both inshore and offshore and deceased remarkably in December. Offshore, the variation in TN was lower in amplitude but coincided in timing with Napoleon Gulf's minor maxima in October.

Maximum total P and its dissolved species was in July-September at both inshore and offshore sites (Figure 2.4 a, b) while maximum total N and particulate N values were measured later in September to November (Figure 2.6 a, b). The major total P maximum in Napoleon Gulf coincided with the total N maximum and with Bugaia's total P maximum (Figure 2.4 a, b, 2.6 a). Total P tended to increase with increases in suspended P, particularly in September when it increased to maximum concentrations and contributed approximately 70 % of the total P concentration in Napoleon Gulf (Figure 2.4 a). Particulate C and chlorophyll-a concentrations were highest between September and March when the lake was thermally stable (Figure 2.2g, 2.7 a, b). Particulate nutrient concentrations and chlorophyll-a were lowest in July when the mixed layer was most turbulent and deepest (Z_{mix} 65 m) in Bugaia. Overall, Napoleon Gulf maintained higher total N as well as higher particulate nutrient and chlorophyll-a concentrations than Bugaia.

Table 2.5 Average ammonium, nitrate, total dissolved inorganic nitrogen (DIN), total dissolved nitrogen (TDN) and total nitrogen (TN) and standard deviation in inshore (0-5 m) and offshore (0-10 m) surface waters of Lake Victoria during 1994-1998. Numbers in brackets = N.

Station	Ammonium (μM)	Nitrate (μM)	DIN (μM)	TDN (μM)	TN (μM)
Bugaia	1.4 ± 1.1(25)	3.0 ± 2.5 (25)	4.5 ± 3.2 (25)	26.3 ± 4.2 (25)	37.1 ± 18.7 (25)
Far Station	1.6 ± 1.0 (3)	0.6 ± 2.0 (2)	3.9 ± 1.2 (2)	24.1 ± 4.8 (2)	
Itome Bay	2.4 ± 3.7 (16)	1.4 ± 2.2 (16)	3.7 ± 4.6 (16)		
Buvuma	4.5 ± 4.9 (12)	1.4 ± 1.8 (12)	6.0 ± 5.7 (12)	54.0 ± 5.3 (12)	81.4 ± 13.0 (12)
Pilkington	4.5 ± 5.9 (12)	0.2 ± 1.0 (12)	4.7 ± 9.6 (12)	63.4 ± 8.6 (12)	100.2 ± 24.0 (12)
Napoleon	2.0 ± 3.6 (18)	1.3 ± 1.7 (18)	2.4 ± 1.2 (18)	70.4 ± 18.2 18)	106.4 ± 28.2 (22)

Total P and N and their species in the surface waters of Lake Victoria

The relative distribution of phosphorus between the dissolved and particulate form was different for inshore and offshore surface waters. Particulate P was by far the largest form of P inshore accounting for 40-60 % of total P (Table 2.3, 2.4 & Table 2.4). In Napoleon Gulf, particulate P was approximately 55% of the total P most of the year, except in September when it peaked and contributed 70-77% of the total P (Figure 2.4). Particulate P contributed a lesser fraction of 16% and 27% of the total P stock in the offshore Bugaia and Far stations, respectively. Buvuma Channel and Bugaia had much higher total dissolved P than any other stations (Table 2.3). SRP made up a dominant fraction (48-80%) of the total dissolved P offshore (Bugaia) and was approximately 30-60% of the total dissolved P in Napoleon Gulf and Pilkington Bay. However, SRP was frequently more variable in Napoleon Gulf, being undetectable to as high as 3.0 μM (Figure 2.4 a).

Particulate N was the dominant form of N inshore accounting for 52-61 % of total N (Table 2.4 & Table 2.5). In Napoleon Gulf, particulate N was approximately 51% of the total N most of the year, except in September when it peaked to 187.0 μM, accounting for 87% of the total N (Figure 2.6a). Particulate N contributed a lesser fraction (average 35%) of the total N stock in the offshore. In Bugaia, a particulate N maximum (24.0 μM) accounting for 37% of the total N was observed in October, but the largest suspended N: total N fraction (55%) was observed in May when PN was only half (12.0 μM) as high as in October and total N was also lower. In both Napoleon Gulf and Bugaia, maximum algal biomass (chlorophyll-a) occurred close but prior to the particulate N maximum.

Total dissolved N made up approximately 49% and 65% of the total N in Napoleon Gulf and Bugaia surface waters, respectively. Dissolved inorganic N contributed small proportions of 17% and 3-11% of the total dissolved N in Napoleon Gulf and Bugaia, respectively, and dissolved organic N (DON) contributed the greater fraction. A major DON maximum coincided with the TN maximum in October in Napoleon Gulf. Nitrite as a component of the total N was negligible and was always ≤ 0.1 μM in Lake Victoria. Ammonia made up a larger fraction (65%-87%) of the total dissolved inorganic N inshore and constituted only 37%-48% offshore. Ammonia concentrations were 50% lower in Napoleon Gulf, and Itome Bay, and 30 % lower in Bugaia, compared to concentrations in Pilkington Bay and Buvuma Channel. Nitrate unlike ammonia constituted a larger fraction (65-67%) of the DIN offshore and a lesser fraction (23-38%) inshore. Average nitrate concentrations in Bugaia were almost double Buvuma Channel, Itome Bay and Napoleon Gulf values. Pilkington Bay on average had 15 times lower nitrate concentrations compared to Bugaia.

Inshore to offshore trend of nutrients and chlorophyll concentrations.

Particulate nutrient, total N and chlorophyll-a concentrations were much higher in the shallow inshore regions than offshore during cross-lake transects (Figure 2.8 a, b, c). Nutrient concentrations were low and remained relatively constant at Bugaia and other offshore stations. Chlorophyll-a and particulate P, N and C decreased along the transect from Portbell in Uganda to the Tanzania offshore waters and then increased again on the Tanzanian inshore waters (Figure 2.8 b, c). Total N was higher in the Ugandan and Tanzania inshore portions of Lake Victoria while total P remained fairly constant.

Inshore-offshore nutrient transects show that Bugaia marked the beginning of deep offshore waters, while the Far station and XL1-XL5 were typical offshore sites with low chlorophyll-a and particulate nutrient concentrations (Tables 2.4 & 2.5).

Total N and total P relationship and their ratios in Lake Victoria.

Total nitrogen: total P (TN:TP) ratios were in the range 8-42, average 15.7 ± 9.3 (std) in Lake Victoria (Table 2.6). Average and minimum TN: TP ratios in Napoleon Gulf were almost double the corresponding values in Bugaia. In Bugaia, TN:TP ratios were low (≤ 20) most of the year with exceptions in September-October. Overall, higher TN:TP ratios occurred between September and April when the lake was thermally stable and low ratios occurred on destratification and deep mixing in May-August (Figure 2.9 a). Based on the criteria of Guildford and Hecky (2000), Napoleon Gulf tended toward N deficiency (TN:TP ratios < 20) for most of the year while Bugaia was only N-deficient in October when TN: TP ratios rose to maximum values. The particularly high TN:TP ratios in September to October (43.2) and February to March (42-43.2) in Napoleon Gulf were slightly lower than the accepted value of 50 which suggests P-deficiency on a system scale (Guildford and Hecky 2001). Based on the TN:TP ratios, Lake Victoria may be classified as a P-sufficient ecosystem with inshore shallow bays tending to N-deficiency during the mixing. Total N was strongly correlated with total P (Figure 2.9 b) and gave a regression slope (19.7) that was significant ($p < 0.01$). This regression slope approximately corresponds to the average TN:TP ratios which suggests that N may be limiting in Lake Victoria.

Table. 2.6. Minimum, average and maximum total nitrogen (TN): total phosphorus (TP) molar ratios in surface waters of Lake Victoria during 1994-1998.

Station	Depth (m)	Minimum	Average	Maximum
Bugaia	Surface (0-10)	8.1	14.5	27.2
Bugaia	Bottom (50-60)	4.4	8.1	11.9
Napoleon Gulf	Surface (0-5)	14.3	29.1	43.2

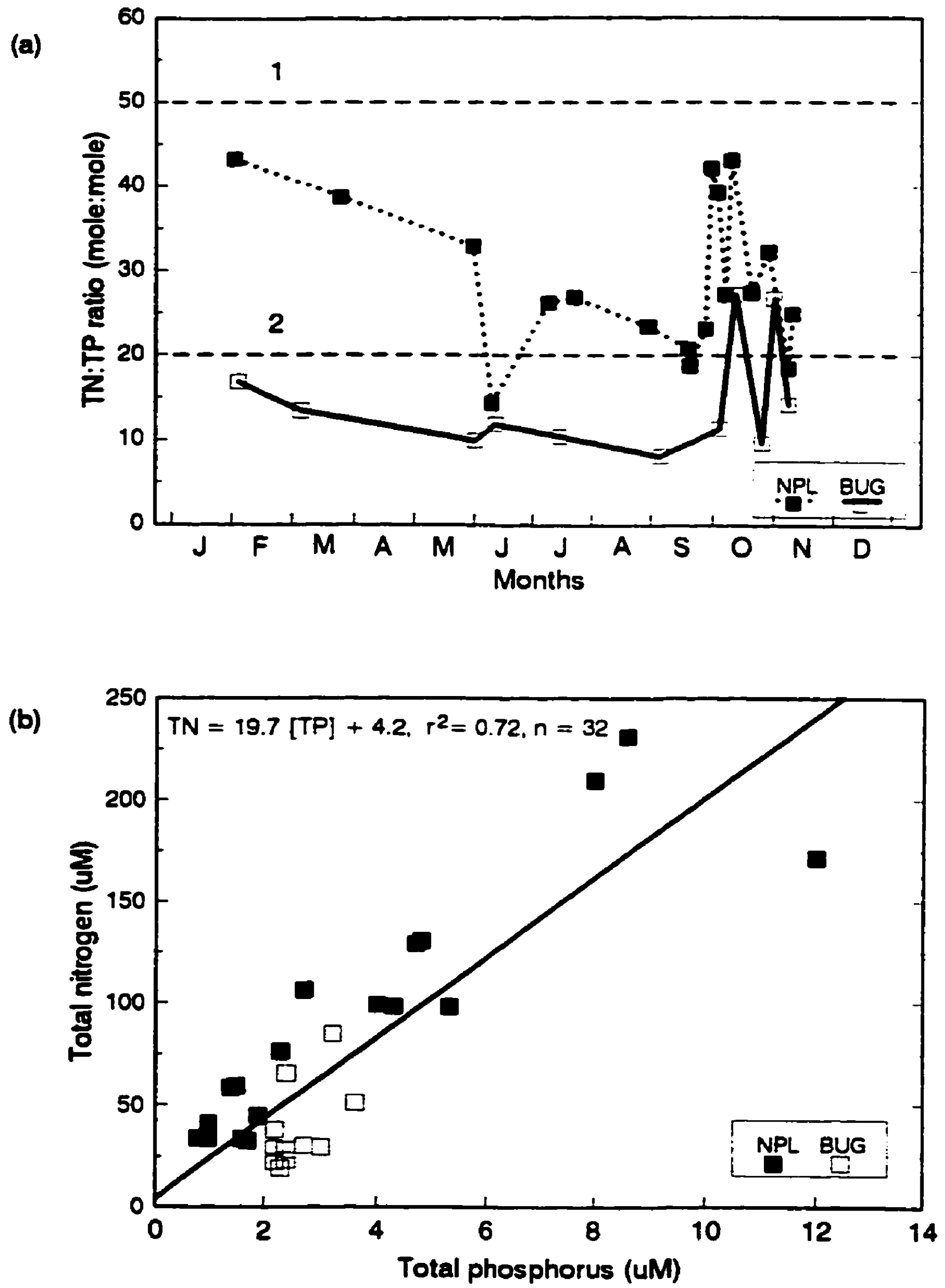


Figure. 2.9. Surface total nitrogen (TN):total phosphorus (TP) ratios for Napoleon Gulf (NPL) and Bugaia (BUG) and (b) relationship of average TN and TP within the euphotic zone of 0-5 m in Napoleon Gulf (NPL) and (0-10 m) in Bugaia (BUG). Dashed line, 1, = 20 and 2, = 50 indicating possible N and P deficiency (Guildford and Hecky (2001).

Discussion

Lake Victoria experienced phases of thermal stratification and destratification in 1994-1998 that were similar to those reported by Talling (1966). As in the 1960s, surface waters were coolest around July and the timing of this cool period remained relatively constant in 1994-1998 and consistent with earlier findings of the 1960s (Fish 1957; Talling 1966) and the recent measurements of the 1990s (Hecky et al. 1994). As in the 1950-60s, destratification and complete mixing in Lake Victoria occurred during periods of increased southerly wind stress around June-July. This windier season is a result of strong and cool Monsoon winds that blow towards Lake Victoria leading to a seasonal fall in air temperatures and lake-wide cooling (Newell 1960; Talling 1969). Talling (1966) found that increased evaporative cooling made the cooler and denser surface waters descend into the hypolimnion. However, current water temperatures, especially during mixing, were consistently higher compared to values reported in the 1960s (Talling 1966, Fish 1957) but were consistent with observations of higher temperatures and increased thermal stability in the lake in the 1990s (Hecky and Bugenyi 1992; Hecky 1993; Lehman et al. 1998).

Despite decreases in Wedderburn numbers in December and March, Lake Victoria remained thermally stable between September and March as indicated by the persistent thermoclines and nutriclines, and bottom water anoxia at Bugaia. Decreases in Wedderburn numbers during the stratified phase were likely a result of internal waves (seiches). Fish and Talling observed strong oscillations of offshore waters and thermocline tilts due to internal waves that could bring deep waters near the surface during periods of maximal thermal stability (Fish 1957, Talling 1966). These seiches lasted a period of 40 days and had the capability to spread their effects from offshore (Bugaia) to inshore waters (Buvuma). It seems possible that stronger thermal stratification in December in Napoleon Gulf may be due to incursion of cooler water at depth as indicated by the relatively lower bottom temperatures in December than November. Seiches or episodes of incursions of cooler water can be ecologically important as they permit partial return of various dissolved nutrients accumulated in deep waters to the mixed layer. Kitaka (1971) observed spikes in nutrient concentrations in surface waters during similar thermal events described by Fish (1957). and interpreted them as cyclonic upwelling.

The annual cycle of thermal stratification and destratification influenced the vertical distribution of dissolved oxygen and nutrients in Lake Victoria. Destratification allowed oxygen-rich surface waters to reach the hypolimnion, as indicated by substantially higher oxygen concentrations at bottom depth in June-July. In addition, strong and deeper mixing allowed nutrients, in particular P, from the hypolimnetic reservoirs to return to surface waters as indicated by the weak vertical nutrient gradients and the almost even distribution of total dissolved P and DIN in the water column. In contrast, during the stratified period (September to April) a stable thermocline extended through Napoleon Gulf and Bugaia, and limited exchange and supply of nutrients from the hypolimnion to the epilimnion resulting in a build up of regenerated nutrients in the hypolimnion. Thermal stratification was a strong barrier to P and N exchange between surface and bottom waters during the advanced phase (December-April) as more concave nutrient and oxygen profiles indicate. Duration of thermal stratification also contributed to concavity.

Thermal stratification isolated the epilimnion from the hypolimnion and. increased the potential for deoxygenation of bottom waters. Indeed. thermal stratification delimited the deeper oxygen-poor waters from the surface oxygen-saturated waters leading to a hypoxic hypolimnion for 80% of the year in Lake Victoria. Deoxygenation did occur rapidly, particularly inshore, resulting in deep water hypoxia that has spread upward to 25-40 m in Bugaia and horizontally further into the shallow nearshore Napoleon Gulf. Hecky et al. (1994) observed a hypoxic hypolimnion in Bugaia, but did not report similar observations in nearshore regions of Lake Victoria. The persistent deep water hypoxia during this study (1994-1998) and earlier studies of 1990-1992 (Hecky et al. 1994) indicate that hypoxia has become almost a persistent feature of 40% to 60 % of the bottom waters of Lake Victoria. Talling (1966) observed brief moderate hypoxia at the deepest depths (60 m) during brief periods of stratification in offshore waters (Bugaia) of Lake Victoria.

Oxygen concentration tended to be higher in the upper surface waters of Lake Victoria, where photosynthesis occurs, and lower below the thermocline as a result of respiration. Increased algal biomass (Mugidde 1992, 1993) likely contributed to increased photosynthesis and increased respiration. Oxygen consuming reactions are likely to have increased with increased organic substrate and in concert with increased temperatures (Hecky 1993, Hecky and Bugenyi 1992) in Lake Victoria. Lehman et al. (1998) suggested that increased stability may have contributed to higher algal biomasses in Lake Victoria today. This is because thermal stratification has a direct impact on the mixing depth, which in turn affects the vertical distribution of dissolved oxygen and nutrients. Thermal stratification reduces the mixing depth and improves light for algal growth. Dissolved oxygen availability has consequences for various redox biochemical reactions as well as aerobic life in Lake Victoria. Oxygen availability or deficiency is likely to influence nutrient cycling (Hecky 2000) and availability, and nutrient availability in turn put checks on algal biomass production and species composition in Lake Victoria (Chapter 5).

Examination of the SRP and DIN profiles show that thermal stratification and hypoxia affect P and N recycling differentially in Lake Victoria. Generally, SRP increased with depth during the stratified period while DIN decreased below the thermocline by end of the stratified period in March. This is because PO_4 is released from insoluble iron oxides under reducing hypoxic hypolimnion conditions, but N can be lost to denitrification at the oxycline (Hecky et al. 1996). This, in part, explains high SRP in bottom waters as indicated by low average TN:TP ratios (8:1), as well as low N availability in surface waters. Bugaia had 40-50 % lower TN: TP ratios than Napoleon Gulf. The almost 3-fold higher total N concentrations in Napoleon Gulf were the reason, because average total P was of similar magnitude in both nearshore and offshore surface waters. TN:TP ratios ≤ 20 suggest that N was likely to be limiting algal growth at Bugaia and is consistent with previous suggestions that N may be limiting in Lake Victoria (Talling 1966, Hecky 1993, Lehman and Branstrator 1993).

Phosphorus was in excess on a system scale given that TN:TP ratios were always $\leq$ 50, a critical value above which P is likely to be limiting algal growth and frequently < 20 offshore indicating N-deficiency (Guildford and Hecky (2000). The considerably higher SRP in Bugaia is consistent with earlier findings of excess P in Lake Victoria (Hecky 1993; Lehman et al. 1998) and further suggest a P-sufficient environment offshore. The simultaneous occurrence of the higher TN:TP ratios in September-October in Napoleon Gulf and Bugaia likely indicates N income via biological N-fixation (Chapter 4). It is difficult to assess algal nutrient status at community level using ambient nutrient concentrations and TN:TP without analyzing the particulate stoichiometry and/ or physiological indicators. These will be addressed in Chapter 3.

In this study, it was not possible to quantify the impacts of oxygen depletion and oxic-hypoxic interface on dissolved inorganic nitrogen. But depth profiles of DIN show a minimum of N at oxic-hypoxic interface, regeneration of ammonia in the hypolimnion and formation of nitrate above the oxic-hypoxic interface. The ammonium maximum that occurred usually below the oxycline between September and December may be a result of ammonium regeneration in the anoxic hypolimnion. Apparently, much of the ammonium that might have diffused through the thermal boundary may be transformed to nitrate and much of the nitrate was denitrified at the low oxygen concentrations near the oxic-anoxic interface (Hecky et al. 1996). This process may appear in the profiles as low DIN concentrations between the nitrate maximum in the epilimnion and ammonium maximum in the hypolimnion as observed in December. Loss of DIN at the oxic-hypoxic interface due to denitrification is common in productive lakes (Hecky 1993). Upon oxygen depletion, nitrate can replace oxygen as a terminal electron acceptor during dissimilatory metabolism by anaerobic microorganisms (Hecky et al. 1996). Denitrification results in N loss and may explain the mid-water sink of dissolved inorganic N between the nitrate and ammonium maxima in Lake Victoria. A mid-water N sink has been previously reported in Lake Victoria (Hecky et al. 1996) and is also known to occur in other African Great Lakes. such as lakes Malawi and Tanganyika (Hecky 1993. Bootsma & Hecky 1993).

Despite ammonium loss at the oxic-anoxic interface. ammonium concentrations in surface waters of Lake Victoria today are higher compared to values of the 1960s. Talling (1966) failed to measure ammonia concentrations, but suggested that N was a limiting nutrient for many phytoplankton of Lake Victoria. The very presence of N-fixing cyanobacteria (Chapter 5) suggests that regeneration and re-mineralization processes alone are unlikely to meet the algal N demand in Lake Victoria. The N demand enhanced by denitrification and increased P loading is likely to be met through biological N-fixation by the heterocystous cyanobacteria (Chapter 4. 5) as N loading from the watershed is insufficient to support the observed algal production in the lake (Lehman and Branstrator 1993).

Chapter 3: Particulate nutrient concentrations and nutrient status of Lake Victoria

Abstract

Phytoplankton nutrient status was determined using seston ratios and physiological nutrient indicators (P and N-debt) collected between 1994-1998 from inshore and offshore waters of Lake Victoria. Examination of particulate N: P, C: P and C: N ratios indicates that N and P-deficiency were more common in inshore than in offshore surface waters of Lake Victoria. N and/or P-deficiency were present when the lake was thermally stable and were absent when the lake was deeply mixing. Inshore, P rather than N-deficiency had a somewhat stronger control of phytoplankton biomass development, as N-fixers can draw on the atmospheric N source when the light climate is good. Offshore, phytoplankton was less constrained by N and P availability, as N and P-deficiency were absent most of the year. Despite the absence of nutrient deficiency, phytoplankton biomass (as chloropyll-a) and particulate nutrient concentrations were consistently lower offshore, probably due to light limitation, as grazing pressure is low in Lake Victoria. Consequently, total P (TP) and total N (TN) were only weakly correlated with chloropyll-a in Lake Victoria. These weak chl-a-TP and chl-a-TN correlations suggest that further P and N input into Lake Victoria may not result in further increases in algal biomass as light now limits biomass maxima.

Introduction

Eutrophication has become a global problem responsible for changes of chemical properties and biological processes in freshwater (Vollenweider 1968, Schindler 1977, Hecky 1993) and marine ecosystems (Smith 1998, 1999) around the world. Consequently, many studies have been carried out to tackle eutrophication and its attendant problems. Many of these studies aimed at identifying nutrient(s) and other factors that contribute to eutrophication. Nutrients, especially P, have been identified as the major factors responsible for eutrophication (Schindler 1977) and for changes in algal biomass, productivity and species composition (Kanda and Hattori 1988, Hecky and Kilham 1988). The relationship between nutrient concentrations, algal growth and occurrence of nuisance cyanobacterial blooms has been studied in temperate lakes (Hendzel et al. 1994, Guildford et al. 1994). Several studies show that aquatic primary productivity is frequently limited by the availability of nutrients (Howarth 1989, Sommer 1990). Nutrient deficient algae may be low quality food for consumers and may contribute to food webs high in contaminants (Taylor et al. 1991). The ability to identify nutrients limiting algal growth is of considerable importance to our understanding of the ecology of aquatic plants and to water management practices. Such knowledge has also proven useful in the management of the northern temperate Great Lakes, and will possibly be important in the management of Africa's largest Great Lake, Victoria.

Algae have basic metabolic requirements for nutrients in relatively fixed proportions and most algae are near the Redfield molar ratio of C: N: P: 105:16:1 when they attain maximum growth rates (Goldman et al. 1979, Hecky and Kilham 1988). Growth of an algal species will be limited if the cellular nutrient concentration falls below a critical level. But individual algal species can achieve optimal growth at different nutrient ratios of C: N: P. Therefore, nutrient ratios may predict the outcome of competition among algal species when nutrients become limiting (Tilman 1982)

Algae show markedly similar compositional and physiological responses to nutrient-limitation (Healey and Hendzel 1980, Hecky and Kilham 1988). Some responses are specific to a given nutrient while others are general responses to nutrient limitation of any kind. A decrease in the internal stores of nutrients, which often determines nutrient uptake kinetics and growth rates, is a general response to nutrient limitation. An algal C: N: P ratio near the Redfield Ratio (105:16:1) indicates near nutrient-sufficient status and near-optimal growth rates for given set of light and nutrient conditions (Goldman et al. 1979, Goldman 1980). Variability in particulate C: N: P ratios from the Redfield ratio does occur, and higher ratios of C to N and N to P are indicative of a nutrient deficient algal community as a whole (Healey and Hendzel 1980; Hecky and Kilham 1988).

Of the macronutrients, nitrogen and phosphorus are most often identified as the principal nutrients limiting algal growth in many aquatic ecosystems, while silicon is essential for diatom growth (Hecky and Kilham 1988). Phosphorus and/or nitrogen can be limiting in temperate marine and fresh waters (Hecky and Kilham 1988, Guildford and Hecky 2000) and in tropical freshwaters (Guildford et al.2000). However, large and small-scale experiments show that P is often the primary nutrient limiting algal growth and biomass in freshwaters lakes. Indeed phosphorus has been found to limit algal growth and biomass in many temperate aquatic freshwater ecosystems (Schindler 1977, 1978, Dillon 1991) and in several small East African lakes (Melack et al. 1982).

However, P-limitation in freshwaters is not always the rule. Studies conducted at the Experimental Lake Area (ELA). Ontario. Canada. demonstrated that increased P loading induces an N-deficiency and leads to increases in planktonic cyanobacteria that can fix atmospheric nitrogen (Schindler 1977. Hendzel et al. 1994).

Nitrogen has been found to limit algal growth in a number of tropical waters (Levine and Schindler 1987, Phlips and Inhat, 1995) including the African Great Lakes such as Lake Malawi (Guildford et al.2000). A potential for N-limitation in Lake Victoria was suggested by historic evaluations in the 1960s (Evans 1962 a. Talling and Talling 1965, Talling 1966). More recent studies conducted in the early 1990s led to the conclusion that N may limit many phytoplankton species in Lake Victoria (Hecky 1993) because soluble reactive P was in excess and nitrogen fixing species were present in the lake. Hecky (1993) demonstrated a tendency to P-limitation in the shallow inshore waters with high algal biomass based on nutrient composition. Further indications of increasing N-limitation in Lake Victoria come from nutrient bioassay experiments that were done to determine algal response to nutrient conditions (Lehman and Branstrator 1993, 1994, Lehman et al. 1998). Nitrogen additions were found to increase algal growth and biomass (as chlorophyll-a) in Lake Victoria. Most recently, Lehman et al. (1998) hypothesized that increased P input into Lake Victoria has caused algal biomass to increase as in temperate lakes similarly subjected to increased P loading. However, extrapolations from temperate lakes must be made cautiously, because of Lake Victoria's tropical location and associated differences in physical and biological dynamics that go with it, such as continuous high temperatures and solar irradiance (Kilham and Kilham 1989). Nutrient enrichment (Hecky and Bugenyi 1992, Hecky 1993, Hecky 2000) with subsequent increases in algal biomass and productivity (Mugidde 1992, 1993) and cyanobacterial blooms confer upon Lake Victoria some characteristics typical of large eutrophied temperate lakes during summer.

In temperate regions, algal stoichiometry and other nutrient status indicators (for example, N and P debt) have proven useful diagnostic tools in understanding the relative availability of nutrients, and the specific nutrient(s) causing water quality deterioration. A combination of dissolved and particulate nutrient ratios and physiological assays all contribute to assessing phytoplankton nutrient status (Healey and Hendzel 1980, Guildford et al. 1994). In the dark, phosphorus or nitrogen deficient algae will take up phosphorus or nitrogen that is made available and the amount taken up relative to cellular biomass (as chloropyll-a) is referred to as a debt. Nitrogen and P uptake rates normalized over chlorophyll-a per 24 hours are known as N and P debt and are used as algal physiological indicators of N and P deficiency (Healey and Hendzel 1980). N and P debt as indicators of nutrient-deficiency, are feasible because algae adapt to nutrient deficiency by increasing their active sites for transport (V_{max}) to overcome low nutrient concentrations in their surroundings, while maintaining cellular growth and metabolism. Nutrient uptake rates depend on algal nutrient status and growth rates (Berzezinski and Nelson 1988, Kanda and Hattori 1988).

Based on the assumptions that algal particulate ratios are meaningful indicators of limiting nutrient(s) at a community level, and that N and P debt are useful diagnostic tools of phytoplankton nutrient status (Healey and Hendzel 1980), N: P, C: P and P-debt and C: N and N-debt were used to determine P and N deficiency in Lake Victoria. Previous nutrient limitation inferences in Lake Victoria, based on ambient nutrient concentrations, sestonic composition ratios (Hecky 1993), nutrients kinetics and enrichment experiments (Lehman and Branstrator 1994, Lehman et al. 1998), were narrow in spatio-temporal coverage and did not allow firm conclusions on the extent of nutrient limitation in Lake Victoria. The seasonal cycle of phytoplankton nutrient status and the extent of nutrient limitation in Lake Victoria remained unknown. Complex patterns of nutrient deficiency are likely to emerge in Lake Victoria, given large spatio-temporal variations in the physico-chemical environment. Because of this, field sampling and measurements covered the annual thermal stratification cycle and were done in both shallow nearshore bays with high algal biomass and deep offshore regions with lower algal biomass. The goal of this study was to determine which nutrients limit phytoplankton biomass production as a basis for effective strategies for control/reversal of eutrophication in Lake Victoria. The specific objectives of this study were to determine if P and/or N limit the algal community of Lake Victoria, and if so, which nutrient was most limiting.

Materials and Methods

Study areas

To examine spatio-temporal variability, samples were collected between 1994 and 1998 in both inshore and offshore regions of northern Lake Victoria (Figure 2.1. a, b, c). Sampling was done most frequently at three inshore locations (Napoleon Gulf, Buvuma Channel and Pilkington Bay) and one offshore station (Bugaia). The inshore areas were relatively shallow, generally much less than 30 m and mixed more frequently than the deep offshore site (Bugaia, depth 65 m) which thermally stratifies most of the year, but mixes completely around June-July when the south-east trade winds blow across the lake (Talling 1966) causing increased cooling by evaporation. Further measurements were made in Itome Bay (30 m), but less frequently, to enable a comparison with the corresponding inshore locations in the lake.

Field sample collection, treatment and analysis

Measurements of Secchi transparency, under water light attenuation and temperature and dissolved oxygen profiles were done during sample collection at all sites. Secchi readings were recorded using a 20-cm white disk. Profiles of photosynthetically available radiation (PAR) were measured with a Li-Cor sensor (model LI-192S sensor, model LI 185 meter) at 0.5 m to 1m interval. Field sampling was done regularly and intensely in 1998 compared to 1994-1997. In 1998, nutrient concentrations and nutrient status measurements were done more frequently (monthly) in the shallow nearshore regions and at least bimonthly in the deep open waters (Bugaia) of Lake Victoria. The offshore (Bugaia) site was sampled monthly from July to December 1998 in an attempt to capture events during complete vertical mixing (July-August) and stable thermal stratification (September-December).

Nutrient status samples were drawn from several depths within the surface waters. but within twice the Secchi depth. using a Van Dorn water sampler. In general. 2x Secchi depth was 1-2 m inshore and 4-6 m offshore. At each site, water samples were pooled in 10 –L polyethylene carboys and kept in the cool and dark. Sub-samples were taken from the pooled samples for nutrient status bioassays (N & P debt), particulate chemistry (C, N & P), chlorophyll-a (Chl-a) and initial ammonium and soluble reactive phosphorus concentrations. Samples for vertical nutrient concentrations were taken from discrete depths in the water column and dispensed in 1-L brown polyvinyl bottles. Water samples of 200-300 ml from offshore and of 50-100 ml from inshore were filtered onto Whatman GF/F filters and filters used for chlorophyll-a and particulate nutrient analyses. The filters were desiccated over silica gel in the field or in the oven at 55 ° C overnight in the laboratory at the Fisheries Resources Research Institute (FIRRI), Uganda. The filtrate was used for analyses of ambient dissolved inorganic nutrients (ammonium, SRP) following methods of Stainton et al. (1977) as described in Chapter 2. Within 1 to 3 hours the unfiltered pooled lake sample was used for N and P-debt bioassays.

Laboratory measurements

Phytoplankton nutrient status: Suspended nutrient ratios.

Particulate and total dissolved P and N and Chl-a were analyzed as described in chapter 2. Known volumes (40 to 300 mL) discrete depth and/or from pooled surface samples were filtered onto pre-ignited Whatman GF/C filters and used for analyses of particulate P. C and N. These filters were desiccated over silica gel or in the oven at 55° C, sealed in dark aluminum bags and shipped to FWI. Winnipeg. Canada for analyses. because this analyses was not possible at FIRRI. Uganda. At FWI. analyses of suspended nutrients were done following methods of Stainton et al. (1977). Seston composition ratios of N: P, C: P and C: N were used and interpreted in terms of nutrient deficiency as in Healey and Hendzel (1980, Table 3.0).

Table. 3.0. Indicator values of phytoplankton nutrient deficiency (Healey and Hendzel 1980). All elemental ratios of phosphorus. carbon and nitrogen are expressed on a molar basis. Units for chlorophyll-a are ug L^{-1} or mg m^{-3} and N and P debt are μM chl-a^{-1} day^{-1}.

Indicator/ ratio	Nutrient	No deficiency	Moderate deficiency	Extreme deficiency
N:P	P	< 22		> 22
C:P	P	< 129	129-258	> 258
P-debt	P	< 0.075		> 0.075
C:N	N	< 8.3	8.3 –14.6	> 14.6
N-debt	N	< 0.15		> 0.15

Phytoplankton nutrient status: Nitrogen and phosphorus debt.

In darkened flasks, 0.5 mL of 1.0 mM concentration of potassium dihydrogen phosphate solution was added to 100 mL unfiltered lake sample to yield a final concentration of approximately 5.0 μM. Similarly, a 100 mL of sample was spiked with 0.5 mL of ammonium chloride solution to give a final concentration of approximately 5.0

μM. Triplicate samples were removed at the beginning and approximately 24 later after incubation at room temperature (26-29 °C) and ammonium and soluble reactive phosphorus were measured spectrophotometrically as in Stainton et al. (1977). The difference in ammonium and soluble reactive phosphorus concentrations between the beginning and the final concentration (24 hours) was the net assimilation. N and P debt were calculated as the amount removed during the 24-hour period per unit of chlorophyll-a, and were interpreted in terms of nutrient deficiency as in Healey and Hendzel (1980). The Wedderburn number (W), which is a lake thermal structure index that describes the potential for mixing was calculated as described in Chapter 2. When W is $\leq$ 0.5, the water column is not stable and little work is needed to mix it (Coulter and Spigel 1996).

Data analysis

Statistical analyses were done using SYSTAT 9. Analyses of variance (ANOVA) was used to examine differences in particulate nutrient concentrations, particulate nutrient ratios, and N and P-debt between surface and bottom waters, locations, months and years. When ANOVA indicated significant differences in the test variable, Tukey HSD multiple comparison tests were used to differentiate means. Ratios of N: P, C: P and C: N were $\log_{10}$ transformed to achieve normality, and their variability due to station, years, month, and unexplained variance was partitioned using ANOVA. ANCOVA was also used to test for differences in regression slopes and constants.

Results

Spatio-temporal variability of particulate nutrients.

Concentrations of particulate nutrients (C, N & P) in the water column covered a very broad range in Lake Victoria (Table 3.1). Particulate N was in the range 0.7-338μM, particulate P in the range 0.03-12μM, and particulate C in the range 22-1269 μM. Spatio-temporal variability of particulate C was much less than for particulate P and N. Particulate nutrient concentrations were significantly lower ($P<0.01$) at deeper depths than in the corresponding surface waters (Table 3.1) likely as result of nutrient regeneration at deeper depth. Particulate P was about 60% higher in surface than in the corresponding bottom waters, while PN was 2-3x higher. Similarly, PC was 2-3 fold higher in surface waters.

The shallow inshore locations (Pilkington Bay, Napoleon Gulf, Itome Bay and Buvuma Channel) supported significantly higher PP, PN and PC ($p < 0.001$) concentrations than the offshore surface location (Bugaia) (Table 3.2). Particulate N, PP and PC concentrations were 2 to 4-fold higher inshore. There were no significant differences ($P > 0.05$) in average PN, PP and PC concentrations among inshore locations, despite the higher average suspended nutrient concentrations in Napoleon Gulf and Pilkington Bay.

Table 3.1. Average particulate nutrient concentrations (μM) and their standard deviation at inshore and offshore regions of Lake Victoria, during 1994-1998. Number in Parentheses = N

Nutrient	Inshore		Offshore (Bugaia)	
	(0-5 m)	(15-20) m	(0-10 m)	(50-56 m)
PP	1.6 ± 1.4 (205)	1.0 ±0.4 (31)	0.5 ±0.2 (24)	0.3 ±0.5 (24)
PN	35.6 ± 38.1 (206)	18.6 ±11.2 (31)	10.6 ±6.0 (24)	3.5 ±3.5 (24)
PC	245.7 ± 228.0 (206)	111.1 ±66.7 (31)	79.1 ±45.1(24)	29.0 ±22.7 (24)

Table 3.2 Average particulate nitrogen (PN), phosphorus (PP), nitrogen (PC) and their standard deviation from the surface mixed waters of Lake Victoria, 1994-1998. Number in bracket = N, the number of months.

Location	PN (μM)	PP (μM)	PC (μM)
Napoleon Gulf	42.8 ±47.1(33)	1.9 ± 1.7 (33)	289.7 ± 283.0 (33)
Pilkington Bay	31.1 ± 14.9 (31)	1.4 ± 0.6 (31)	230.6 ± 103.1 (38)
Buvuma Channel	25.5 ± 20.8 (33)	1.0 ± 0.6 (33)	178.4 ± 127.4 (33)
Itome Bay	20.3 ± 10.9 (19)	1.0 ± 0.5 (19)	138.8 ± 73.9 (19)
Bugaia	10.6 ± 4.4 (24)	0.5 ± 0.2 (24)	79.1 ± 31.1 (24)

Slopes of the linear relationship of PN and PC regressed as dependent variables of PP, and PC as a dependent variable of PN, correspond to the more conventional particulate N:P, C:P and C:N ratio respectively (Figure 3.1). Particulate P was strongly (r^2 = 0.89) related to PN and PC and the relation between PC and PN was even much stronger (r^2 = 0.97). The slopes of regressions of PN on PP (26.7), PC on PP (162.3) and PC on PN (6.0) were close to the average corresponding values of particulate nutrient ratios (Table 3.3). Overall the particulate N:P and C:P values had a small range and were close to the lines whose slopes denote nutrient deficiency (Figure 3.1). The inshore values had a wider scatter from their respective lines. Most of the C:N values were lower than a slope of 8.3 which is considered indicative of N-deficiency.

Table 3.3. Particulate N: P. C: P and C: N molar ratios in the surface waters of Lake Victoria, 1994-1998.

	Inshore					Offshore
Nutrient Ratio		Napoleon Gulf	Buvuma Channel	Pilkington Bay	Itome Bay	Bugaia
N:P ratio	Minimum	7.3	8.6	10.0	2.7	3.3
	Average	23.6	23.0	22.4	21.2	20.1
	Maximum	77.6	75.5	40.0	30.0	31.1
	Std.	11.1	11.1	6.2	6.2	6.2
	N	33	33	33	19	24
C:P ratio	Minimum	46.6	64.9	65.3	24.3	56.8
	Average	164.1	163.7	168.6	148.0	151.4
	Maximum	465.4	501.4	291.8	276.7	290.0
	Std.	68.9	71.1	49.2	48.5	50.3
	N	31	31	31	19	24
C:N ratio	Minimum	4.5	5.5	5.2	4.5	5.7
	Average	7.2	7.4	7.6	7.1	7.9
	Maximum	14.8	11.1	10.1	9.2	17.5
	Std.	1.4	1.3	1.5	1.0	2.3
	N	31	33	38	19	24

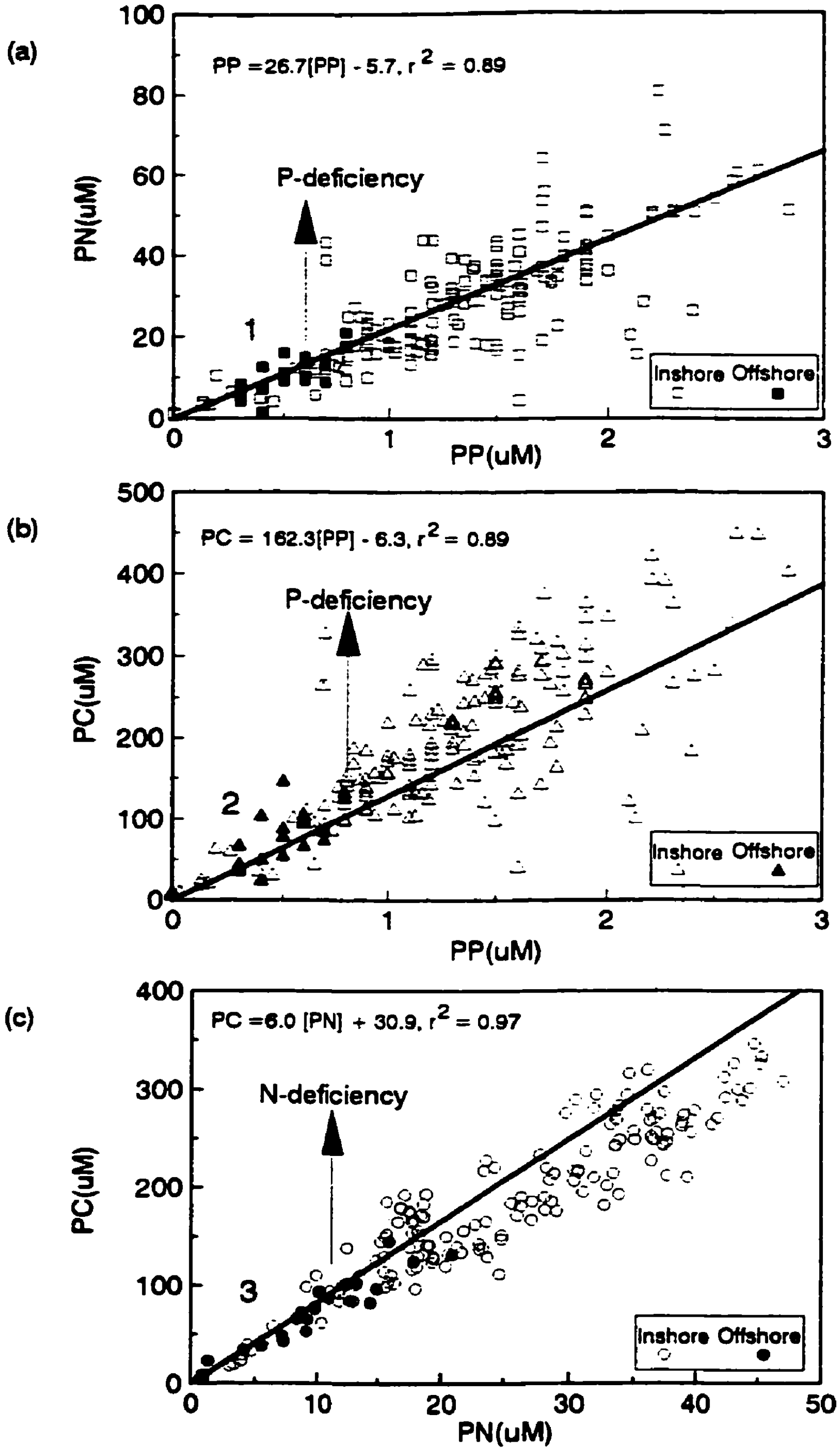


Figure. 3.1. (a) Particulate N(PN) vs particulate P(PP), (b) particulate N(PN) vs PP, (c) PC vs PN from surface waters of Lake Victoria, 1994-1998. Slope in a, b, and c are equal to values 22, 129 and 8.3 that are indicative of P and/ or N deficiency according to the criteria of Healey and Hendzel (1980). The equations in a, b, & c are fitted regression equations to the data and the r^2 values.

Spatial patterns of nutrient deficiency

Particulate N:P and C:P ratios had a wider range inshore than offshore (Figure 3.1, a, b, c & Tables 3.3, 3.4). Generally particulate N:P and C:P ratios were approximately 30% to 40% higher in the surface than in the corresponding bottom waters with exception in July when ratios had almost a homogeneous vertical distribution (Figure 3.2). Vertical distribution of particulate N:P and C:N ratios often showed a decrease below 40 m depth during the stratified period at Bugaia (Figure 3.2). A decrease of surface N:P and C:P ratios was also observed in July-August at both inshore and offshore and in November at Bugaia (Figure 3.3 a, b, d, e). Phosphorus was often in excess in both inshore and offshore bottom waters as indicated by the low percentage frequency (6%-10%) of N: P values indicative of low P availability (Table 3.5). Extremely low hypolimnetic N:P ratios (≤ 4.0) are also indicative of low N availability in deeper depths at both inshore and offshore sites. (Table 3.4).

Although average particulate C:N ratios were about 20% higher in the surface than in the corresponding bottom waters, no coherent vertical distribution pattern of C:N ratios was evident at Bugaia (Figure 3.2 & Tables 3.3, 3.4). Hypolimnetic average particulate C:N ratios were similar at both inshore and offshore but maximum C:N ratios were almost double inshore (Table 3.4). The higher maximum C:N ratios were indicative of lower N availability in the inshore than in offshore bottom waters. Although low hypolimnetic N availability was more extreme inshore, it was rare as indicated by the low percentage (10%) of C:N ratios indicative of sufficiency (Table 3.5).

Table. 3.4. Particulate nutrient ratios in the inshore (15-30 m) and offshore (50-65 m) bottom waters of Lake Victoria during 1994-1998.

Nutrient ratio		Inshore	Offshore (Bugaia)
N:P	Minimum	2.7	2.5
	Average	15.5	15.9
	Maximum	28.4	25.0
	N	31	24
C:P	Minimum	29.4	22.5
	Average	106.0	151.0
	Maximum	159.0	255.0
	N	31	19
C:N	Minimum	4.5	7.0
	Average	9.2	9.6
	Maximum	31.0	14.4
	N	31	19

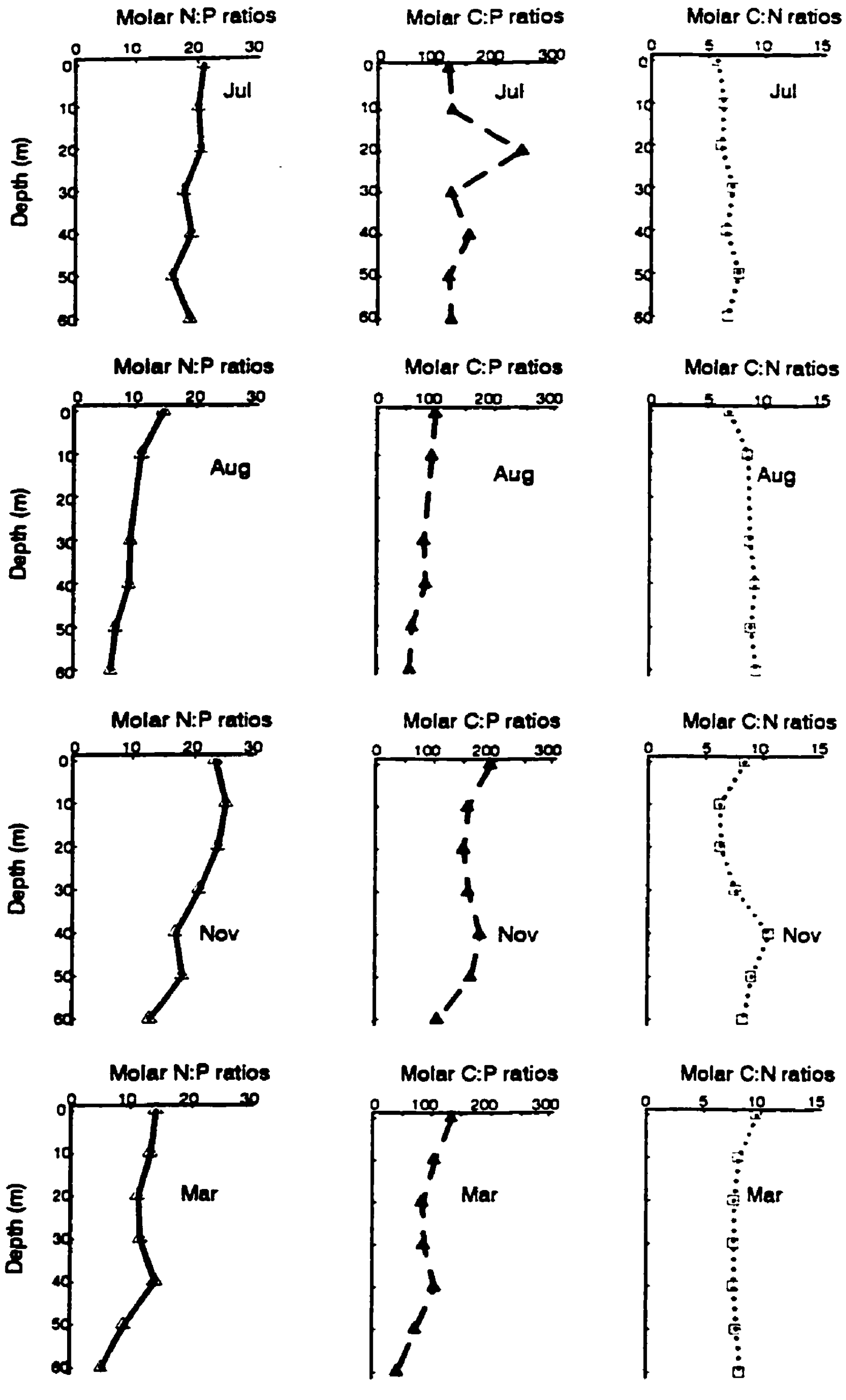


Figure. 3.2. Depth profiles of particulate nutrients ratios from offshore (Bugaia) Lake Victoria, during 1998.

Phosphorus deficiency was more common in inshore than offshore surface waters as indicated by the higher percentage frequency of N:P and C:P ratios greater than values indicative of deficiency (Figure 3.3.a b. d.e. Table 3.5). The almost double maximum N:P and C:P ratios indicate that P-deficiency was more extreme in inshore than in offshore surface waters of Lake Victoria (Figure 3.3 a, b.d. e, Table 3.3). However. average surface water C: P ratios did not differ markedly in their composition from values indicative of moderate P deficiency at all sites. Average N: P ratios indicated marginal P-deficiency in shallow Napoleon Gulf. Buvuma Channel and Pilkington Bay and no P-deficiency in the inshore Itome Bay and offshore (Bugaia) stations (Table 3.4). Occasionally, low epilimnetic N:P ratios (≤ 5) indicative of excess P were measured in both inshore and offshore surface waters of Lake Victoria (Figure 3.3 a. b. d. e & Table 3.3).

Table 3.5. Percentage frequency of particulate nutrient ratios indicative of N and P-deficiency in the surface and deeper inshore and offshore waters of Lake Victoria. 1994-1998. Inshore (surface = 0-5 m, bottom =15-30 m), offshore (surface 0-10 m, bottom 50-65 m).

Station	N-deficiency		P-deficiency			
	% of C:N ratios		% of C:P ratios		% of N:P ratios	
	Surface	Bottom	Surface	Bottom	Surface	Bottom
Inshore	21	10	83	20	58	10
Offshore	29	63	70	6	33	6

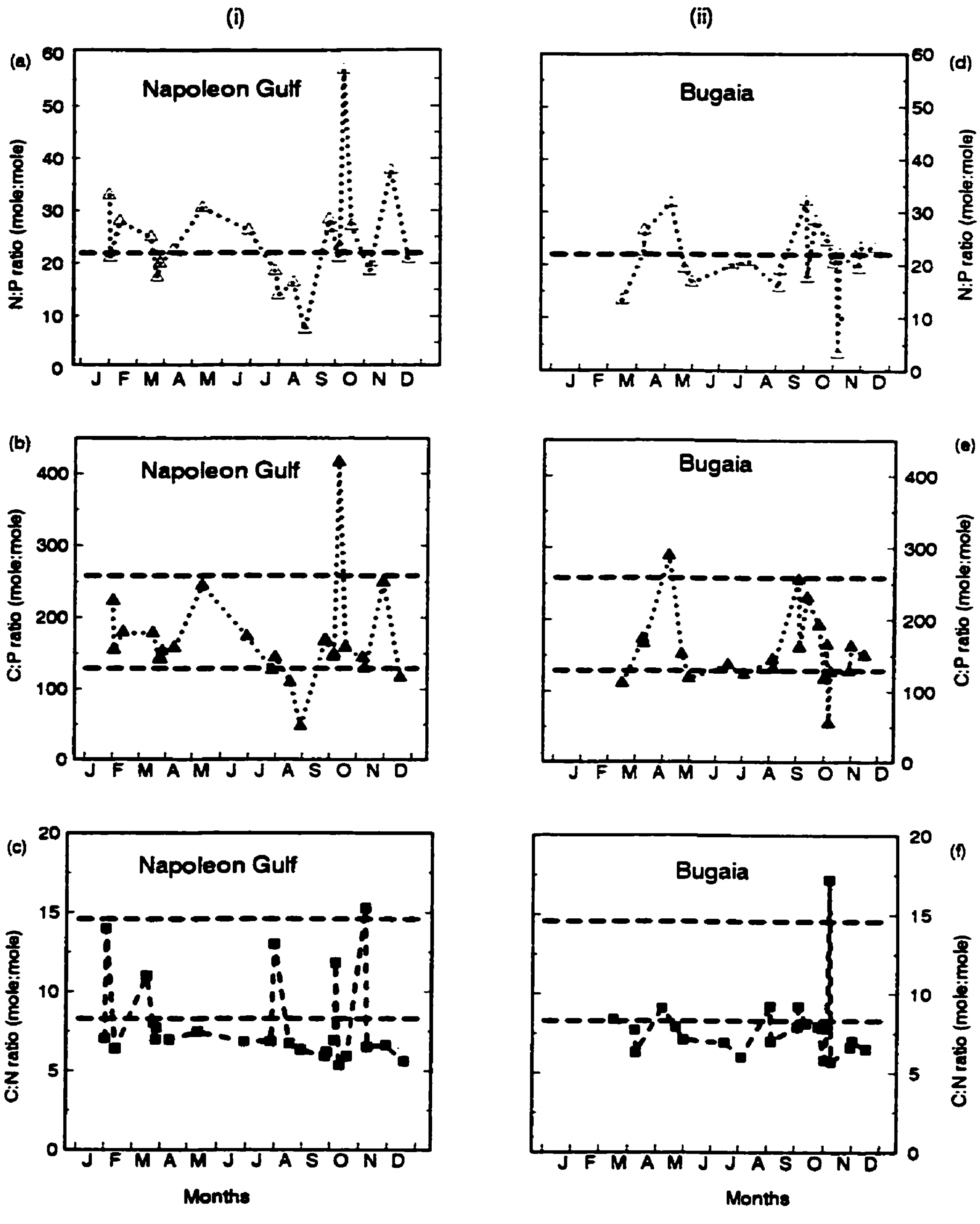


Figure. 3.3. Particulate N:P (a & d), C:P (b & e) and C:N (d & f) ratios from surface mixed waters of (i) Napoleon Gulf and (ii) Bugaia during 1994-1998 Dashed lines indicate P and N deficiency.

Nitrogen deficiency, as indicated by particulate C: N ratios, was almost as frequent in inshore (21%) as in offshore (29%) surface waters of Lake Victoria (Figure 3.3 c, f, Table 3.6). However, the relatively higher C: N ratios indicate stronger N-deficiency events offshore than inshore (Table 3.4). The overall average C: N ratios in the range 7.2-7.9 (Table 3.3) were indicative of no N-deficiency in both inshore and offshore surface waters, according to the criteria of Healey and Hendzel (Table 3.4). Average particulate nutrient ratios (N: P, C: P & C: N) from the surface waters did not differ significantly between locations in Lake Victoria ($p > 0.05$), but highest N: P and C: P ratios were inshore. Although there were shifts from conditions of N and P-sufficiency to N and P-deficiency, particulate C: N and N:P ratios did not vary significantly among months nor months nested into seasons ($p \geq 0.05$). Months nested into seasons accounted for a significant ($p \leq 0.05$) proportion of the C:P ratios in the surface waters of Lake Victoria. Unexplained variation accounted for the largest proportion (≥ 60%) of the variation in N: P, C: P and C: N particulate ratios from the surface mixed waters of Lake Victoria (Table 3.6).

Table 3.6. Percentage of the total sum of squares explained by station, month and unexplained variance of particulate nutrient ratios in Lake Victoria.

Variable	Station	Month	Unexplained
C:N	4.3	23.9	71.8
C:P	4.0	29.5	66.5
N:P	4.0	17.4	78.6

Temporal trends in deficiency as indicated by particulate nutrient ratios

Temporal trends of particulate N: P, C: P and C: N ratios indicate that P and N deficiency were present and absent at particular times in both inshore and offshore surface waters (Figure 3.3). Particulate nutrient ratios were frequently low and indicative of no P and N deficiency between April and July in Napoleon Gulf and between May and August in Bugaia (Figure 3.3 a, b, d, e). During that period, Wedderburn numbers of $\leq$ 0.5 were frequent (Figure 3.3 c) and indicating strong mixing of the water column. P-and N-deficiency was often present between September and April when the lake was thermally stable as indicated by the increasing Wedderburn numbers. Severe P-deficiency indicated by high ratios of N: P ($\geq$ 30) coincided in timing (September – October) but not in magnitude in Napoleon Gulf and Bugaia (Figures 3.3 & 3.4 a, b).

Extreme N-deficiency (N: C > 14.6) was rare and was only observed in October and February in Napoleon Gulf. In Bugaia, extreme N-deficiency occurred once at the end of October but was rapidly relieved in November to December (Figure 3.4 b). In Bugaia, extreme N-deficiency (C: N > 14.6) at end the of October coincided with conditions of P-sufficiency as indicated by both low N: P (< 5) and C: P (< 100) ratios (Figure 3.3 b). N- and P-deficiency occurred contemporaneously in October and (Figure 3.4 a) and N- and P-sufficiency coincided in December and in July-August in Napoleon Gulf.

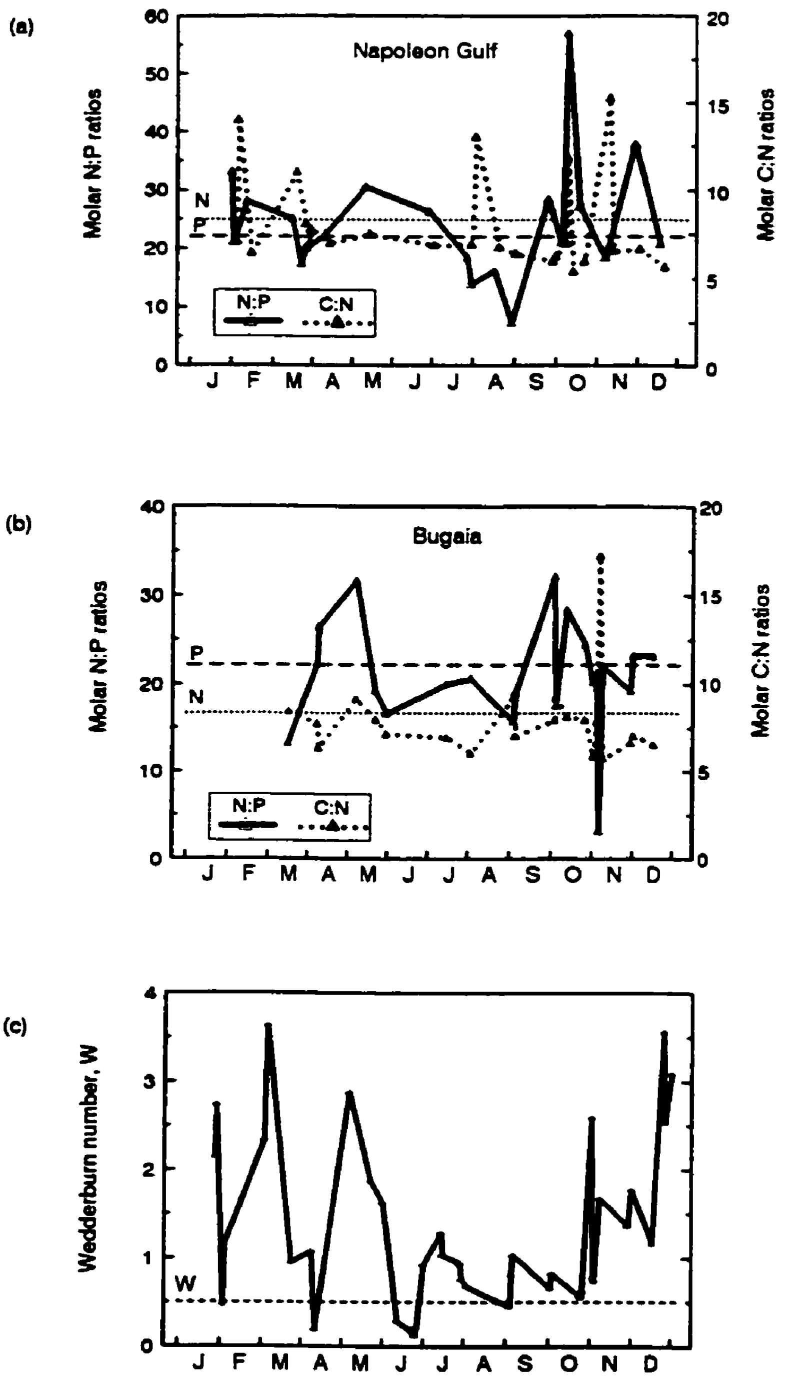


Figure. 3.4. Molar N:P and C:N ratios in the surface waters of (a) Napoleon Gulf, (b) Bugaia and (c) Wedderburn numbers (W) for Lake Victoria. Dashed line, W, = 0.5, is indicative of strong deep mixing.

Physiological indicators of P and N status in Lake Victoria

Figures 3.5 shows temporal patterns of P-debt and particulate N:P ratios used as indicators of P-deficiency in this study. P-debt was in the range 0.01-0.25 μM P chl-a^{-1} 24 h^{-1}. P-debt indicates that P was only occasionally limiting in both inshore and offshore surface waters of Lake Victoria (Figure 3.3 a, b). Uptake rates (P-debt) indicated P-deficiency in August, October and June in Napoleon Gulf and in September and April in Bugaia (Figure 3.5 a, b, Table 3.7, 3.8). P-debt indicates that P deficiency was almost as frequent inshore as offshore. Out of 19 P-debt measurements from Napoleon Gulf, 3 (16%) indicated P-deficiency and only 2 were in agreement with other indicators of P-deficiency (Table 3.7). In Bugaia, three (14%) out of 21 P-debt measurements showed P-deficiency and all the 3 correlated with deficiency determined from particulate N:P and C:N ratios (Table 3.8). Overall, elevated phosphate uptake rates indicative of P-deficiency coincided with elevated particulate N:P and C:P ratios indicative of P-deficiency. But high N:P and C:N ratios indicating P-deficiency were not always accompanied by high P-debt.

Table 3.7. Particulate nutrient ratios. P-debt and N-debt in the surface waters (0-5 m) at Napoleon Gulf, during 1994-1998. Presence = + and absence = - of deficiency of P or N.

Date	N:P	C:P	P-debt	C:N	N-debt
06-Oct-94	+	+	-	-	
04-Nov-94			-		
10-May-95	+	+		-	
02-Nov-95	+	+		+	
31-Jan-96	-	+		+	
15-Mar-96	+	+		+	
27-Jul-96	-	+		+	
02-Oct-97	+	+		+	-
01-Oct-97	+	+	-	-	
03-Dec-97			-		-
30-Jan-98	+	+	-	-	-
10-Feb-98	+	+	-	-	
23-Mar-98	-	+	-	-	-
03/27/98	-	+	-	-	
26-Mar-98	-	+	-	-	
10-Apr-98	+	+	-	-	-
27-May-98			-		-
27-Jun-98	+	+	+	-	-
25-Jul-98	-	-	-	-	-
14-Aug-98	-	-	+	+	+
26-Aug-98	-	-	-	-	-
24-Aug-98					-
21-Sep-98	+	+		-	
23-Sep-98	+	+		-	-
14-Oct-98	+	+	+	-	-
04-Nov-98	-	+	-	-	
24-Nov-98	+	+	-	-	-
13-Dec-98	-	-	-	-	-
Total +	14/24	20/24	3/19	5/24	1/15

Table 3.8. Particulate nutrient ratios. P-debt and N-debt in the surface waters (0-10 m) of Bugaia, during 1994-1998. Presence = + and absence = - of deficiency of P or N..

Date	N:P	C:P	P-debt	C:N	N-debt
29-Jan-94					-
16-Apr-94			_		-
17-Jul-94			_		-
01-Sep-94	-	+	_	+	
29-Sep-94	+	+	_	-	
30-Oct-94	-	+	_	-	-
24-Nov-94	-	-	_	-	-
02-Feb-95			_		-
06-May-95	+	+	_	+	-
21-May-95	-	+		-	
13-Jul-95	-	+	_	-	-
01-Sep-95	-	+		-	
21-Oct-95	+	+		-	
01-Nov-95	-	-		+	
06-Apr-96	-	+		-	
08-Oct-97	+	+	+	-	-
06-Dec-97			_		-
16-Mar-98	-	-	_	+	+
08-Apr-98	+	+	+	-	-
29-May-98	-	-	_	-	-
31-Jul-98	-	-	_	-	-
08-Aug-98	-	-	_	+	-
30- Sep-98	-	+	-	+	-
27-Oct-98	-	-	_	-	-
11- Nov-98	-	-	_	-	-
26-Nov-98	+	+	_	-	-
11-Dec-98	+	+	+	-	-
Total +	7/21	14/20	3/22	6/21	1/20

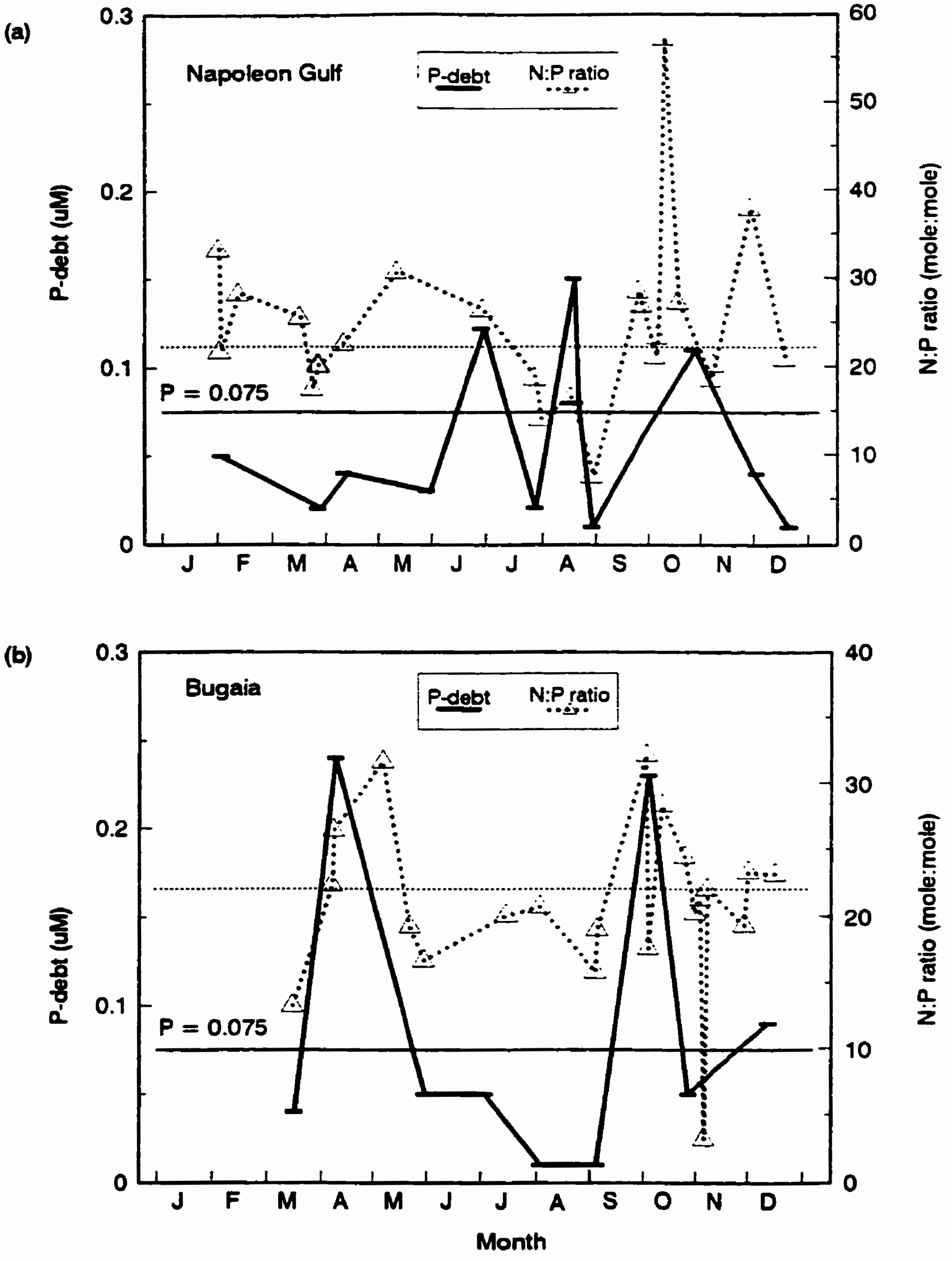


Figure. 3.5. Temporal variation of P-debt and particulate N:P ratios at (a) Napoleon Gulf and (b) Bugaia, during 1998. Dashed line = 22 and solid line marked P = 0.075, indicating P-deficiency

Ammonium uptake per unit of chlorophyll-a (N-debt) ranged from 0.01-0.15 μM N chl-a^{-1} 24 h^{-1} (Figure 3.6 a, b). At both inshore and offshore sites, N uptake was often well below critical values of 0.15 μM N chl-a^{-1} 24 h^{-1} denoted by the horizontal line 1, indicating N-deficiency. N-debt indicated marginal N-deficiency in August in Napoleon and in March in Bugaia. Low N-debt values indicative of no N-deficiency were measured even when high C: N ratios indicating deficiency were present (Figure 3.6 a, b). Clearly, N-debt and C:N as indicators of N deficiency were not always in agreement in Lake Victoria.

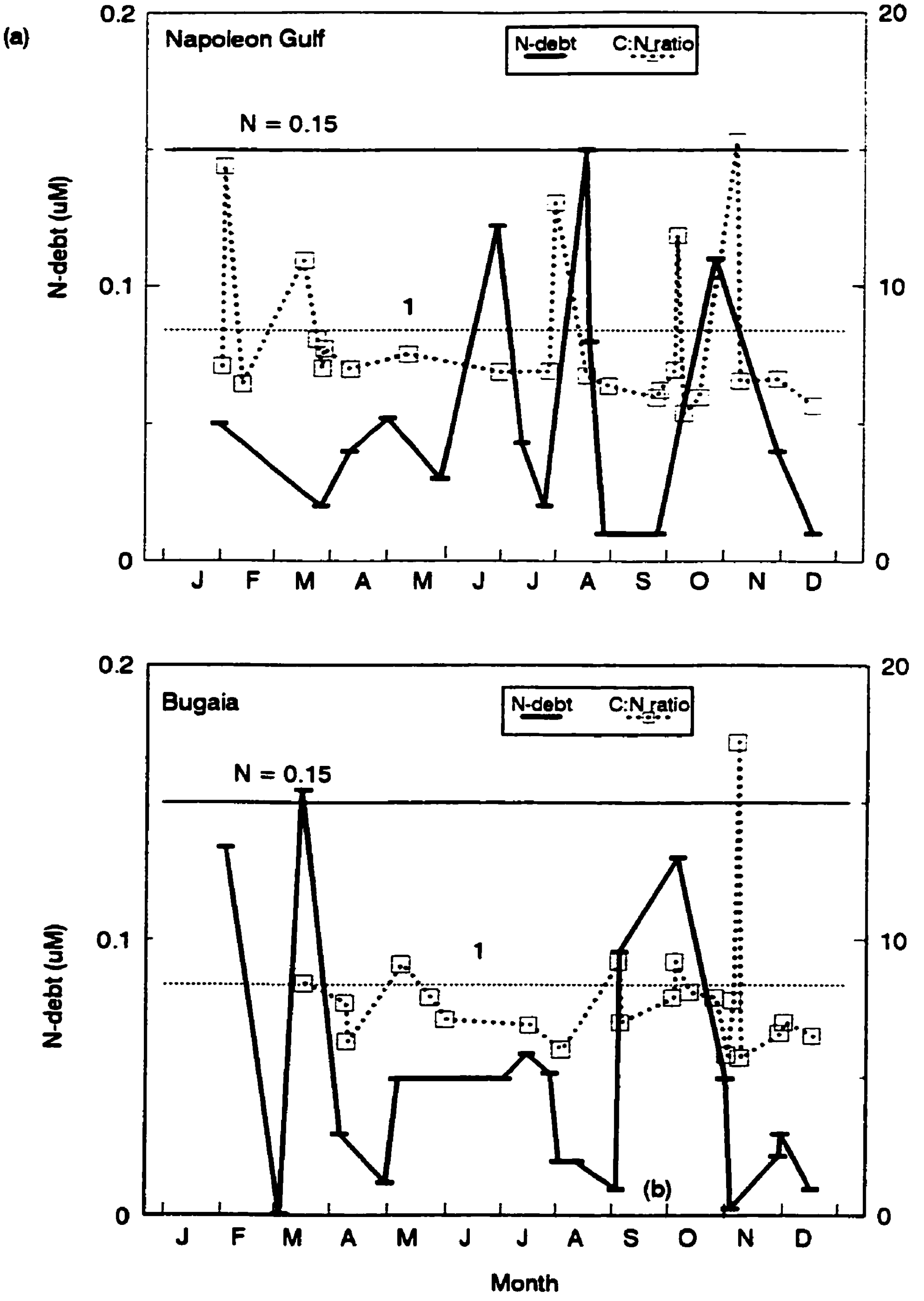


Figure. 3.6. Temporal variation of N-debt and particulate C:N ratios at (a) Napoleon Gulf and (b) Bugaia, during 1998. Dashed line = 8.3 and solid line marked N = 0.15, indicating N-deficiency

Algal biomass (Chloropyll-a) –nutrient relationship

Chlorophyll-a (chl-a) concentrations ranged from 2.5 to 657.0 mg.m^{-3}. mean 46.4 mg m^{-3} in the surface waters of Lake Victoria (Figure 3.7 a. b). Epilimnetic chlorophyll-a concentrations exhibited a much wider range inshore than offshore. and average concentrations were 3 to 5-fold higher in inshore than in offshore Lake Victoria (Table 3.9). In the surface waters of Lake Victoria. chlorophyll-a was lowest when the lake was deeply mixing around July as indicated by the low $W \leq 0.5$ and was highest during the stratified phase when $W \geq 0.5$ (Figure 3.6 a.b.c). A temporal algal biomass plot shows a major chlorophyll-a maximum in September in Napoleon (Figure 3.7a) that coincided with N and P-sufficient conditions in the Gulf (Figure 3.3 a. b). After the maxima. chloropyll-a concentrations declined and remained relatively constant from November to April despite a relief in N and P-deficiency in Napoleon Gulf. At Bugaia. the September-May chlorophyll-a concentrations were almost double the June- August values (Figure 3.7 b). Despite N and P-sufficiency at Bugaia, chlorophyll-a concentrations remained low during periods of strong wind stress and lower water column stability indicated by $W \leq 1.0$

Table 3.9. Average chlorophyll-a concentrations in the surface inshore (0 -5 m) and offshore (0-10) waters of Lake Victoria during 1994-1998.

	Location	
	Inshore	Offshore
Minimum	14.8	2.5
Average	59.6	13.5
Maximum	655.8	29.0
Std	79.4	5.8
C.v.	1.3	0.4
N	105	42

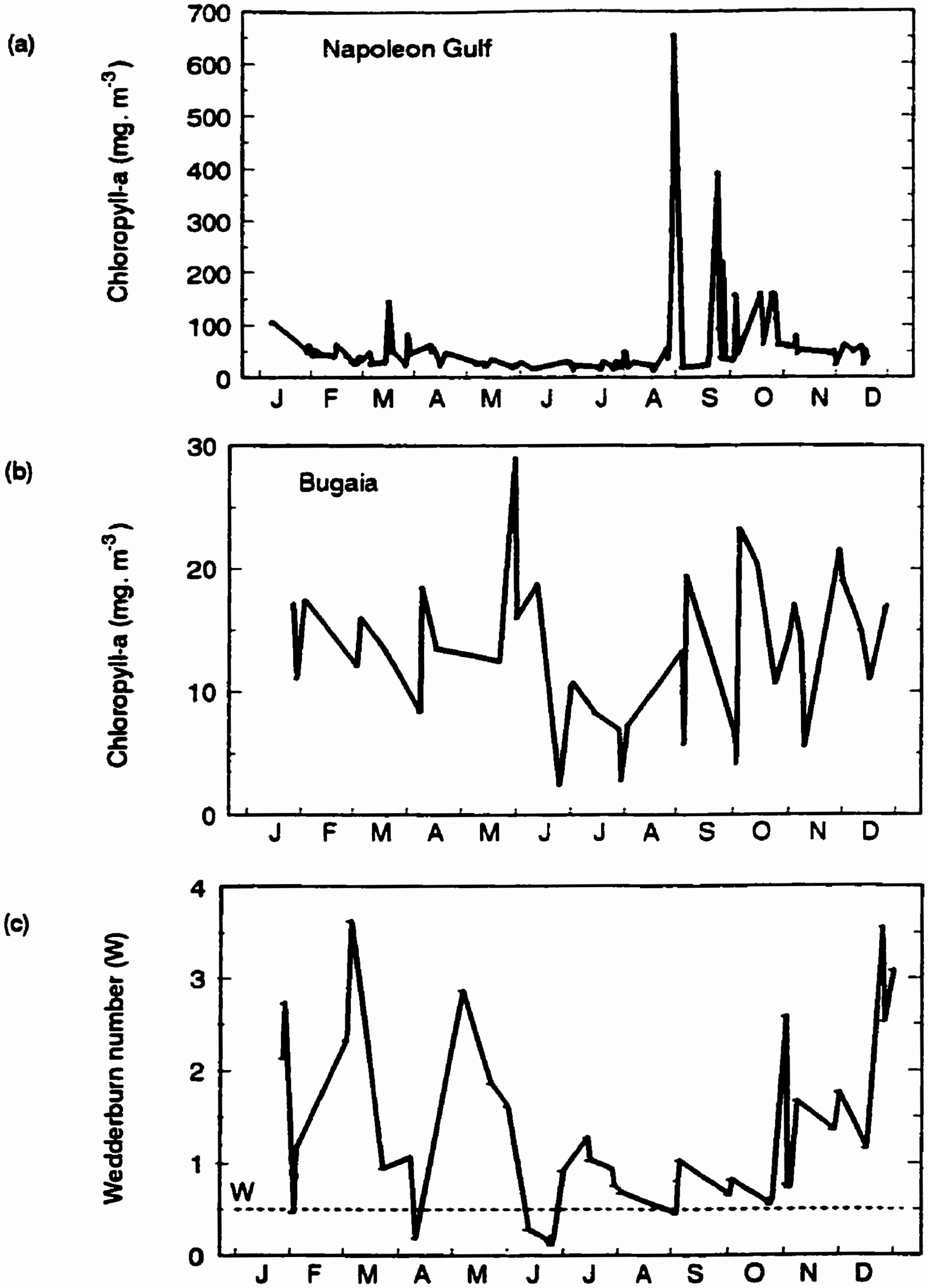


Figure. 3.7. Chloropyll-a concentrtations at (a) Napoleon Gulf, (b) Bugaia, (c) estimates of Wedderburn number(W) for Lake Victoria 1994-1998. Dashed line = W of 0.5, indicative of strong deep mixing.

Chlorophyll-a – total P and total N relationship

Data of total P and chlorophyll-a concentrations split into inshore and offshore sets exhibited fundamental differences in TP- chl-a relationship (Figure 3.8a). The coefficient of determination for the relationship of chl-a to TP for inshore was higher ($r^2 = 0.52$, $n = 26$) and the slope (15.6) was significant ($p = < 0.01$) compared to offshore where the relationship was very weak ($r^2 = 0.11$, $n = 20$) and not significant ($p > 0.05$). Offshore, chlorophyll-a did not increase with increases in total P concentrations as indicated by the negative slope (-1.8). The chlorophyll-a vs. total N relationship was fairly strong ($r^2 = 0.42$, $n = 27$) and the slope was significant ($p < 0.05$).

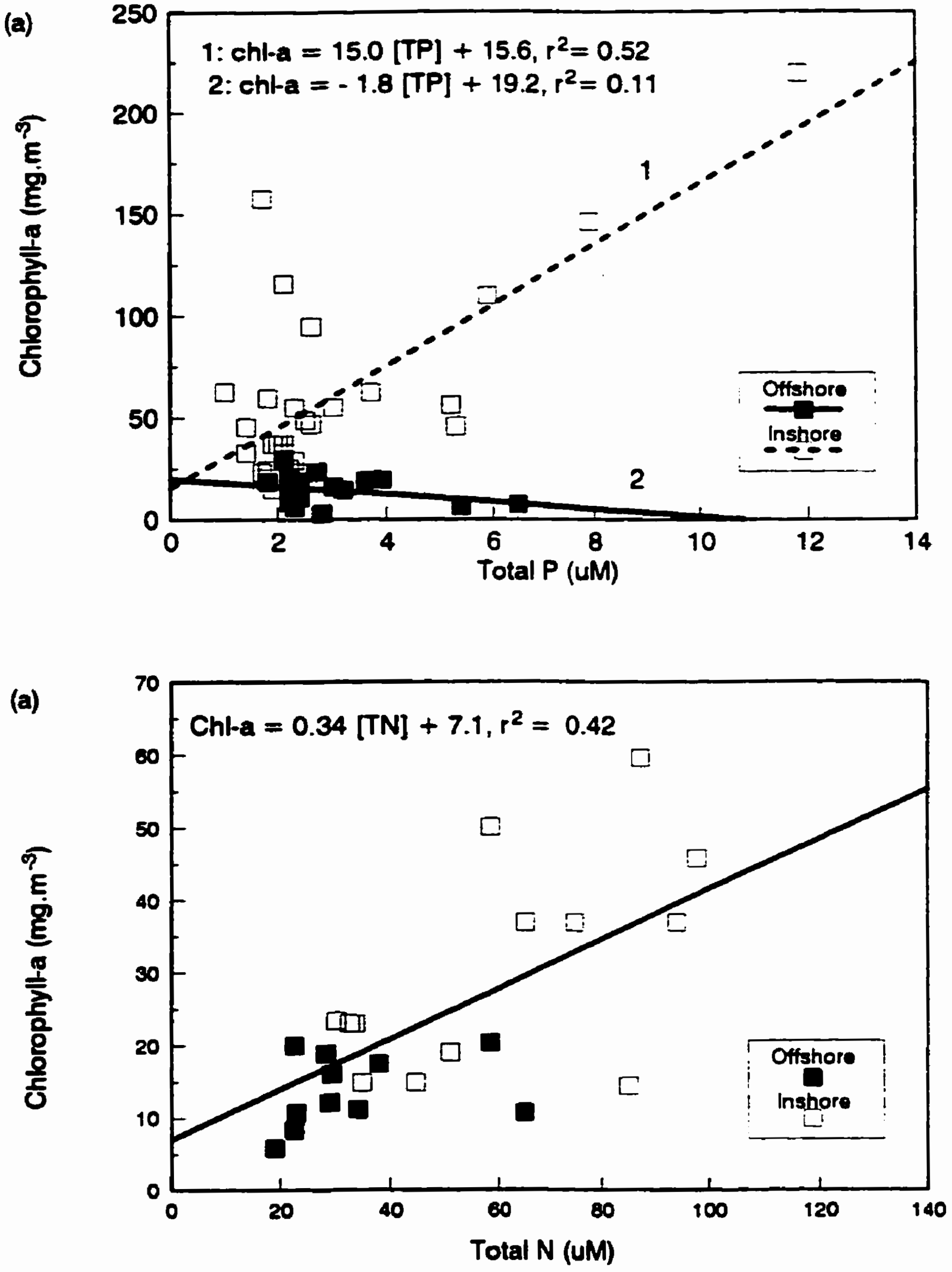


Figure.3.8. Relationships between epilimnetic chlorophylla concentrations and (a) total P and (b) total N.

Discussion

Use of particulate nutrient ratios as a tool for assessing nutrient availability indicated that both P and N may limit the phytoplankton community in the surface waters of Lake Victoria. Examination of the distribution and frequency of many particulate nutrient ratios indicate that the algal community offshore was more nutrient sufficient compared to those growing in the inshore regions of the lake. Indications of P-deficiency were more common (33-58%) than indictors of N-deficiency (21-29%), especially inshore where high sestonic N: P and C:P ratios indicated that P might limit further biomass increases at biomass maxima. P and N-deficiency were infrequent offshore and only occurred during the stratified period when algal biomass increased. Offshore, the algal community was less likely to be suppressed by P-deficiency as stocks of dissolved inorganic P were large and often in excess of 1.0 μM. Given the infrequent P and N deficiency offshore, the low algal biomasses (as chlorophyll-a and particulate nutrients) were likely a result of stronger light limitation (Chapter 4,5). The very weak and negative chlorophyll-a- total P relationship indicates that phytoplankton in offshore regions of Lake Victoria are insensitive to high P enrichment. This implies that further P loading may not increase algal biomass offshore, but could stimulate larger cyanobacterial blooms inshore.

Temporal variability of particulate nutrient ratios indicates that P and N deficiency was absent during periods of deeper and stronger mixing (June-July) in Lake Victoria. Absence of nutrient deficiency was likely due to impacts of stronger and deeper mixing that relaxed nutrient demand. Strong mixing reduces nutrient demand in surface waters as regenerated nutrients are re-distributed and algal biomass mixed deeply and has less light. Deeper and stronger mixing limits the algae's ability to utilize dissolved inorganic P because of reduced light availability (Chapter 4). Consequently, dissolved inorganic nutrients, in particular P, remain unutilized in offshore surface waters because algal biomasses remain consistently low. However, increases in algal biomass in September-October did lead to conditions of P-deficiency followed by severe N-deficiency at Bugaia. This deficiency in N favors N-fixing cyanobacteria (Chapter 5) and their biomass will be determined by light availability. Light limitation of N-fixers limits N availability for other algal species (Hendzel et. al. 1994) and without such light limitation, N-fixers could possibly fix adequate N to allow other algal species to increase using regenerated N.

Lake Victoria was frequently driven to conditions of N and P deficiency during periods of stable thermal stratification (September to April). This was indicated by the relatively high particulate C: N (>10) and low N: P (>22) ratios that occurred when thermal stratification was established (Figure 3.3 c, Hecky et al. 1994). Shallower mixing during early stable stratification (September-December) creates favorable light conditions that allow development of algal biomass and nutrient demand in the lake. These high algal biomasses consume nutrients and reduce dissolved inorganic concentrations, and subsequently the phytoplankton became increasingly P and N deficient with persistent thermal stratification. Continuous P and N removal by uptake and sedimentation, in addition to restricted nutrient exchange between the epilimnion and hypolimnion during sustained thermal stratification, result in reduced dissolved inorganic P and N concentrations in the surface waters. This was more evident in Napoleon Gulf where high algal biomasses occurred contemporaneous with elevated sestonic N: P (> 22) and C: P (> 129) ratios indicative of P deficiency.

In addition, stable thermal stratification restricts dissolved oxygen exchange between the epilimnion and hypolimnion, thus enhancing hypolimnetic anoxia. Hypolimnetic anoxia has intensified and is almost a permanent feature of Lake Victoria during the periods of stable thermal stratification (Chapter 2, Hecky et al. 1994). Anoxia promotes N loss in Lake Victoria (Hecky 1993, Hecky et al. 1996) as it promotes denitrification that converts nitrate to nitrous oxide and dinitrogen gas, both of which are lost to the atmosphere. Consequently, Lake Victoria becomes reduced in N relative to P during periods of stable thermal stratification. This result is consistent with observations in some temperate freshwater such as Lake 227 at the ELA, where denitrification reduced TN: TP to <8:1 in the hypolimnion resulting in an overall low N: P ratio upon mixing of deep waters into surface waters (Findlay et al. 1994). This low N: P ratio favored growth of N_2-fixing-cyanobateria (Schindler 1977, 1978; Flett el. 1980; Findlay et al. 1994). Similarly, in bottom waters of Lake Victoria, low sestonic N: P ratios of < 8 occur as well as low TN: TP ratios of < 20 occur (Chapter 2, Hecky and Guildford 2000) due to denitrification (Hecky et al. 1996). These low hypolimnetic ratios are more common during periods of prolonged stable thermal stratification in Lake Victoria, whereas epilimnetic values are generally in excess of 16 (Chapter 2, Hecky et al. 1996). This difference is maintained by N-fixation (Chapter 4) which offsets hypolimnetic losses to denitrification.

Given that N supply from the hypolimnion is reduced by denitrification and N from the catchment is insufficient to support observed algal production (Lehman and

Branstrator 1993), the phytoplankton in Lake Victoria have resorted to the more energy expensive diazotrophic activity (Turpin 1991) to mitigate perpetual N-deficiency. In Lake Victoria, conditions of N-deficiency are quickly overcome by the N-fixing cyanobacteria that maintain low C: N ratios (<8.3) in the euphotic zone, indicating that N requirements of the phytoplankton are frequently met through N-fixation. This observation is not in conflict with the finding that N sometimes limits the phytoplankton community in the surface waters of Lake Victoria. In aquatic ecosystems with diverse algal communities, it is possible for non-nitrogen fixers to be limited by N while N-fixing algae with ability to fix molecular N_2 remain N-sufficient. However, this condition may lead to dominance of by N-fixing algae. As a range of nutrient ratios is required by different algae for optimal algal growth (Hecky and Kilham 1988), an algal community can be limited by both P and N as frequently observed in Lake Victoria. Moreover, algae have different abilities to assimilate nutrients at low concentrations which allows different algal species to be limited by different nutrients.

Seston N: P, C: P and C: N ratios were more sensitive as indicators of P and N deficiency than the physiological nutrient status indicators P and N-debt. The consistently low N-debt values even when C: N values were high and indicative of N-deficiency casts doubt on the suitability of N-debt as an indicator of N-deficiency in Lake Victoria. The particulate N: P and C: P ratios and P-debt were often in agreement as a measure of P-deficiency. Overall N: P ratios were sensitive and may be the best measures of P-deficiency in Lake Victoria.

Use of N-debt as an indicator of N-deficiency in Lake Victoria suggested no or minimal N-deficiency even when high C: N ratios indicative of moderate to extreme N-deficiency were present. This inconsistency is not unique to Lake Victoria. In P-deficient culture experiments (Healey and Hendzel 1980) and in Lake Superior, irrespective of high C: N ratios, N-debt was always observed (Guildford and Hecky 2000). N-debt as a measure of N-deficiency is expected to be ineffective for N-fixing algae as they possibly can fix adequate N and lower their N-debt when light and other factors are favorable. So, when N-fixers dominate, N-debt may be low although the very presence of N_2-fixers indicates N-deficiency in the system. In temperate systems, there is often a time lag in the onset of N-deficiency during which N-debt can be useful in predicting the succession of N_2-fixing algae (Hendzel et al. 1994). However, in tropical systems that are continuously warm, illuminated and with a tendency to N-limitation (Guildford et al.2000), the succession may be very rapid (within hours of onset of N-debt).

Particulate nutrient ratios of N: P, C: P and C: N allow the general conclusion that both P and N limit the algal phytoplankton community in the surface waters of Lake Victoria. However, surface inshore waters were more frequently P-deficient than offshore due to higher N-fixer biomass that draws on the atmospheric N given better light conditions (Chapter 4, 5). These high algal biomasses, in turn, draw down the available dissolved inorganic P, leading to more frequent P-deficiency inshore than offshore. But, the N-fixers do not provide the entire required N to balance P because this process is energetically expensive and primary production in Lake Victoria is light limited (Mugidde 1992, 1993). Although P and N co-limit biomass production, hence contributing to eutrophication, reduction of P loads is key to the control and reversal of eutrophication that threatens the ecosystem health of Lake Victoria. Phosphorus reduction will lead to reduced frequency of N-deficiency, and consequently reduced N-fixation and cyanobacteria biomass and blooms, including genera known to produce phycotoxins. Reduced biomass will improve the underwater light availability and expand the euphotic zone. It is possible that increased light availability will maintain current primary productivity with less anoxia or even increase fish production in Lake Victoria.

Chapter 4: Planktonic nitrogen fixation in Lake Victoria, Africa

Abstract

Planktonic N-fixation provides up to 80% of the total N input in the surface waters of Lake Victoria. Rates of biological N-fixation in Lake Victoria were high and often exceeded 0.5μg N L^{-1} h^{-1}. Average rates of volumetric N-fixation at optimal irradiance were 8 times higher inshore than offshore. Rates of annual areal N-fixation, modeled from the N-fixation light-response per unit chlorophyll-a and light attenuation in the lake, were moderate to high (1.8-23.1 g N m^{-2} y^{-1}), and were only twice as high inshore as offshore. Variation in the light extinction coefficient explained a small but significant proportion of the variation in the optimal N-fixation in Lake Victoria. N-fixation increased significantly with increases in algal biomass (chloropyll-a). Algal biomass and N-fixation were lower in the more deeply mixing (> 20 m) offshore waters, because of the persistently low mean light intensities over 24 hours (I_{24}) in the water column most of the year. N-fixation increased with increases in light availability associated with shallower mixing depths, and maximal rates occurred when the lake was thermally stratified and shallowly mixing.

At both inshore and offshore, minima of algal biomass and N-fixation were consistent with low light conditions around July when the lake was most deeply mixing. The ratio of I_{24} to the irradiance at which N-fixation approaches saturation (I_k) was often <1, and provides evidence that N-fixation was light-limited, particularly offshore. Light limitation lessens the algal demand for N, and constrains algal biomass development and N-fixation more in the offshore compared to the shallower and more protected inshore surface waters of Lake Victoria.

Introduction

Lake Victoria, a large (68, 800 km^2) eutrophic lake (Hecky 1993), is recognized as one of the most productive freshwater ecosystems, with the largest freshwater fishery in the world (Ogutu-Ohwayo 1990, 1992, Goldschmidt & Witte 1992) and high rates of phytoplankton primary production (Mugidde, 1992, 1993, Ogutu-Ohwayo et al. 1996). With commercial fish yields that can exceed 500,000 metric tonnes a year, the lake constitutes a huge fishery resource for human consumption within the East African region, and even beyond to international markets. Lake Victoria and its tributaries provide drinking water for about 10 million people, and for a huge livestock and wildlife population in the region. However, the lake's importance as a reservoir of biodiversity and a source of clean drinking water, hydroelectric power and transport as well as tourist attraction is threatened by undesirable changes in the water quality since the early 1960s. Unwanted water quality effects in Lake Victoria include objectionable taste and odors of drinking water, fish kills associated with cyanobacterial blooms (Ochumba and Kibaara 1989, 1990, Hecky 1993) and deep water anoxia (Hecky 1993, Hecky et al. 1994).

Despite the increasing nutrient enrichment that is recorded in the sediments (Lipatou et al. 1996) and documented in the water column (Hecky and Bugenyi 1992, Hecky 1993), ambient dissolved inorganic nutrients can be low in the surface mixed waters of Lake Victoria (Chapter 2, Hecky 1993, Lehman et al. 1998). Total dissolved inorganic nitrogen concentrations can be low in surface waters and even in the mid-waters, where high rates of N loss through denitrification at the oxic-anoxic interface in the water column occur (Hecky et al. 1996). The oxic-anoxic interface is present during the thermally stratified phase that persists for approximately 80 % of the year, from

September through May (Chapter 2, Hecky et al. 1994) and limits nitrogen return from the deep waters of Lake Victoria (Hecky et al. 1996). In contrast, seasonal anoxia favors P regeneration from the sediments (Hecky et al. 1996). Consequently, the bottom waters become enriched with phosphorus relative to nitrogen. This imposes low N: P ratios when deep waters are mixed into surface waters around July. Moreover, Lake Victoria is heavily loaded with P relative to N from the catchment (Lehman and Branstrator 1993) which exacerbates the already low N: P ratios and imposes a nitrogen deficit that favors large populations of nitrogen fixing cyanobacteria (Schindler, 1977, Levine and Schindler 1992, Hendzel et al. 1994). Consequently Lake Victoria has one of the lowest recorded TN: TP ratios for a large water body (Chapter 2, Guildford and Hecky 2000).

The shift in dominance from the historic algal community dominated by diatoms, such as *Aulacosiera (Melosira)* and *Cyclostephanos*, and chlorophytes (Talling 1957 a, b, Evans 1962) to cyanobacteria including N-fixing, filamentous cyanobacteria (Kling et al. 2001) also provides evidence of increased P loading in Lake Victoria. The persistence and abundance of the blue-green algae *Cylindrospermopsis* and *Anabaena* that can fix atmospheric N_2 provides additional evidence of N-deficiency in Lake Victoria. Given that N-fixation is an energetically expensive biochemical process catalyzed the by oxygen–sensitive enzyme nitrogenase (Gallon, 2001), the light-N-fixation relationship was evaluated. Mugidde (1993) has previously demonstrated that phytoplankton primary productivity is light-limited, which implies that light possibly limits N-fixation in Lake Victoria.

Although indirect evidence suggests that algal N-fixation must be high, the quantitative importance of N-fixation and its relative importance to other sources of N loading have not been previously determined. N-fixation of gaseous nitrogen by cyanobacteria such as *Cylindrospermopsis* may be important to maintaining high primary productivity (Mugidde 1992, 1993), and thus the transfer of energy to higher levels in the food web in Lake Victoria. The objective of this study was to determine nitrogen fixation rates in Lake Victoria, and put those rates in the context of N-budget of Lake Victoria and to the nitrogen requirement of the phytoplankton.

Methods

Study areas

Lake Victoria has two ecologically distinct regions, the shallow inshore bays (< 30 m) along the irregular coastline and behind the extensive northern archipelago of islands (Figure 1a) and the deeper offshore region (> 60 m) that experiences stable thermal stratification between September and April and complete vertical mixing in June-July. The upper mixed layer depth averages 10 m in protected inshore areas and 30 m offshore during periods of stable thermal stratification (Fisheries Resources Research Institute (FIRRI) unpublished data). N-fixation measurements were made between 1994-1998 at inshore and offshore locations (Figure 1b). The inshore sites in Napoleon Gulf (19 m), (Pilkington Bay (11 m), Itome Bay (30 m) and offshore sites Bugaia and Far station (65 m) were sampled frequently between 1994-1998. Buvuma Channel (21 m) was sampled once in 1997, and monthly in 1998. Further offshore sites XL1 to XL12 (> 65 m, Figure 1c) were sampled once or twice between 1995-1996.

Water samples were drawn from the epilimnion, but within twice the Secchi depth, that generally was 0-2 m inshore and 0-6 m offshore. Water samples were passed through a 100 μM nylon mesh to exclude large zooplankters, and were returned to the laboratory at FIRRI, or used on deck, for N-fixation bioassays as well as dissolved nutrients and chlorophyll-a analyses. Water was filtered onto GF/F filters for determination of suspended nutrients (C, N & P) and chlorophyll-a. Desiccated filters were sent to the Freshwater Institute Winnipeg, for analysis of suspended C, N & P following procedures as in Stainton et al. (1977). Chlorophyll-a samples were extracted in 90% methanol, kept in the cold (4 °C) and dark for about 20 hours, and the absorbances of the extracts were measured spectrophotometrically at FIRRI, Uganda. Chlorophyll-a concentrations were calculated as in Stainton et al. (1977).

N-fixation was measured using the modified acetylene reduction method of Flett et al. (1976). N-fixation samples were incubated in light and dark syringes filled with lake water. A control syringe (acetylene blank) was filled with de-ionized water. Light-tight syringes wrapped in alumnium foil were used to measure dark N-fixation. With little or no aeration, 50-ml pyrex glass syringes (Luer-Lock) fitted with a three-way valves were filled with 30-40 ml of lake water or de-ionized water. Each sample was injected with 5 ml of acetylene, shaken vigorously to dissolve the acetylene into the liquid phase, and incubated for 4 h under simulated *in situ* light conditions either in the laboratory or in the on-deck incubators, maintained within 2 °C of ambient lake surface temperature. Light syringes were placed in an incubator at positions of decreasing light intensity. A 1000 watt white lamp provided a constant light source that gave a gradient of light intensities in various positions in the laboratory incubator. Natural light adjusted with fibre-glass window screen was used to produce high to low light intensities in on-deck incubations. A spherical light sensor and meter (Li-COR 1000) were used to measure the light intensity at each syringe position in the incubators.

Stripping the incubated samples with 10 mL of clean air to extract ethylene ended the N-fixation incubations. The resulting gas samples were stored in vacutainers and measured using the flame ionization gas chromatography as in Hendzel et al. (1994). The ethylene measured in the control was subtracted from the light values to estimate biological N-fixation. Nitrogen fixation was estimated from the ethylene production using a conversion factor of 3:1 (atom: atom) as in (Flett et al. 1976) and 1:5.57 (weight: weight), and volumetric rates of N-fixation are reported in μg N L^{-1} h^{-1}.

N-fixation vs. irradiance curves from the incubator were used to calculate three N-fixation parameters, N_{opt} (N-fixation at optimal irradiance in μg N L^{-1} h^{-1}), N^B (maximum rate of N-fixation normalized to chlorophyll-a in μg N μg chl-a^{-1} h^{-1}) and α^B, the slope of chlorophyll-a normalized N-fixation at nonsaturating irradiances in μg N μg chl-a^{-1} mE^{-1} m^{-2} (E = Einstein). The light saturating irradiance (I_k) in mE m^{-2} min^{-1} for N-fixation was determined as the ratio N^B/α^B (Figure 4.3). The modified numerical photosynthesis model of Fee (1990) was used to estimate daily and annual rates of N-fixation from the temporal distribution of photosynthetically available radiation (PAR), the underwater extinction of PAR and volumetric N-fixation as a function of light intensity in the incubator or deck box. Daily and annual N-fixation were calculated using light attenuation coefficients and actual global radiation data, integrated each 30 minutes from sunset to sunrise as described in Fee (1990). The fraction of solar PAR that reaches each depth relative to surface light (I_z) was calculated as in Hutchinson (1957) with the following equation:

$$I_z = I_S e^{-kz}$$

where k is the vertical extinction coefficient of PAR. I_s is the surface irradiance. I_z is the solar irradiance at depth z . The mean irradiance in the water column over 24 hours (I_{24}, mE m^{-2} min^{-1}) was calculated as in Hecky and Guildford (1984) with the following equation:

$$I_{24} = I_s \frac{(1 - e^{-kz})}{kz}$$

where, I_s is the surface light and z is the mixed layer depth. I_s was obtained from cloudless solar irradiance and was corrected for altitude and latitude of Lake Victoria as in Fee (1990).

The daily N demand was determined from the particulate C:N ratios and daily areal C-fixation calculated from gross oxygen production assuming a photosynthetic quotient of 1.25. Gross photosynthesis was estimated as changes in dissolved oxygen evolved in the light and dark bottles as in Talling (1965). Water sub samples drawn from the same sample as N-fixation samples were siphoned into either clear or blackened 60 mL glass bottles. These dark and light bottles were placed in the laboratory incubator, where irradiances and temperatures closely approximated in situ conditions, for three hours. In other cases, light and dark bottles were filled with water taken from several depths in the euphotic zone (0-6 m) and then incubated in situ at irradiances received at those specific depths. At the end of the incubation, samples were fixed using manganese chloride and potassium iodide with sodium azide.

Data on $\delta\ ^{15}N$ of particulate organic matter (POM) was from the multidisciplinary Lake Victoria Ecosystem study and was provided by Ms. P. Ramlal who performed the analysis. I participated in the Lake Victoria Ecosystem research program and did C-and N-fixation measurements. Statistical tests were conducted with SYSTAT version 9.0.

Results

N-fixation in inshore and offshore Lake Victoria

Table 4.1 gives measured volumetric rates at optimal light for N-fixation, and Table 4.2 presents areal N-fixation modeled from N-fixation parameters N^B and α^B (derived from incubator N-fixation - light response) and in situ light attenuation. Napoleon Gulf and Bugaia were chosen to represent typical inshore and offshore stations. Measured and modeled daily rates for 1998, the year of most frequent sampling for Napoleon Gulf and Bugaia, are used to illustrate seasonality of N-fixation and the importance of light.

Optimal rates of volumetric N-fixation were in the range 0.0 -5.0 μg N L^{-1} h^{-1} during 1994-1998 in Lake Victoria (Figure 4.1a, Table 4.1). Overall, N-fixation decreased from nearshore to offshore and average inshore rates (0.90 μg N L^{-1} h^{-1}) were significantly higher ($p<0.01$) than offshore average values (0.11 μg N L^{-1} h^{-1}). Maximum rates of volumetric N-fixation were orders of magnitude higher and average rates were approximately 8 times higher in inshore than in offshore regions of Lake Victoria. Annual and optimal average N-fixation did not differ significantly ($p>0.05$) among inshore stations Napoleon Gulf, Buvuma Channel and Pilkington Bay (Table 4.1 & 4.2). However, Itome Bay, the deepest inshore station, did have lower average and maximum rates than the other inshore stations, being intermediate between inshore and offshore rates. There were significant differences ($p<0.01$) in average N-fixation among offshore stations near at Bugaia, XL9, XL12 and farther offshore stations at XL1 to XL8, X10 to XL11.

Table 4.1. Optimal volumetric rates of N-fixation ($\mu g\ N\ L^{-1}\ h^{-1}$) for inshore and offshore Lake Victoria, during 1994-1998. Std = standard deviation.

Station	Minimum	Average	Maximum	Std	N
Napoleon Gulf	0.023	0.889	4.886	1.195	36
Pilkington Bay	0.154	0.996	3.885	0.996	18
Buvuma Channel	0.360	1.200	4.390	1.120	11
Itome Bay	0.271	0.571	1.122	0.327	11
Bugaia, XL9, XL12	0.000	0.167	0.378	0.117	19
FAR Station, XL1-XL8, XL10-XL11	0.000	0.004	0.009	0.005	13

Table 4.2. Annual (areal) rates of N-fixation (g N m^{-2} y^{-1}) and their coefficient of variation (c.v. standard deviation expressed as percentage of the mean) in Lake Victoria during 1994-1998. N = number of measurements during the year.

Location	Inshore regions			Offshore regions				
Year	Napoleon Gulf	Pilkington Bay	Buvuma Channel	Bugaia	XL7	Far	XL1	XL5
1998	15.0 (19)	23.1 (12)	13.2 (11)	10.4 (9)				
1997	10.9 (2)	18.1(2)		6.1 (2)				
1996	9.1 (4)		11.5 (4)	7.8 (3)		1.3 (1)	0.5 (1)	0.0 (1)
1995	16.0 (4)		8.5 (3)	1.8 (2)	13.1 (1)	0.0 (1)	0.0 (1)	2.2 (1)
1994	14.4 (2)			4.5 (1)		0.0 (1)		
Average	13.1	20.6	11.0	6.1	13.1	0.4	0.3	1.1
C.v.	20%	12%	17%	48%		141%	100%	100%

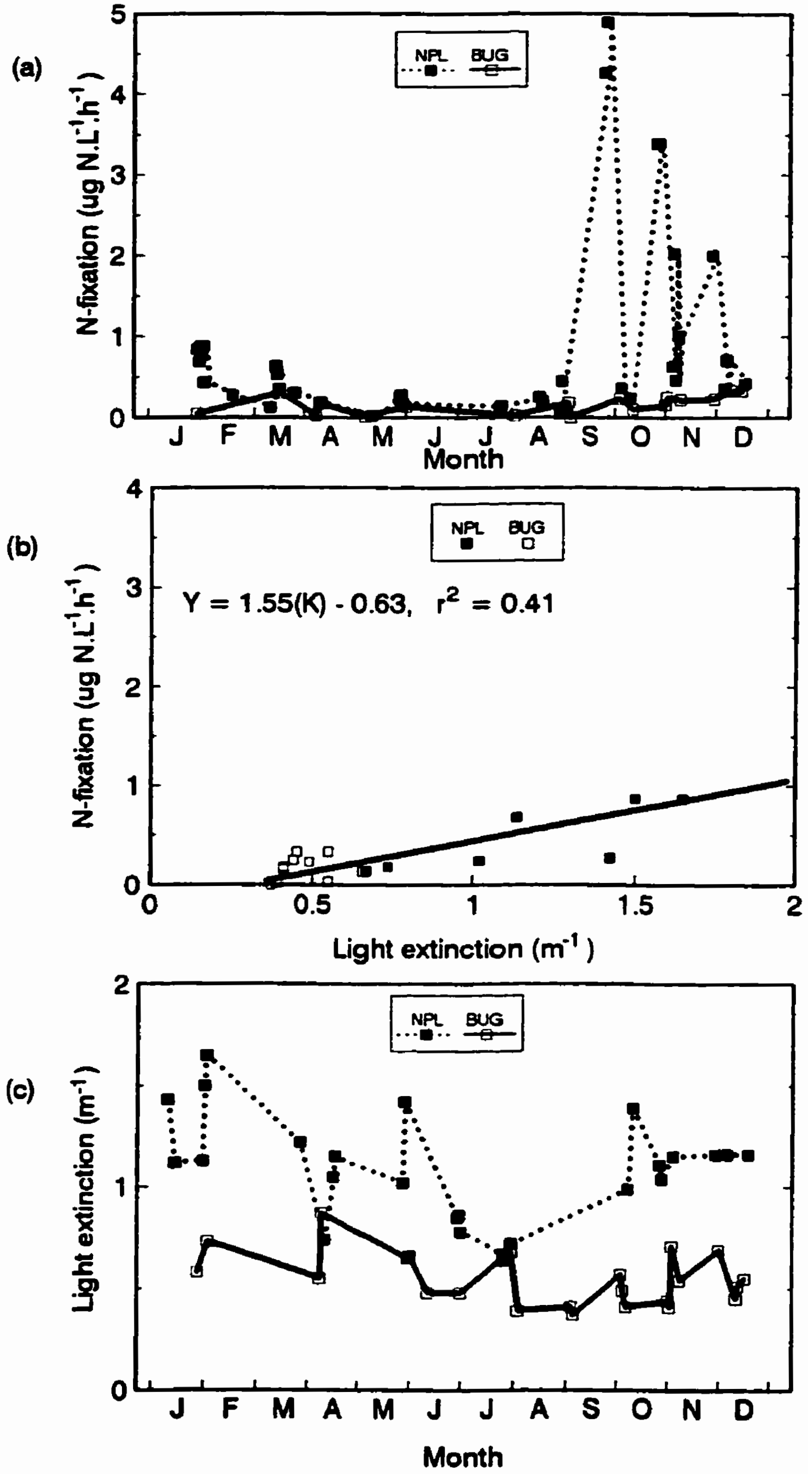


Figure. 4.1. (a) Optimal rates of volumetric N-fixation at inshore in Napoleon Gulf (NPL) and offshore at Bugaia (BUG) between 1994 and 1998, (b) optimal N-fixation vs light extinction (k) at NPL and BUG and (c) temporal variation of k at NPL and Bugaia

Modeled annual rates of integral N-fixation were quite variable and in the range 0.5 to 23.1 g N $m^{-2}y^{-1}$, average 8.1 g N m^{-2} y^{-1} (Figure 4.2 a, Table 4.2, 4.3). Areal rates of N-fixation did not vary significantly ($p > 0.05$) between years in Lake Victoria. The shallower inshore bays with high light extinction coefficients (Table 4.4) had significantly higher ($p = 0.002$) average daily areal rates of N- fixation than offshore (Table 4.2, 4.3). Estimated annual N-fixation was four times higher in the shallower inshore areas than in the deeper offshore (Bugaia & Far) waters of Lake Victoria. Annual average integral N-fixation was significantly higher ($p < 0.01$) in the offshore Bugaia region than in the further offshore Far region that was sampled less frequently (Table 4.3).

Table 4.3. Average integral N-fixation and standard deviation from of the inshore and offshore regions of Lake Victoria during 1994-1998. Std = standard deviation, N= number of measurements.

Location	Average N-fixation (g N m^{-2} y^{-1})	Std	N
Inshore: Napoleon Gulf, Pilkington Bay and Buvuma Channel region	14.0	4.2	62
Offshore Bugaia, XL7, XL9, XL12 region	7.3	3.7	18
Offshore Far, XL1-XL5, XL10-XL11 region	0.6	0.8	7

Table 4.4 Average light characteristics and their standard deviation for inshore and offshore Lake Victoria, from measurements between 1994 and 1998. Number of measurements is reported in parentheses.

Parameter	Inshore (Napoleon Gulf)	Offshore (Bugaia)
Light extinction coefficient (m^{-1})	1.1 ± 0.3 (25)	0.6 ± 0.1 (23)
Mean light in water column (I_{24}, mE m^{-2} min^{-1})	13.3 ± 0.8 (12)	6.5 ± 2.7 (12)
Secchi transparency (m)	1.5 ± 0.4 (22)	2.4 ± 0.6 (25)
Euphotic depth (m)	4.7 ± 1.2 (24)	9.2 ± 2.0 (22)
Mixing depth (m)	7.1 ± 2.6 (24)	35.0 ± 12.6 (24)
Chlorophyll-a (mg m^{-3})	71.0 ± 100.4 (47)	13.5 ± 5.8 (42)

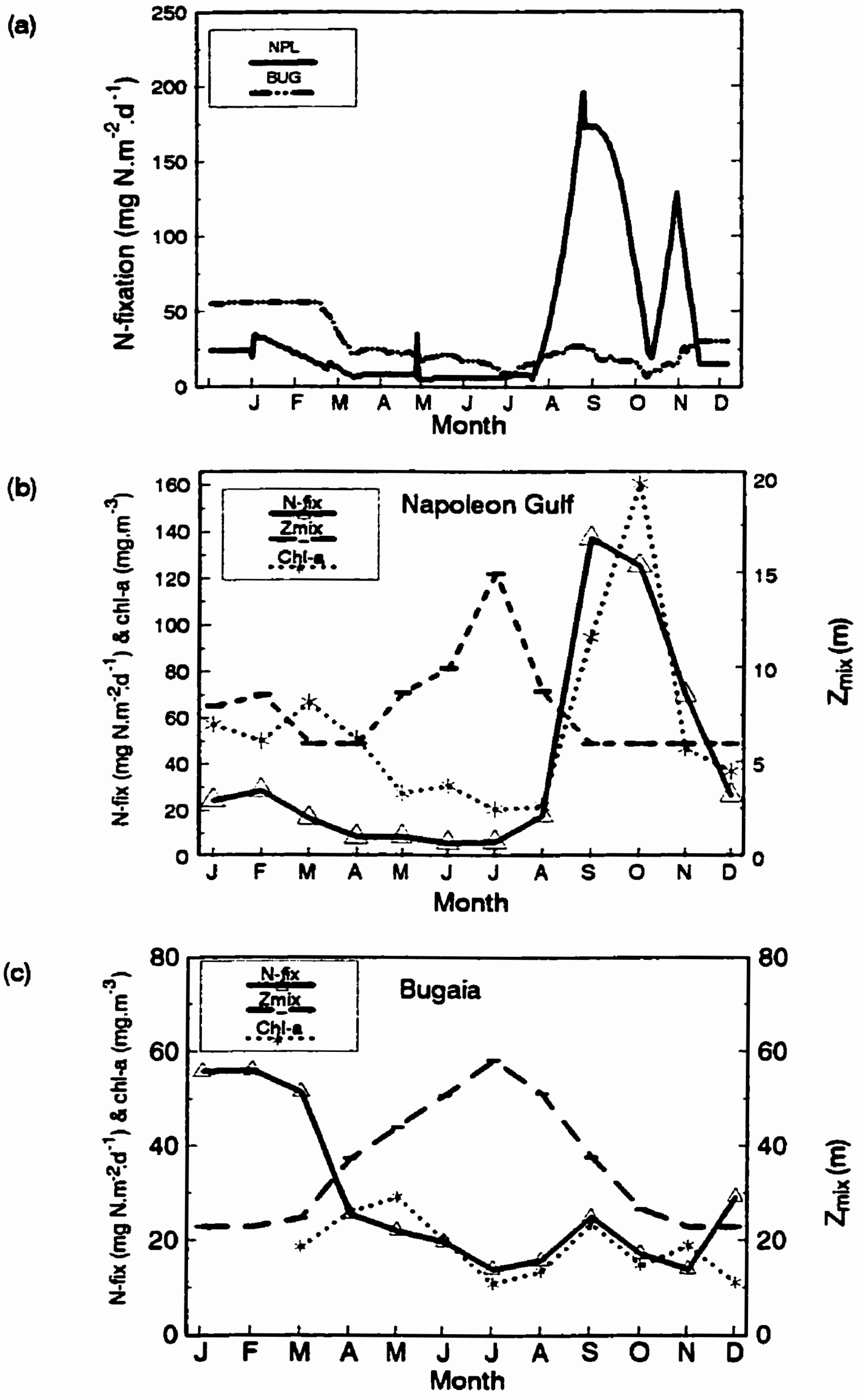


Figure. 4.2. (a) Modeled daily rates of N-fixation in Napoleon Gulf (NPL) and Bugaia (BUG). N-fixation (N-fix), mixing depth (Zmix) and chlorophyll-a at (b) Napoleon Gulf and (c) Bugaia

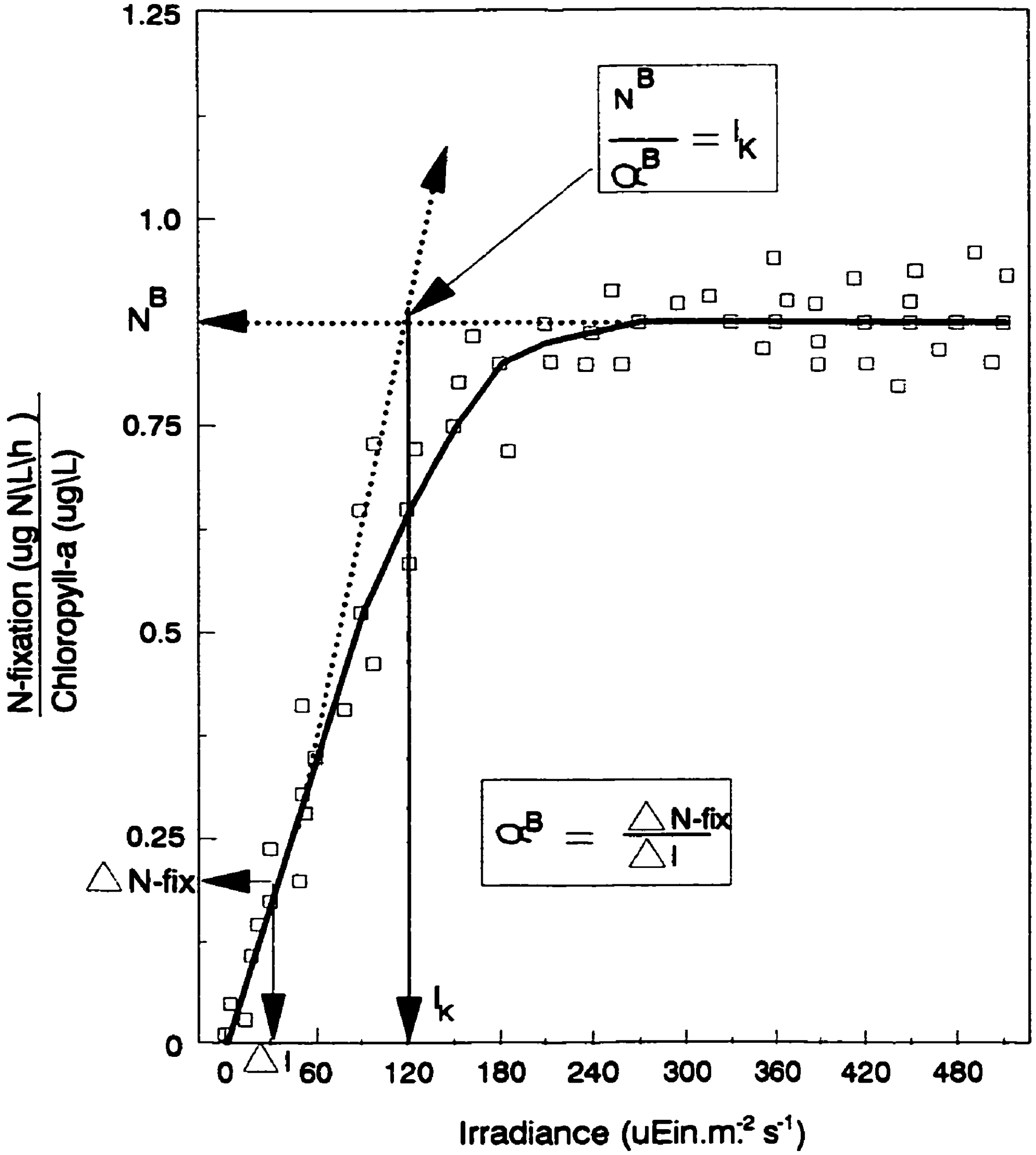
N-fixation parameters and light response

Algal N-fixation increased with increased light intensity until light-saturated N-fixation was achieved between irradiances of 100-130 μE $m^{-2}s^{-1}$. The shape of the N-fixation-light response curve was similar both inshore and offshore, but a steeper gradient of nonsaturated N-fixation and higher rates of maximum N-fixation were measured inshore (Figure 4.3, Table 4.5). Maximum chlorophyll-a –normalized N-fixation rate (N^B) ranged by two orders of magnitude, from 0.001 to 0.1 μg N chl-a^{-1} h^{-1}, and the N-fixation coefficient at nonsaturating irradiances ($\propto^B$) ranged by over one order of magnitude, from 0.003-0.085 μg N chl-a^{-1} $E^{-1}m^{-2}$. Highest values of both parameters were in inshore surface waters, and average N^B and $\propto^B$ values were significantly different ($P < 0.05$) amongst inshore and offshore sites (Table 4.4). The light saturation parameter (I_k) ranged from 45 to 347μEin $^{-1}m^{-2}$ s^{-1} and average inshore and offshore mean values were not significantly different among stations.

Selected volumetric N-fixation depth profiles provide a simple means of assessing light constraints on phytoplankton N-fixation (Figure 4.4 a, b). Rates of volumetric N-fixation were typically higher in the shallower photic depth (approximate 5m) in Napoleon Gulf than in the deeper euphotic depth (10 m) offshore. Further evidence of higher N-fixation inshore was provided by patterns of δ ^{15}N content of particulate organic matter (POM) that were consistent with higher diazotrophic activity fixing atmospheric N_2 (δ $^{15}N = 0$) inshore than offshore. The δ ^{15}N of POM ranged from 0.8 to 16.3 (Figure 4.5 a, Table 4.5). The δ ^{15}N of POM was strongly ($r^2 = 0.94$) and significantly ($p<0.01$) correlated with the daily integral rates of N-fixation in Lake Victoria (Figure 4.5 b), calculated for the same stations. Increases in δ ^{15}N POM were accompanied by decreased N-fixation as indicated by the negative linear regression slope (Figure 4.5 b). Concentrations of δ ^{15}N in POM were 3- to 6-fold higher offshore than inshore reflecting the higher degree of diazotrophy inshore. The higher δ ^{15}N offshore implies that internal cycling processes with the recycled DIN having a high δ ^{15}N were a larger source of N offshore than inshore. The y-intercept of the relation in Figure 4.5 b may represent the isotopic signature (δ ^{15}N = 9) of regenerated deep water δ ^{15}N after annual mixing.

Table 4.5. Average values with standard deviations of N-fixation parameters and δ ^{15} N of POM for inshore and offshore Lake Victoria. Number of measurements is reported in parentheses.

Parameter	Inshore (Napoleon Gulf)	Offshore (Bugaia)
N^B (μg N μg chl-a^{-1} h^{-1})	0.018 ± 0.018 (32)	0.011 ± 0.01 (18)
α^B (μg N μg chl-a^{-1} Ein^{-1} m^{-2})	0.098 ± 0.098 (32)	0.062 ± 0.085 (18)
I_k (μEin^{-1}m^{-2} s^{-1})	130.59 ± 76.25 (32)	108.150 ± 41.28 (18)
δ ^{15}N POM.	2.8 ± 0.7 (13)	8.9 ± 3.6 (25)
Percentage N demand	4.4 ± 5.0 (38)	3.1 ± 1.9 (25)
N-turnover (days)	67 ± 42 (33)	83 ± 46 (16)



4.3. N-fixation (N-fix)-light (I) curve for Lake Victoria, 1994-1998 and graphical definition for the N-fixation parameters normalized to chlorophyll-a and used in modeling areal N-fixation.

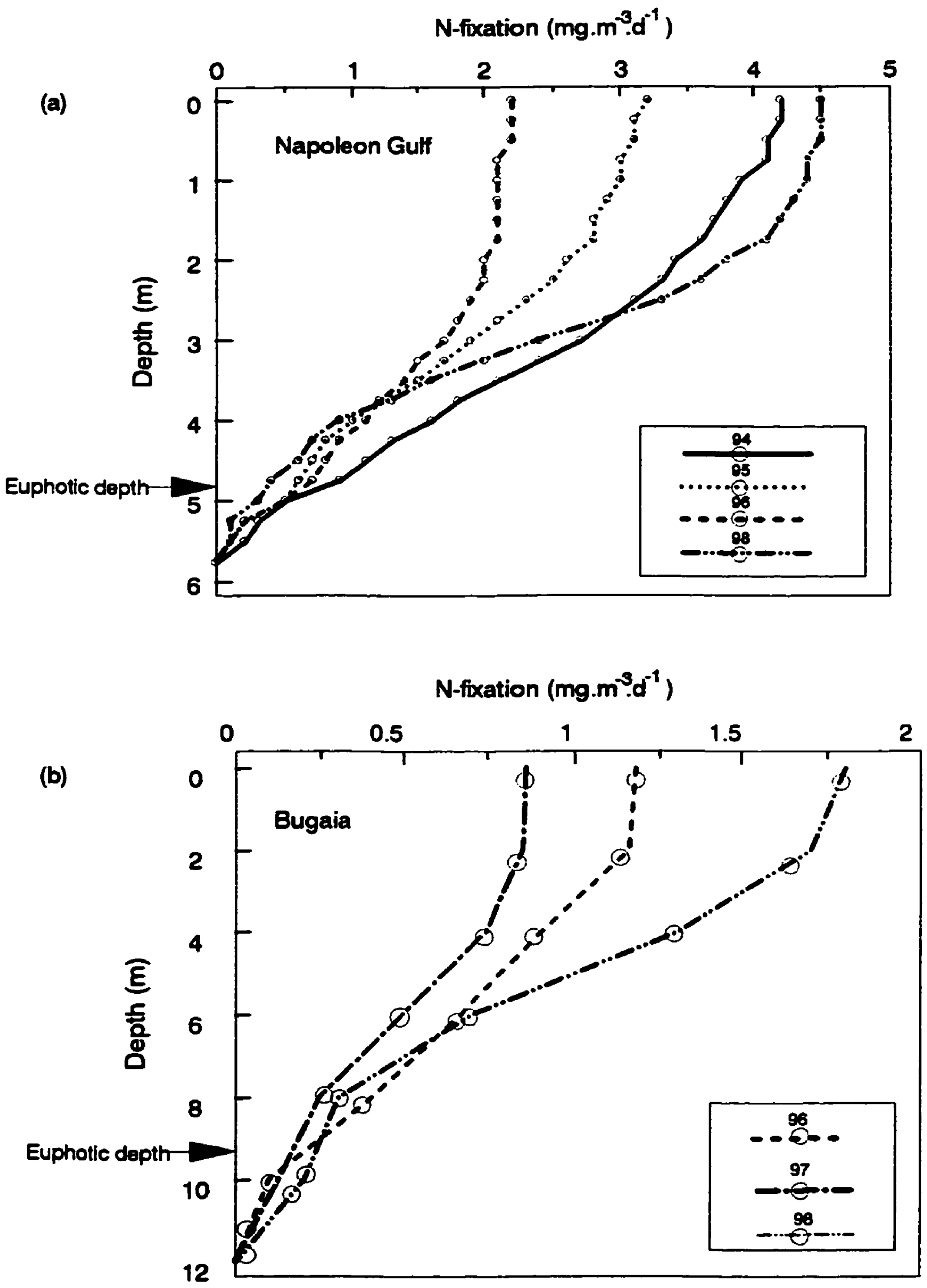


Figure. 4.4. Simulated in situ mean N-fixation depth-profiles from Napoleon Gulf and Bugaia. Daily surface irradiance (PAR) depth profiles of PAR and incubator-derived data of maximum and nonsaturating rates of N-fixation normalised to chlorophyll-a were used in the generation of these N-fixation depth profiles.

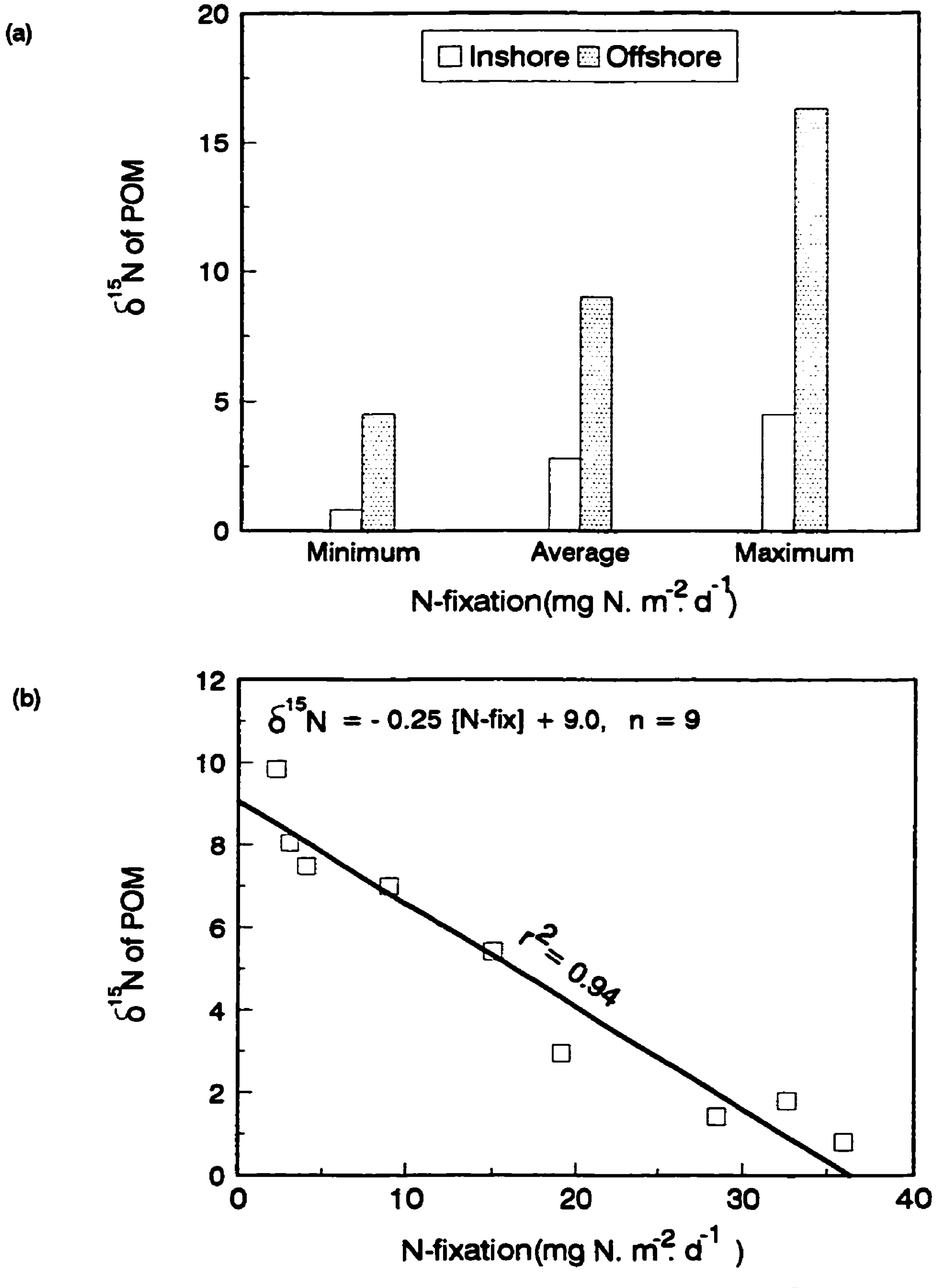


Figure. 4.5. (a) Minimum, average and maximum δ^{15}N of POM
(B) relationship of δ^{15}N of POM and N-fixation

N-demand and turnover times in Lake Victoria

Simultaneous measurements of the higher contribution to the daily N-demand calculated from the primary production measurements (Figure 4.6 a) and faster N turnover times of particulate N (Figure 4.6 b) provide further evidence of higher dependence on N-fixation by phytoplankton inshore than offshore. The daily N-demand, calculated from particulate C:N ratios and daily carbon fixation, contributed 1% to 20 %, average 4% of the daily N requirement in Lake Victoria. The N-fixation contribution to the daily N-demand varied with season ($p<0.01$) and was slightly higher inshore (1-20%) than offshore (1-9%). The highest N-fixation contribution to the daily N-demand occurred during the early stratified period (September-December) at both inshore and offshore and also in February-March in Bugaia.

The fact that N-fixation contributed a small proportion (≤ 20%) of the daily N demand, especially offshore, suggests that a large fraction of the daily N requirements originate from internal recycled N. It thus follows that N turnover times, calculated from particulate N concentrations and daily rates of N-fixation, were longer offshore than inshore. N turnover due to fixation varied remarkably, and was in the range 4 to 173 days, average 73 days (Figure 4.6 b). Shortest N turnover times occurred between September and December in Napoleon Gulf and in September-October and February-March in Bugaia. Overall, shortest N turnover occurred during the stratified period (Figure 4.6 b) when rapid increases in phytoplankton biomass occurred in September-November especially in the inshore surface waters (Figure 4.2 a, b). At this time of the year, the new N delivered via N-fixation would take approximately 60 days to increase algal biomass and dependent daily N-fixation rates to maximum values (Figure 4.2 a, b) and this increase can be accounted for by N-fixation rates during this time interval. Total N also increases to its annual maximum (see chapter 5, Figure 5.5 f) at this time. Longest turnover times of the particulate N pool occurred in July-August (Figure 4.2 a, b, 4.6 b) when biomasses were low, but N-fixation was minimal. Recycling of N was adequate to meet the low N demand (Figure 4.6 a) at this time.

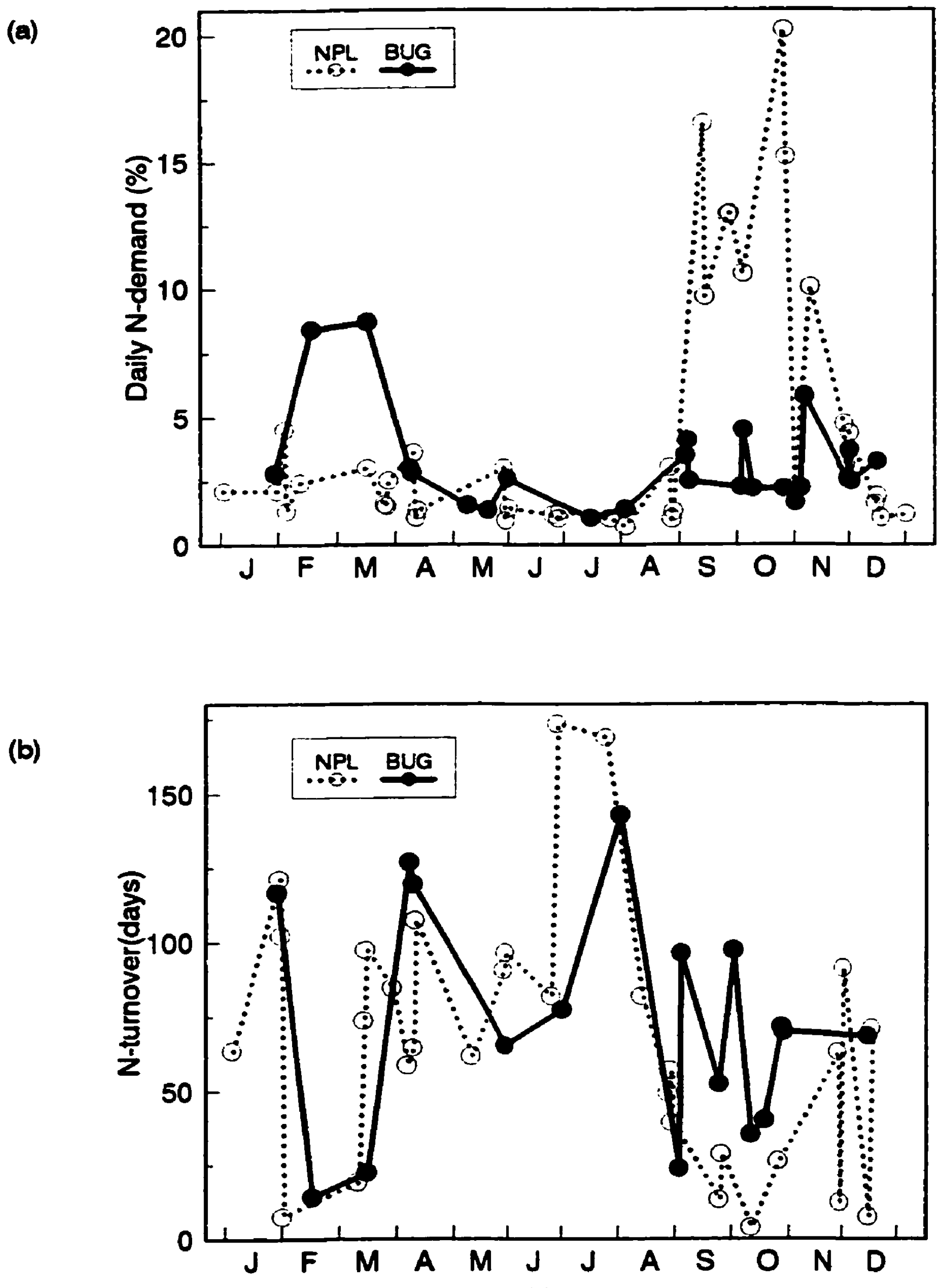


Figure. 4.6. (a) Percentage N-fixation contribution to the daily N-demand at Napoleon Gulf (NPL), Bugaia (BUG) and (b) nitrogen- turnover times due to N-fixation, 1994-1998.

Spatio-temporal variation of N-fixation, algal biomass and light

The relationship between optimal rates of volumetric N-fixation and the light attenuation coefficient (k) is illustrated in Figure 4.1 b. Optimal rates of N-fixation varied with fluctuations in light extinction coefficient, and yielded a weak linear correlation ($r^2 = 0.41$) that was statistically significant at $p < 0.05$. Inshore (Napoleon Gulf), the light extinction coefficient was double the offshore (Bugaia) coefficient, and the Secchi and euphotic depth were half as deep (Table 4.5). Despite higher light extinction coefficients inshore, the shallower depths for mixing resulted in higher light availability (I_{24}). More light availability (I_{24}) in the shallower mixed water column inshore supported higher rates of planktonic N-fixation and algal biomass (chlorophyll-a) than in the deeper mixed water column offshore (Figure 4.2 a, b, c, Table 4.3, 4.5).

The volumetric and areal rates of N-fixation showed similar temporal and quantitative trends in Lake Victoria (Figure 4.1 a, 4.2 a). Optimal (volumetric) and daily N-fixation varied significantly ($p<0.05$) with season in Napoleon Gulf. Highest rates of N-fixation occurred between September and November when the lake was thermally stable and algal biomass had reached its maximum (Figure 4.2 b, c, 3.3 c). Minimal fixation occurred between April and August, when light extinction coefficients were relatively low ($k < 1.0$ m^{-1}) but mixing depths were greatest all over the lake. There was little seasonality in volumetric rates of N-fixation and light extinction coefficients in offshore (Bugaia) Lake Victoria (Figure 4.1 b, 4.2 b, c). N-fixation did not vary significantly with months and seasons ($p > 0.05$) in the optically more clear but more deeply mixed offshore (Bugaia) waters of Lake Victoria. However, both measured (volumetric) and modeled (areal) N-fixation rates were particularly low around July when the lake was deeply mixing in both Napoleon Gulf and Bugaia.

Algal biomass (chlorophyll-a) was much higher inshore, with average chlorophyll-a concentrations approximately 5-times higher in Napoleon Gulf than at Bugaia (Table 4.4). Chlorophyll-a concentrations were correlated to volumetric N-fixation ($r = 0.80$, $n = 30$) in Lake Victoria (Figure 4.7a). In Napoleon Gulf, high chlorophyll-a concentrations were associated with high rates of N-fixation (Figure 4.2 b). The N-fixation maximum occurred just prior to increased and maximum chlorophyll-a concentrations in Napoleon Gulf in September-October. After this, chlorophyll-a decreased 3-fold and remained lower until further decreases in April in Napoleon Gulf. Variation in chlorophyll-a concentrations and N-fixation was less in Bugaia, although slightly higher values between September and May and minimal values in June-July were measured (Figure 4.2 c). Algal biomass (chlorophyll-a) in the range 6.5-160 mg m^{-3} was significantly related to light extinction ($r^2 = 0.38$, $n = 58$) (Figure 4.7 b).

The ratio of I_k to in situ I_{24} is an indicator of the light available in the water column to saturate rate of N-fixation (Hecky and Guildford 1984). Evidence obtained from the ratio I_{24}/I_k, shows that planktonic N-fixation was often light deficient and may be light limited (Figure 4.8 a & b), especially in the deep offshore regions (Bugaia). The deeper mixing depth (> 20 m) contributes to the low I_{24} (Figure 4.2 c, 4.8 c) which, in turn, supports low algal biomass and N-fixation at Bugaia. The I_{24}/I_k ratio < 1 indicates that N-fixation is light-limited in Bugaia most of the year, with exceptions in September, December and March (Figure 4.8b). Light was adequate to saturate N-fixation in September-October, when the lake was warming and shallowly mixing. The high chlorophyll-a concentrations in Napoleon Gulf are made possible by the shallower mixing depth (< 10 m) and relatively higher I_{24} than offshore (Figure 4.8c). Light was more available in the shallow inshore waters as indicated by the higher I_{24} most of the year (Figure 4.8a). Extremely low I_{24}/I_k (< 0.5) values were measured during destratification (May-August) offshore because of deeper mixing depths at that time of the year.

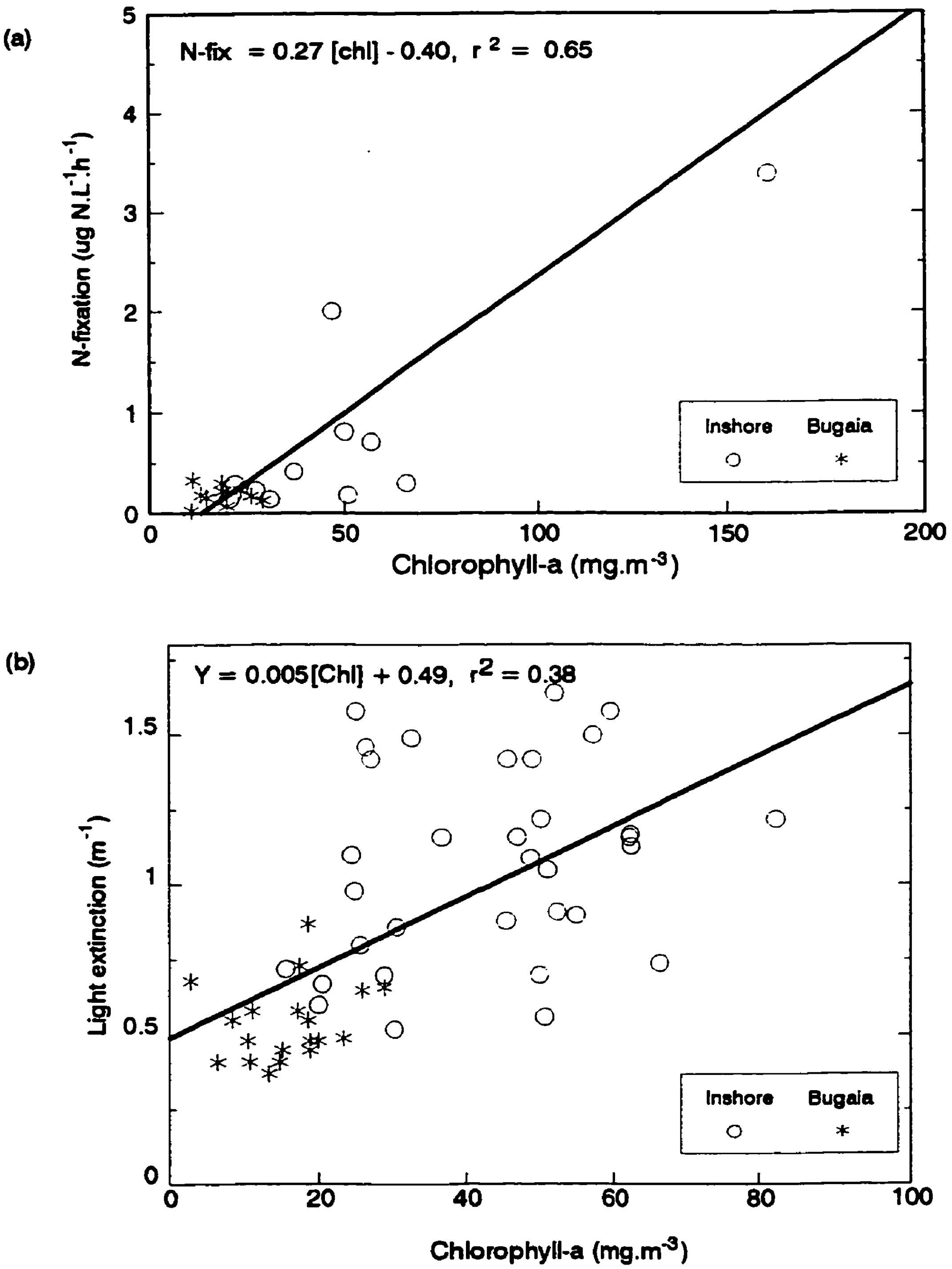


Figure. 4.7. Relationship between epilimnetic algal biomass (chlorophyll-a) and (a) volumetric N-fixation, (b) vertical light extinction coefficients in Lake Victoria between 1994-1998.

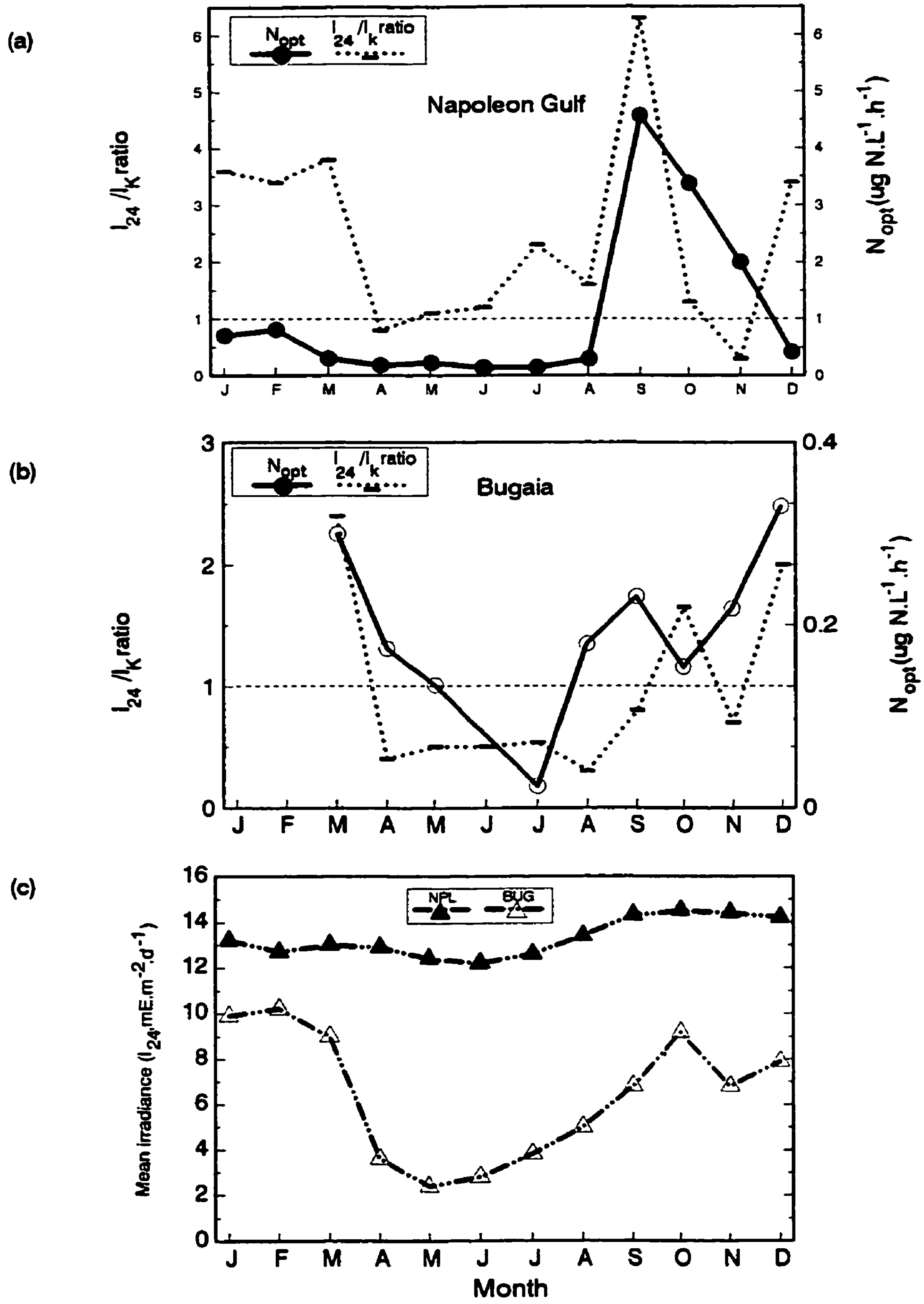


Figure. 4.8. Temporal variation of optimal N-fixation and light characteristics in (a) Napoleon Gulf, (b) Bugaia and (c) mean water column irradiance in Napoleon Gulf (NPL) and Bugaia (BUG)

Discussion

Rates of planktonic N-fixation in Lake Victoria were among the highest observed in the world (Table 4.6). The annual average integral fixation rates in the range 0.6-23.1 g N m^{-2} y^{-1} for Lake Victoria stations often exceed the moderate to high fixation rates (0.2-9.2 g N m^{-2} y^{-1}) measured in other eutrophic lakes of the world (Table 4.6, Howarth et al. 1988a). Although N-fixation contributed a small fraction on average to the daily N demand of the phytoplankton community, it was important in the N-budget of Lake Victoria and contributed approximately 80% of the total annual N input into the lake (Table 4.7). This relatively high N contribution via fixation is not unique to Lake Victoria as fixation contributes over half of the total N input in the shallow tropical Lake George in Uganda (Horne and Viner 1971), and as much as 7-60 % of total N into other eutrophic freshwaters in the world (Table 4.7). Levine and Schindler (1992) report 14-98 g N m^{-2} y^{-1}, equivalent to 10-80 % of the total annual N input in lakes which have N: P supply ratios as Lake Victoria. In Lake Victoria, epilimnetic and hypolimnetic TN:TP ratios range from 8-44 and 4-12 respectively (Chapter 2, Guildford and Hecky 2000) as internal processing of N and P lowers the effective supply ratio of N:P to the phytoplankton from hypolimnetic waters (Hecky et al. 1996) which favors N-fixing cyanobacteria (Hendzel et al. 1994, Findlay et al. 1994). Phosphorus is supplied primarily by rain and rivers, while N-fixation is the major source for addition of N to Lake Victoria.

Table 4.6. Rates of planktonic N-fixation and N-fixation as a percentage of total N input in selected lakes and other aquatic ecosystems in the world. ^{E} = Eutrophic, ^{M} = mesotrophic and ^{O} = oligotrophic.

Lake/system	Mean N-fixation (g N m^{-2} y^{-1})	Range of N-fixation (mg $Nm^{-2}d^{-1}$)	N input in system (%)	Reference
L.Victoria^{E}	11.4	6 – 322	80.0	this study
ELA, Lake 302	0-98	0 - 42	0-80	Levine and Schindler 1992
ELA, Lake 227^{E} , 1990-1992	1.5	0 – 40	53.0	Hendzel et al. 1994
L. Valencia. Venezuela^{E}	1.3		13.0	Levine and Lewis 1987
Rievtvlei dam, S. Africa ^{E}	9.2		35.0	Ashton 1981
ELA, Lake 226, 1975^{E}	0.62			Flett el. 1980.
L. Washington, Washington^{M}	0.13		0.3	Howarth et al. 1988b
L. Mendota. Wisconsin^{E}	0.97		7.0	Torrey and Lee 1976.
L. Superior, Michigan^{O}	0.0003		0.02	Mague and Barris 1973
L. Erie, western area^{E}	0.23			Mague and Burris 1973.
L. Clear lake, California^{E}	2.6		43.0	Horne and Goldman 1972
L. George, Uganda^{E}	4.4		65.0	Horne and Viner 1971.
Arabian sea		174	25.0	Capone et al. 1998.
Tropical Atlantic ocean		25-65	25.0	Carpenter et al. 1999.

Table 4.7. Provisional nutrient budgets for Lake Victoria based on inflowing river concentrations using annual mean concentrations of the Linthipe River (Malawi) apportioned to river flow into Lake Victoria. volume weighted concentration of the rain measured at Jinja, Uganda, nitrogen fixation (this assumes 10 g y^{-1} for inshore 40% of lake area and 5 g y^{-1} for offshore 60% of lake area), sedimentation rates and denitrification.

Flux	Water mm y^{-1}	TN Kt y^{-1}	TP Kt y^{-1}	TN:TP Molar
Inputs:				
Rainfall	1790[1]	83[2]	4.8[2]	39
Rivers	338[1]	43[3]	9.8[3]	10
External Total		126	14.6	20
N Fixation		480[4]		
Total	2128	606	14.6	
Outputs:				
Nile	524	25	1.8	59
Sedimentation[5]		78	13.9	13
Denitrification[6]		503		
Total	2128	606	15.7	

[1] Xin and Nicholson (1998), [2] Bootsma and Hecky 1999, [3] based on volume weighted concentrations of rain measured at Jinja, Uganda, apportioned to total rainfall, [4] this study, [5] Cornwell and Giblin (1999), [6] denitrification by difference.

In nature, many factors including nutrient and light availability, micronutrients (Paerl et al. 1987) and excessive turbulence (Levine and Lewis 1987, Bell et al. 1999) can influence biological N-fixation. Inshore, the patterns of lower $\delta\ ^{15}N$ of POM, the shorter N turnover due to fixation and higher N-fixation contribution to the daily N demand than offshore emphasize the greater importance of N-fixation. Shortest N-turnover times (4-25 days) and elevated algal biomasses coincided and were measured between September and November in Napoleon Gulf and in February-March in Bugaia. These short turnover times occurred when N-fixation contributed a higher proportion to the daily N-demand. At this time of the year, the phytoplankton were more N limited (Figure 3.3 a, b) and stability of the thermocline was high ($W \geq 1.0$) (Figure 3.3 c). In addition, marked increases in daily areal N-fixation occurred between September and November and approximately 60 days were required to reach maximum total N concentrations observed in Napoleon Gulf. The rate of N-fixation occurring at that time could account for the observed increase in total N. This time scale was close to calculated average N-turnover times (67) for the inshore Lake Victoria (Table 4.5) at this time.

Despite higher N-fixation parameters N^B and $\propto^B$ inshore than offshore, the average I_k values were rather similar at both inshore and offshore. Judging from the average N^B and $\propto^B$ values, both parameters decreased similarly (36-38%) from inshore to offshore (Table 4.5) and, thus similar average I_k values occur lakewide. The high average N^B accompanied by high $\propto^B$ values was an unexpected result given that analogous increases in light saturated photosynthetic rates are frequently associated with decreasing values of the chlorophyll-a specific light-limited photosynthetic rates (Hecky and Guildford 1984, Basterretxea and Arístegui 2000). This was probably because N-fixation system is operating under low light conditions in Lake Victoria. Different vertical light regimes associated with changes in the physical conditions of the water column, particularly thermal stability, may partly be responsible for the overall high N^B values accompanied by high α^B. The lower N-fixation parameter N^B offshore could be interpreted as a result of low light adaptation (Falkowski 1981). But the wide range of α^B and N^B perhaps reflects a process of photoacclimation given the changing irradiances in the water column. Overall, the lower variability of α^B (28-fold) compared to N^B (100-fold) may be expected because α^B is a function of basic photochemical reactions (Côté and Platt 1983). In Lake Victoria, variability in $N^B$and α^B may also be related to shifts in phytoplankton assemblages (Chapter 5) and/or changes in algal photophysiological status, that in turn, respond to changes in the physical conditions of the water column. Since $N^B$and α^B are based on chlorophyll-a and not all phytoplankton fix N, a lot of the variance may be due to abundances of non-fixers. As well $N^B$and α^B can vary with N-deficiency and will likely be inhibited by high ammonia.

Increased thermal stability and a more persistent anoxic-oxic interface (Hecky et al. 1996) in September -October likely had effects on light and nutrient availability which influenced N-fixation and total N concentrations in Lake Victoria. This is because light availability to phytoplankton is a function of mixing depth and was typically higher in the shallower inshore bays that had almost double I_{24} than the deeper mixed offshore regions of Lake Victoria. Consequently, N-fixation was typically higher inshore and during the thermally stratified periods because of the relatively higher I_{24}. The I_{24} was greater than the saturating irradiance (I_K, 11.0 mE m^{-2} min^{-1}) reported for phytoplankton photosynthesis in Lake Victoria (Mugidde 1993), and supported higher algal production as indicated by the chlorophyll- a and N-fixation maxima in September-October. Peaks of algal biomass and N-fixation occurred during periods of lake stratification when phytoplankton had sufficient light for growth, but dissolved inorganic N compounds were scarce.

Overall, N-fixation increased prior to increases in algal biomass production in Lake Victoria, a pattern similar to N-fixation and algal biomass observations made in temperate Lake 227 (Hendzel et al. 1994). This further indicates the critical role N-fixation plays in generating algal biomass maxima. In Lakes 227 and 226 within the Experimental Lake Area (ELA) in Ontario, Canada, N-fixation provided sufficient N to allow proportionate P utilization and algal growth (Schindler 1977, Hendzel et al. 1994, Findlay et al. 1994). In Lake Victoria, soluble reactive P concentrations in the offshore are always in excess of 1.0 μM, but concentrations as low as < 0.1 μM occur inshore, especially, during the biomass maxima (Mugidde unpublished).

Simultaneously low rates of N-fixation and algal biomass, and absence of nutrient deficiency suggest that factors such as light were an important constraint of algal growth in June-July. N-fixation was minimal during complete vertical mixing because complete circulation deepens the mixed layer and mixes algal populations below the critical depth for photosynthesis (Mugidde 1993, Lehman et al. 1998). Consequently, the phytoplankton community becomes light-limited and N-fixation and primary production are low around July. Light-limitation constrains N-fixation because fixation is an energy consuming process and photosynthesis provides much of this energy through direct photo reduction and/ or carbon reserves (Turpin 1991). Light-limited algal photosynthesis has been previously reported for Lake Victoria (Mugidde 1993). Light suppresses photosynthetic production (Mugidde unpublished data), leading to the reduction in the supply of energy (ATP) and the reducing power that ultimately limits the N-fixation potential in Lake Victoria.

The weak correlation between N-fixation and chlorophyll-a suggests that algal biomass production has approached its maximum potential productivity in Lake Victoria. Further additions of N through fixation will not increase algal biomass production in the lake as light limited photosynthesis will set upper bounds on algal biomass as self-shading of algal populations occurs. Algal biomass and N-fixation in Bugaia were subject to less seasonal variation because of severe light limitation most of the year. The offshore region (Bugaia) was more turbulent and had a deeper mixed layer (> 20 m) that resulted in low I_{24} irradiances and light deficiency, as indicated by $I_{24}/I_K < 1$. Light deficiency, rather than nutrient deficiency per se, precludes further development of high algal standing crops and suppresses N-fixation at offshore Lake Victoria.

Light is an important factor affecting N-fixation by cyanobacteria in Lake Victoria, but light alone cannot trigger nor sustain N-fixation in Lake Victoria. During complete circulation (July) the phytoplankton community of Lake Victoria has been found to be nutrient sufficient (Chapter 3, Lehman et al. 1998) due to return of dissolved nutrients from bottom waters to surface waters (Talling 1966, Hecky 1993). Nutrient return from the hypolimnion to surface waters relaxes N-demand and reduces N-fixation in Lake Victoria as indicated by very low rates of N-fixation in the lake around July. At the same time, N removal through denitrification (Hecky et al. 1996) will be reduced due to high amounts (> 4 mg/L) of dissolved oxygen throughout the water column during circulation (Hecky et al. 1994). However, this nutrient return has a low N: P ratio (8:1, Hecky et al. 1996) and will lead to N-limitation as stratification occurs and nitrogen compounds are taken up into algal cells and lost to the sediment.

Increased P-loading from the watershed into Lake Victoria (Hecky 1993, Lipiatou et al. 1996, Table 4.7) is the ultimate force driving the N-demand and, therefore, elevated rates of N-fixation and algal production in Lake Victoria. Observations of higher P concentrations and associated high cyanobacterial biomasses following eutrophication (Hecky 1993, Kling et al. 2001) and high rates of N-fixation are consistent with observations made at ELA Lake 226 and 227 (Findlay et al. 1994) and in many temperate freshwater lakes (Schindler 1977, Flett at al.1980) and in Lake Kinneret, Israel (Gophen et al. 1999). Higher photosynthetic and N-fixation rates allow and maintain high inshore biomasses which consume and deplete dissolved inorganic N and P resulting in higher seston N: P and/or C: N ratios at particular times (Chapter 3). Higher seston N: P ratios inshore indicate that P may limit further biomass increases at biomass maxima if light availability is high, for example, during very shallow diurnal stratification.

Although light is one of the important controls of N-fixation in Lake Victoria, P relative to N concentrations also plays a major role. N-fixation provides the required N loading to respond to anthropogenic P loads that have increased 2 to 3-fold since the beginning of the twentieth century (Hecky 1993). Consequently, increased P and N loads have contributed to the eutrophication and to the modification of the ecology of Lake Victoria. Modification of Lake Victoria includes proliferation of nuisance blooms of cyanobacteria that include heterocystous N_2-fixers as well as the potentially toxic taxa such as *Cylindrospermopsis*, *Anabaena* and *Microcystis*. These algal blooms are often associated with fish kills and undermine the use of Lake Victoria as a source of clean and safe drinking water.

The undesirable algal blooms in Lake Victoria will persist if increased P loads persist and conditions of anoxia and high rates of denitrification continue. External P loads, rather than N-fixation, are controllable and P reductions is the most economically feasible and viable option for water quality and fisheries management of Lake Victoria. Reductions in P loads will lead to decreases in cyanobacterial biomass in inshore areas and, in particular, biomass of heterocystous N_2-fixers including toxic species. This should relax some of the negative consequences of high algal biomass such excess oxygen demand and nutrient-and light-limited algal growth. Reductions in algal biomass will improve the light environment which will led to improved algal productivity and ecological efficiency in the transfer of energy to higher levels in the food-web and sustaining high levels of fish production in Lake Victoria.

Chapter 5: Cyanobacterial blooms and heterocyst abundance in Lake Victoria

Abstract

Abundance of cyanobacteria in relation to environmental factors was studied at a shallow inshore (Napoleon Gulf) and the deep offshore (Bugaia) station in Lake Victoria. The aim was to outline seasonal changes in cyanobacteria and heterocyst biomass and occurrence of dominant species in relation to light and nutrient availability. Average total cyanobacteria, N-fixing and heterocyst biomasses were respectively 4, 7 and 5 times higher inshore than offshore. Improved light conditions during the thermally stratified phase boosted the development of algal biomass, including N-fixing species and heterocysts, especially inshore. The heterocystous N-fixing cyanobacteria, *Anabaena* and *Cylindrospermopsis*, contributed a large fraction (≥ 50 %) of the total cyanophyte biomass during the stratified phase. Overall, *Anabaena* was the most abundant cyanobacteria followed by *Microcystis* in Lake Victoria. *Anabaena* made up a major fraction of the biomass maxima inshore while the non- heterocystous *Aphanocapsa* were most abundant and dominated the cyanobacteria maximum offshore.

Low algal biomass in June-August, when underwater light was low and P and N were sufficient, indicates that light restricts algal standing crop to levels below the potential provided by the available nutrients during periods of mixing. N-fixation was strongly related to heterocyst biomass, so the relationship was used to develop a simple N-fixation model. This model is a useful tool in estimating lakewide N-fixation as it correctly predicts the magnitude and temporal patterns of rates of N-fixation in the lake. It might also be used to predict potentially toxic cyanobacteria blooms.

Introduction

Cyanobacteria can be the primary contributors to algal biomass, primary production and N-fixation in fresh and marine waters (Paerl et al. 1989, Howarth and Mario 1999), especially in nitrogen deficient systems. Eutrophication of freshwaters frequently gives rise to development of cyanobacterial blooms (Schindler 1977, Findlay et al. 1994) that have become an increasing problem worldwide. Blooms of toxin-producing cyanobacteria cause unwanted water quality effects such as fish kills, and can poison drinking water, thus increasing costs of water treatment. Deaths of wildlife and livestock and adverse effects on human health caused by cyanophyte poisoning have been reported from many geographical regions (Hallegraeff et al. 1989, Haugen et al. 1994).

Lake Victoria is one of the world's most productive freshwaters. Phytoplankton biomass evaluated as chlorophyll-a or as biovolume has increased by 6-fold or more since the 1960s (Talling 1966, 1987, Mugidde 1992, 1993, Kling et al. 2001). The eutrophic conditions now favor dominance of blue-green algae while large chlorophytes such as *Pediastrum* and diatoms such as *Aulacosiera* have disappeared. Despite a 7-fold reduction in soluble reactive silica in the water column, diatoms have increased their biomass since the 1960s in Lake Victoria (Kling et al. 2001). These changes in phytoplankton biomass and species composition have been attributed to general increases in P and N loading (Hecky 1993, Lipiatou et al. 1996), changes in fish communities (Ogutu-Ohwayo 1992) and climate change (Lehman et al. 1998). Current evidence of global warming and possibilities of climate change stimulating phytoplankton blooms and driving algal biomass towards blue-green algae drives considerable scientific interest in the phytoplankton ecology of tropical lakes. Already, thermal stability of Lake

Victoria and hypolimnetic temperatures are higher in the 1990s than in the 1960s (Hecky 1993, Lehman et al. 1998).

The success of cyanobacteria and their ability to dominate phytoplankton communities is influenced by many factors, including the ability of some genera to fix atmospheric nitrogen when N: P ratios are low (Levine and Schindler 1992, Findlay et al. 1994), buoyancy-regulation in stratified environments (Bradford et al. 1998), adaptation to elevated water temperatures and resistance to grazing by zooplankton (Paerl 1996). Recently, several authors have addressed cyanophyte dominance in Lake Victoria, and Hecky (1993) attributes it to low N: P ratios. Low N: P ratios have been found to induce cyanobacterial blooms and initiate planktonic N-fixation in freshwater lakes (Schindler 1977, Levine and Schindler 1992, Findlay et al. 1994) as well as marine waters (Kahru et al. 2000). Lehman (1996) found that small-bodied zooplankton cannot effectively graze down and control the algal blooms in modern Lake Victoria. Trophic cascade models (Howarth et al. 1999) support Lehman's conclusion, but do not explain the proliferation of N-fixing cyanobacteria in Lake Victoria. Historically, Lake Victoria was thought to be limited by N supply (Talling and Talling 1965) and has increased its biomass since the 1960s. Much of the increase is accounted for by presence of heterocystous cyanobacteria (Kling et al. 2001) capable of biological N-fixation (Chapter 4).

Although N-fixation is not restricted to heterocystous cyanobacteria (Paerl et al. 1995, 1996, Thiel and Pratte 2001), most N-fixation in freshwater lakes occurs in heterocysts. Consequently, relationships between N-fixation, cyanobacteria and heterocyst abundance have been found for some temperate and tropical lakes (Levine and Lewis 1987, Findlay et 1994) and have proven useful in estimating biological N-fixation

(Levine and Lewis 1987, Hendzel et al. 1994). Prompted by the frequent occurrence of cyanobacteria blooms (Ochumba and Kibaara 1989) including heterocystous N-fixers (Kling et al. 2001), this study examines the spatio-temporal variation of cyanobacteria abundance and also the relationship between heterocyst biomass and N-fixation in Lake Victoria. The goal was to develop a simple and predictive model that would be useful for the lakewide estimation of N-fixation based on empirically derived relationship between heterocysts, measured N-fixation and light attenuation.

Material and methods

Phytoplankton and N-fixation samples were drawn from inshore (Napoleon Gulf) and offshore (Bugaia) surface waters as described in Chapter 1. The major physico-chemical parameters and chlorophyll-a were done as described in Chapter 2, nutrient status as in Chapter 3 and N-fixation was estimated from acetylene reduction bioassays as described in Chapter 4. Chlorophyll-a was used as an estimator of total algal biomass because of its strong and significant relationship ($r^2 = 0.87$) with total phytoplankton (wet) biomass in Lake Victoria (Kling et al 2001). Phytoplankton samples were preserved in acidic Lugol's solution. A 1-2 ml phytoplankton sub-sample was placed in a Utermöhl sedimentation chamber and left to settle for at least three hours. Phytoplankton species and heterocyst identification and enumeration were done using a Zeiss Axioinvert 35 inverted microscope at 400x. Cell measurements were made on each cyanobacteria species to a maximum of 20 individuals. At 400x magnification, ten fields of view were counted for the most numerous coccoid cyanobacteria and a 12.42 mm^2 transect was counted for the numerous and large heterocystous cyanobacteria and heterocysts. Algal and heterocyst bio-volumes were determined using formulae as in Wetzel and Likens (1991). The whole bottom area of the chamber was examined for the big and rare taxa under low (100x) magnification. Heterocysts were enumerated and measured separately from vegetative cells. Cell measurements were converted to biovolumes of cyanophytes and heterocysts (H) from appropriate geometric formulae, and biovolumes were converted to wet biomass assuming a density of 1 pg μm^{-3} (Nauwerck 1963).

Light attenuation, maximum rates of N-fixation normalized to chlorophyll-a (N^B), light limited N-fixation per unit chlorophyll-a ($\propto^B$) and the light saturation parameter I_k, the intercept between initial slope $\propto^B$ and N^B were calculated as in Fee (1990). The relationship between N-fixation and heterocysts was used to estimate maximum optimal N-fixation (NH_{max}) per heterocyst, and the light limited ratio of N-fixation based on heterocyst abundance ($\propto^H$) was derived as a ratio of NH_{max} to I_k. Mean I_k for Lake Victoria was also used to derive a second set of values of light limited N-fixation ($\propto^{HA}$). The calculated N-fixation parameters (N^B, $\propto^B$) were used in the modified Fee (1990) photosynthetic model to calculate daily and annual integral rates of N-fixation. By substituting estimated N-fixation parameters (NH_{max}, $\propto^H$ or $\propto^{HA}$) based on heterocysts in Fee's model, predicted daily and annual integral N-fixation were obtained and compared with estimates based on the direct measurements of N-fixation. Wedderburn numbers were calculated as described in Chapter 2.

Results

Spatio-temporal patterns of algal biomass

Total algal biomass evaluated as chlorophyll-a and cyanobacteria biomass showed a common pattern of higher concentrations at the onset of stable thermal stratification (September-December) and relatively low concentrations during periods of sustained thermal stratification (January-April) and mixing (June-July) (Figure 5.1). The maximum total cyanobacteria biomass and chlorophyll-a concentrations coincided in Napoleon Gulf, but not in Bugaia. Biomasses were always higher inshore than in offshore surface waters (Figure 5.1 a, b, Table 5.1). Average cyanobacteria biomass was typically four times higher in the inshore surface waters than offshore, and maximum biomass was three times higher. Similarly, average non-N-fixing, N-fixing and heterocyst biomasses were 2, 7 and 5 times higher inshore than offshore and were accompanied by 6-fold higher rates of N-fixation (Table 5.0).

Table 5. Average biomasses and optimal N-fixation and standard deviation at inshore (Napoleon Gulf) and offshore (Bugaia) Lake Victoria, during 1998. N = number of samples.

	Inshore	Offshore	Overall (inshore & offshore)
Total cyanobacteria biomass (mg L^{-1})	29.3 ± 36.7	6.9 ± 10.6	18.6 ± 30.3
Non-N-fixers biomass (mg L^{-1})	12.2 ± 17.5	4.6 ± 7.1	8.5 ± 14.1
N-fixer biomass (mg L^{-1})	17.1 ± 36.6	2.3 ± 3.6	10.0 ± 27.5
Heterocyst biomass (mg L^{-1})	0.9 ± 1.1	0.2 ± 2.5	0.5 ± 0.9
Optimal N-fixation (ug L^{-1})	1.2 ± 1.3	0.2 ± 0.1	0.7 ± 1.1
N	16	20	36

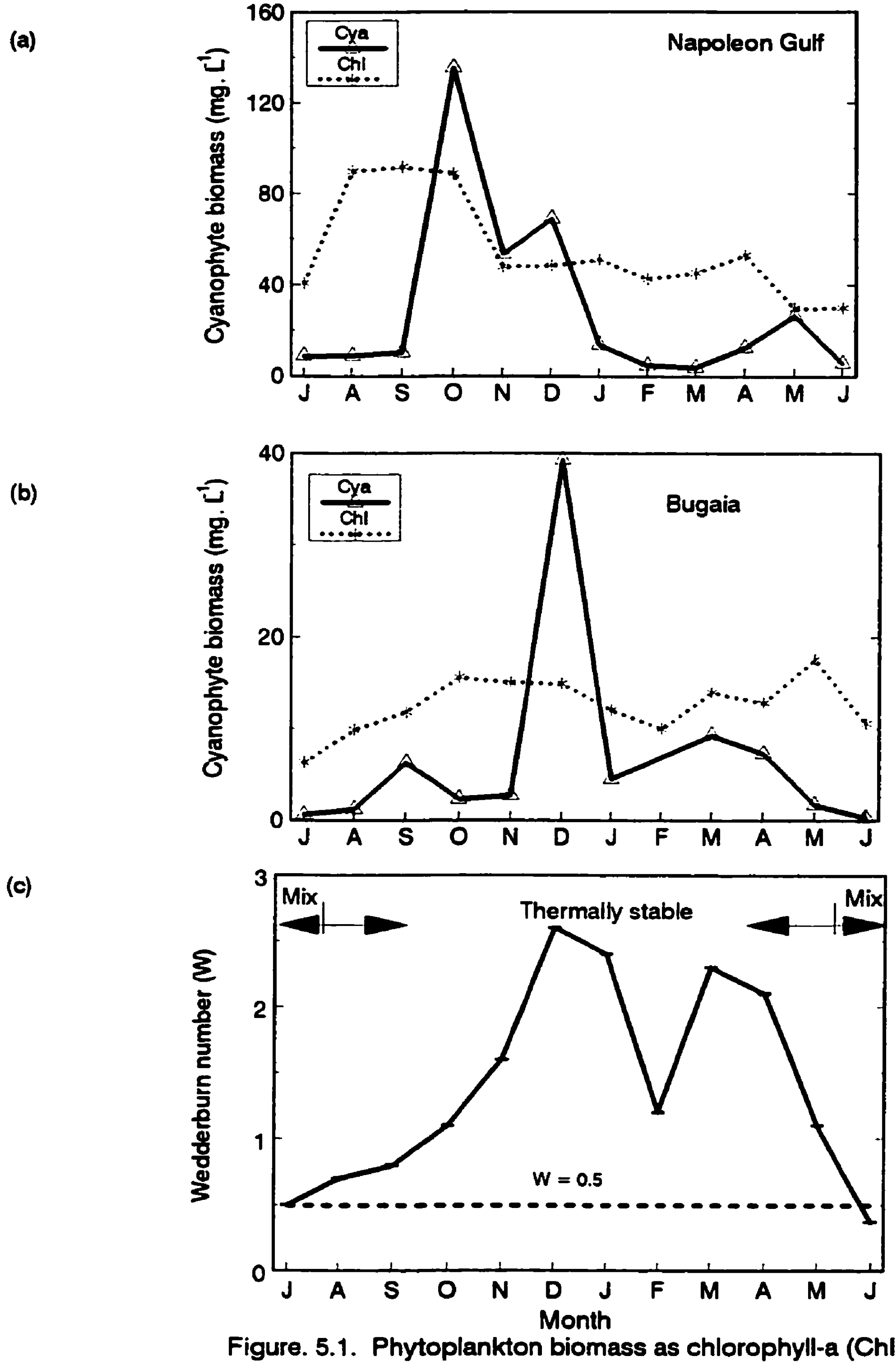


Figure. 5.1. Phytoplankton biomass as chlorophyll-a (Chl) and cyanophyte biomass (Cya) at (a) Napoleon Gulf, (b) Bugaia and (c) Wedderburn numbers (W) for Victoria at Bugaia, 1998. Dashed line, W, = 0.5, indicative of strong deep mixing.

Spatio-temporal variation of cyanobacteria biomass

Total cyanobacteria biomass varied between 0.3 and 136 mg L^{-1} but was often > 5.0 mg L^{-1} in the surface waters (Figure 5.1 a, b). In Napoleon Gulf, cyanobacteria biomass was in the range 5-9.0 mg L^{-1} in June-September and increased to maximum concentrations (135.5 mg L^{-1}) in October. Total cyanobacteria abundance remained relatively high (53-69 mg L^{-1}) in November-December, but deceased 5-fold in January and decreased even further to seasonal minimum concentrations of 3.8 to 4.7 mg L^{-1} in February-March. Biomass increased in April and doubled to a small peak (26.4 mgL^{-1}) in May in Napoleon Gulf (Figure 5.1a). As in Napoleon Gulf, minimal cyanobacteria biomass concentrations (0.3-0.6 mg L^{-1}) occurred in June-July at Bugaia (Figure 5.1 b). Cyanobacteria biomass began to increase in September and achieved a well defined but less persistent biomass maximum (39.3 mg L^{-1}) in mid December in Bugaia. After December, cyanobacteria biomass decreased 4 to 9-fold during periods of prolonged thermal stratification (January to April) and decreased even further in May at the onset of thermal destratification.

N-fixing cyanobacteria exhibited similar spatio-temporal trends as total cyanobacteria biomass and were a significant component of the total cyanobacteria in Lake Victoria (Figure 5.2 a, b, c). Generally, N-fixing cyanobacteria were more abundant when Wedderburn numbers were increasing or near maximum as the lake became stably stratified (Figure 5.1 c) and dominated in Napoleon Gulf, making up 65-98% of the total cyanophyte biomass between October and March. N-fixing cyanobacteria with a predominance of *Anabaena* reached maximum abundances (132.9

mg L^{-1}) in October in Napoleon Gulf. In Bugaia, N-fixing cyanobacteria contributed approximately 60% of the total cyanobacteria biomass in October-November and reached 13.4 mg L^{-1} in December (Figure 5.2 b). Falling Wedderburn numbers led to declines in cyanobacteria biomass that was lowest when the lake was mixing. In Napoleon Gulf, N-fixing cyanobacteria occurred in low abundance (< 1.0 mg L^{-1}) contributing to ≤ 20% of the total cyanobacteria biomass in July-August when the lake was destratified. Similarly in Bugaia, N-fixer biomass was very low (< 1.0 mg L^{-1}) and contributed 8% to 20% of the total cyanobacteria biomass in June-August. Despite elevated total cyanobacteria biomasses in December, N-fixers contributed only 34% and 4% to the total cyanophyte biomass in Bugaia and Napoleon Gulf at that time (Figure 5.2 c).

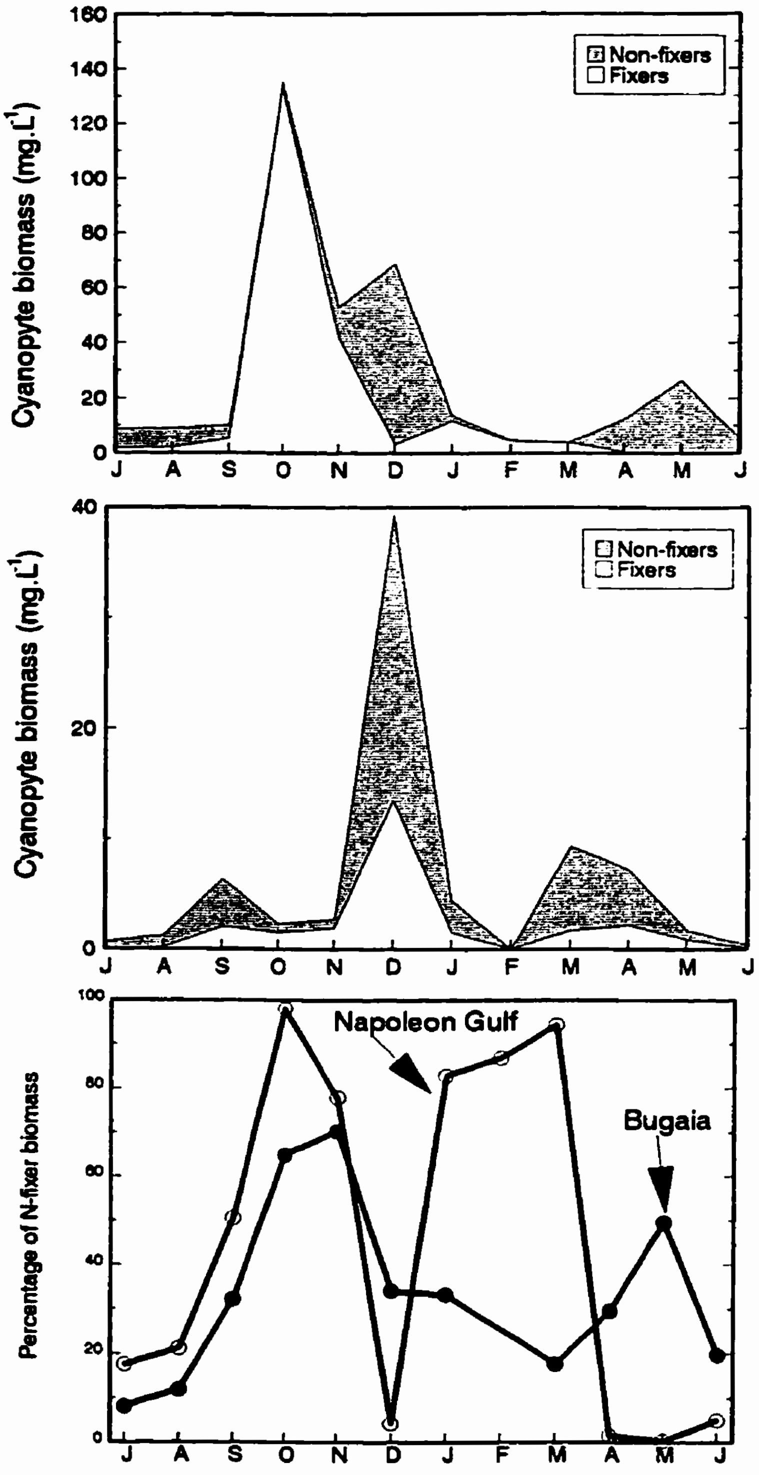


Figure. 5.2. Temporal variation of N-fixer and non N-fixer biomss at (a) Napoleon Gulf, (b) Bugaia and (c) N-fixer biomass as a percentage of total cyanophyte biomass at Napoleon Gulf (NPL) and Bugaia (BUG), during 1998.

Cyanobacteria population dynamics and species composition

Nine cyanobacterial species were frequently encountered during this study (Table 5.1). The large filamentous cyanobacteria (*Anabaena, Cylindrospermopsis* and *Planktolyngbya*) and the colonial mucilaginous forms (*Aphanocapsa, Microcystis, Chroococcus, Coeleospharium* and *Merismopedia)* often formed blooms in Napoleon Gulf and were the 8 most common cyanobacteria during 1998 (Table 5.1, 5.2). Overall, *Anabaena* had the highest biomass, followed by *Microcystis* and then *Cylindrospermopsis* in Lake Victoria (Table 5.2). *Anabaena* biomass was double that of *Cylindrospermopsis* in Napoleon Gulf. *Microcystis* had higher biomass than *Planktolyngbya* while *Chrococcus* and *Coleospharium* biomass was equal in Napoleon Gulf. In Bugaia, *Aphanocapsa* had the highest biomass followed by *Anabaena* and *Cylindrospermopsis* that were equal in biomass (Table 5.2).

Table 5.1. Minimum, average and maximum biomass (mg. L^{-1}) of nine common cyanobacteria species in Lake Victoria, during 1998. N = number of samples

	Minimum	Average	Maximum	Std	C.v.	N
Anabaena	0.00	8.9	131.6	20.3	235	26
Cylindrospermopsis	0.01	3.6	35.5	5.1	117	26
Microcystis	0.02	5.8	23.1	5.4	111	26
Planktolyngbya	0.02	1.9	13.9	2.2	107	26
Aphanocapsa	0.00	1.7	23.2	4.3	221	26
Chroococcus	0.02	0.7	5.5	0.9	112	26
Coeleospharium	0.00	0.6	2.6	0.5	100	26
Merismopedia	0.01	0.5	2.8	0.6	117	26
Aphanotheca	0.00	0.3	1.4	0.5	161	26

Table. 5.2. Average and standard deviation (StD) of cyanobacteria biomass (mg. L^{-1}) in inshore and offshore surface waters of Lake Victoria, during 1998.

	Inshore (Napoleon Gulf)		Offshore(Bugaia)	
Taxon	Average	StD	Average	StD
Anabaena	15.1	36.5	1.1	2.8
Cylindrospermopsis	7.0	10.4	1.1	0.9
Planktolyngbya	2.9	5.3	0.8	0.8
Aphanocapsa	0.7	1.3	2.2	6.6
Microcystis	3.5	7.2	0.7	1.5
Chroococcus	1.1	1.7	0.2	0.2
Coeleospharium	1.1	0.9	0.1	0.1
Merismopedia	0.9	1.0	0.3	0.4

A general succession pattern of increased dominance of N-fixing cyanobacteria during the early stratified period (September- December) followed by non-fixers later in the stratified period and lowest cyanobacterial abundances during the deepest mixing period in June-July was apparent in Lake Victoria (Figures 5.3 & 5.4). *Cylindrospermopsis* was the most common cyanobacterium as it appeared nearly continuously throughout the year and frequently dominated other cyanobacteria in both inshore and offshore surface waters. In Napoleon Gulf, *Anabaena* reached maximum concentrations contributing to > 90% to the cyanobacteria biomass maxima in October (Figure 5.3 a). In November, *Anabaena* declined and was replaced in dominance by *Cylindrospermopsis* (5.3 b). *Anabaena* became dominant again in December, but its abundance began to decrease in January and reached minimum concentrations in June-July. The phytoplankton community of Napoleon Gulf became more diverse as N-fixers declined and non-N-fixing cyanobacteria (*Planktolyngbya*, *Aphanocapsa and Microcystis*) increased to small peak concentrations in December. Although *Cylindrospermopsis* was in low abundance, it dominated again from January to April but was succeeded by *Microcystis* in May. *Microcystis* contributed approximately 89% of the total cyanobacteria biomass in May in Napoleon Gulf. Generally, the non N-fixing species, *Planktolyngbya*, *Aphanocapsa*, *Chroococcus*, *Merismopedia* and *Aphanotheca*, formed small peaks in December and in April (Figure 5.3 d-e) as N-fixers declined in the population. *Merismopedia* became prominent only in July in Napoleon Gulf.

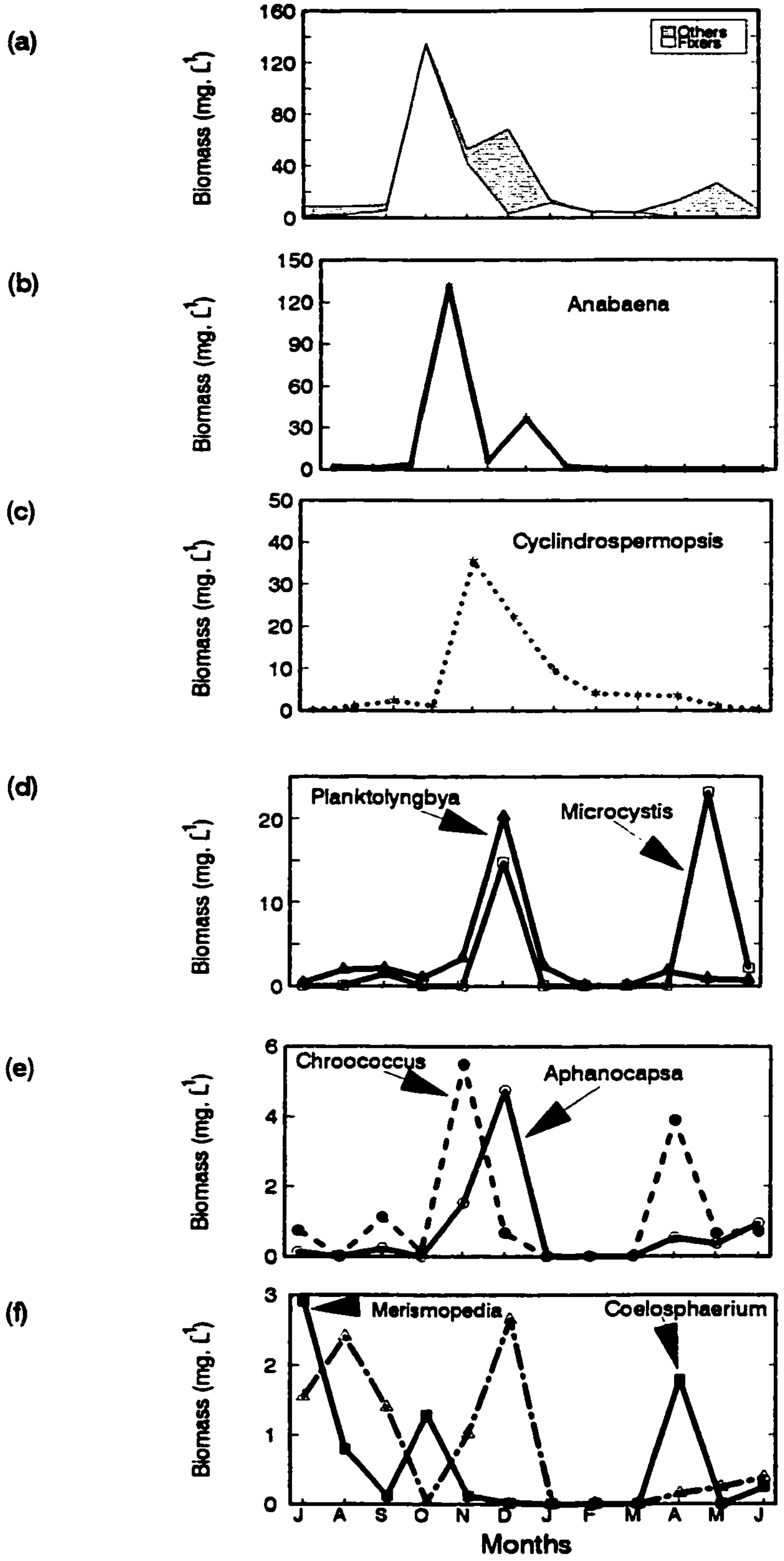


Figure.5.3. Temporal variation of biomasses of N-fixers, non-N-Fixers and major cyanobacetrial taxa at Napoleon Gulf, during 1998.

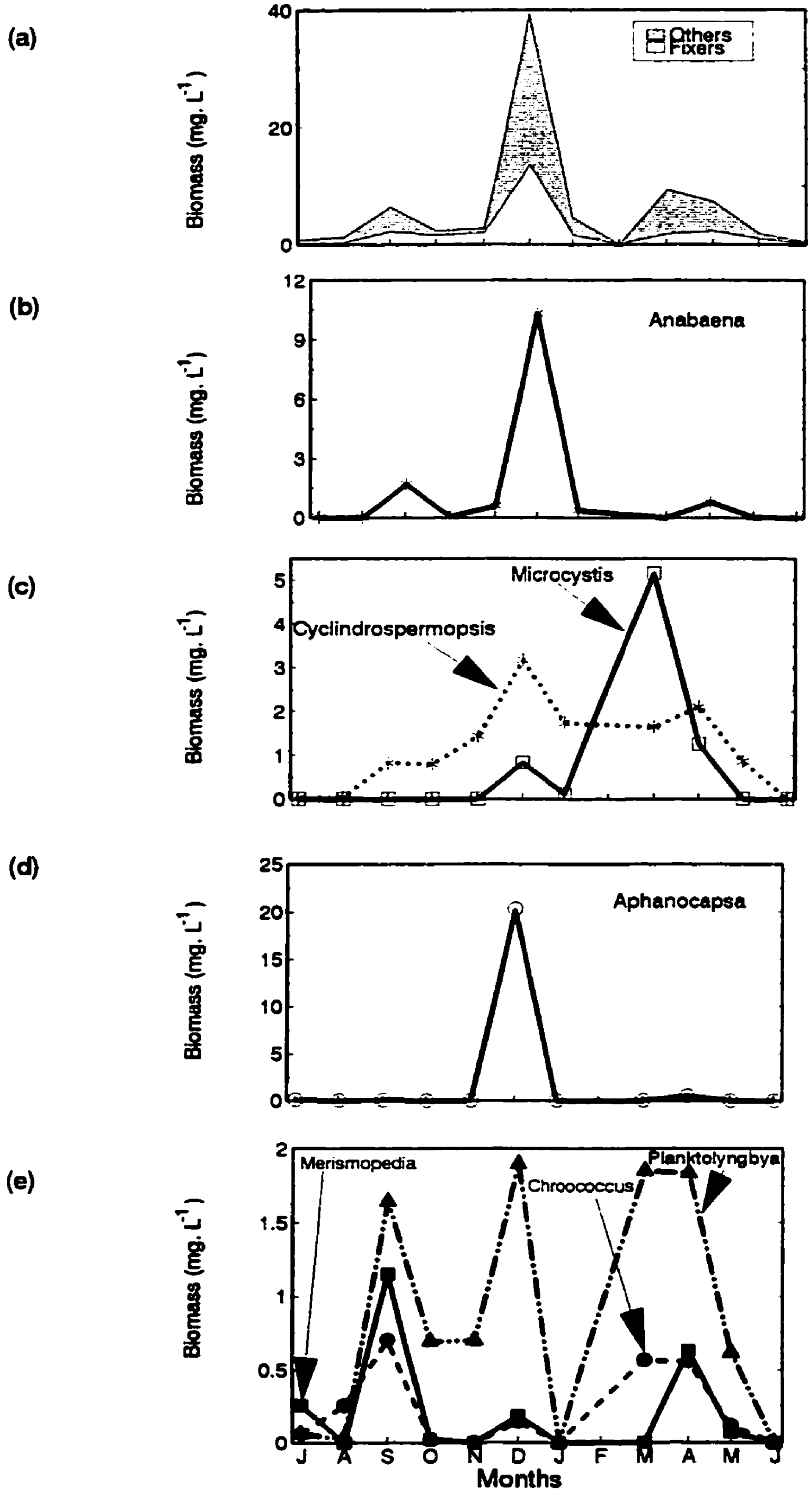


Figure.5.4. Temporal variation of biomasses of N-fixers, non-N-Fixers and major cyanobacetrial taxa at Bugaia, during 1998.

Bugaia had a similar seasonal pattern of cyanobacteria species composition as Napoleon Gulf (Figure 5.4). Peak heterocystous cyanobacterial biomass occurred in December during the stratified phase, but species of non-N-fixing cyanobacteria represented high proportions of the total cyanobacteria biomass most of the year except in October-November (Figure 5.2 c). The filamentous species *Anabaena*, *Cylindrospermopsis* and *Planktolyngbya*, and the small coccoid *Chroococcus* and *Merismopedia* were prevalent in September. *Anabaena* appeared in the plankton for a greater part of the year and had three peaks in abundance, two minors in September and April and a major one in December (Figure 5.4 b). But *Anabaena* dominated only during its small peak in September and was replaced by *Cylindrospermopsis* that contributed a major fraction to the N-fixer biomass maxima in October-November (Figure 5.4 c). *Aphanocapsa* formed a large bloom and became the most dominant cyanobacteria in December at Bugaia (Figure 5.4 d), and at this time *Anabaena* also achieved maximum abundance. *Cylindrospermopsis* remained fairly abundant between January and March and was replaced in dominance by *Microcystis* in March. *Planktolyngbya* had three small peaks of almost equal magnitude that coincided with peaks in N-fixing cyanobacteria in September, December and April in Bugaia. *Planktolyngbya* was nearly as abundant as *Cylindrospermopsis* in April-May, while *Chroococcus* and *Merismopedia* had low background level concentrations most of the year. They achieved small peak concentrations in September and April, as the plankton became more diverse (Figure 5.4 e, c).

Relationship between heterocysts and N-fixation

Seasonality in heterocyst biomass was well defined in Lake Victoria. Heterocyst biomass ranged from 0 to 3.6 mg $L^{-1}$and had similar seasonal and spatial trends as N-fixer biomass. Elevated heterocyst biomass (2.0-3.6 mg L^{-1}) occurred between September and November in Napoleon Gulf, and maximum concentrations were in September just prior to the N-fixer and total cyanobacteria biomass maxima (Figure 5.2 a, 5.5 a). In Bugaia, heterocyst biomass was elevated between October and January and maximum biomass (0.7 mg L^{-1}) coincided with the N-fixer and total cyanobacteria biomass maxima in December (Figure 5.2 b, 5.5 a). Generally, elevated heterocyst biomass occurred at a time when the phytoplankton of Lake Victoria showed indications of N-deficiency (C: N ratios > 8.3, Figure 5.5 b) as the lake became more thermally stable (Figure 5.1c). In Napoleon Gulf, maximum heterocyst biomass in September was preceded by moderate N-deficiency in August. High C: N ratios (≥ 10) also preceded maximum heterocysts biomass in December in Bugaia. Extremely low heterocyst biomass (≤ 10 ug L^{-1}) in April to July in Napoleon Gulf and in May to July in Bugaia coincided with deeper mixing periods (Figure 5.5 c) and conditions of reduced N-deficiency (Figure 5.5 b).

The higher heterocyst biomasses inshore than offshore were accompanied by higher volumetric rates of N-fixation (Figure 5.5 a, d). Maximum rates of N-fixation coincided with heterocyst biomass maxima in Napoleon Gulf and their minima occurred contemporaneously in June-August. Similarly, increases in concentrations of total N coincided with elevated heterocyst biomass production and rates of N-fixation in September- December. Consequently, the linear regression of N-fixation on heterocyst biomass was strong ($r^2 = 0.89$, $n = 29$) and significant ($p< 0.01$) in Lake Victoria (Figure

5.6 a). N-fixation was also significantly correlated with the biomass of N-fixing (r^2 = 0.83) and total cyanobacteria (r^2 = 0.76).

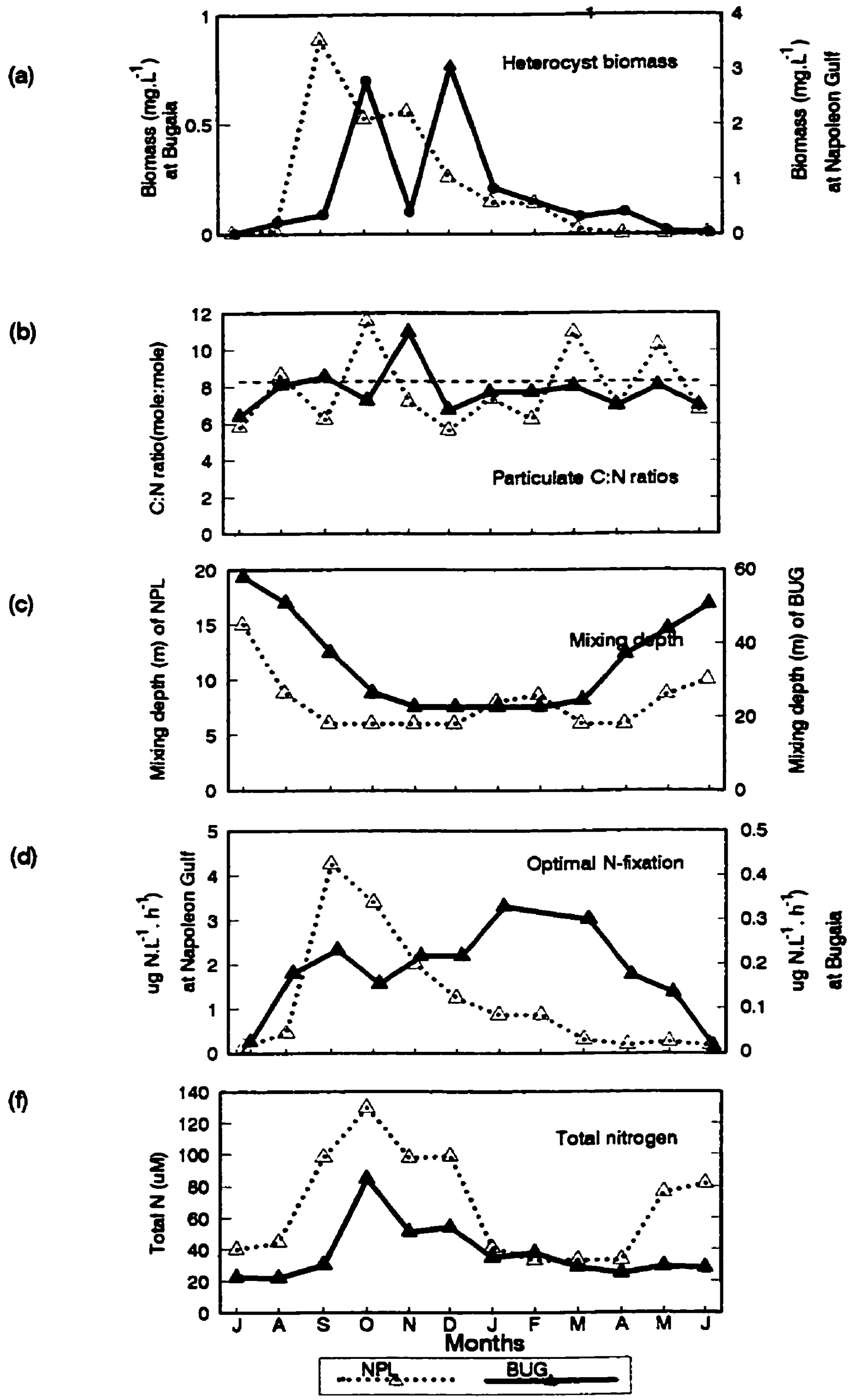


Figure. 5.5. Temporal distributions of (a) heterocyst biomass (b) C:N ratios, (c) mixing depth, (d) N-fixation and (e) total nitrogen concentrations in Napoleon (NPL) and Bugaia (BUG).

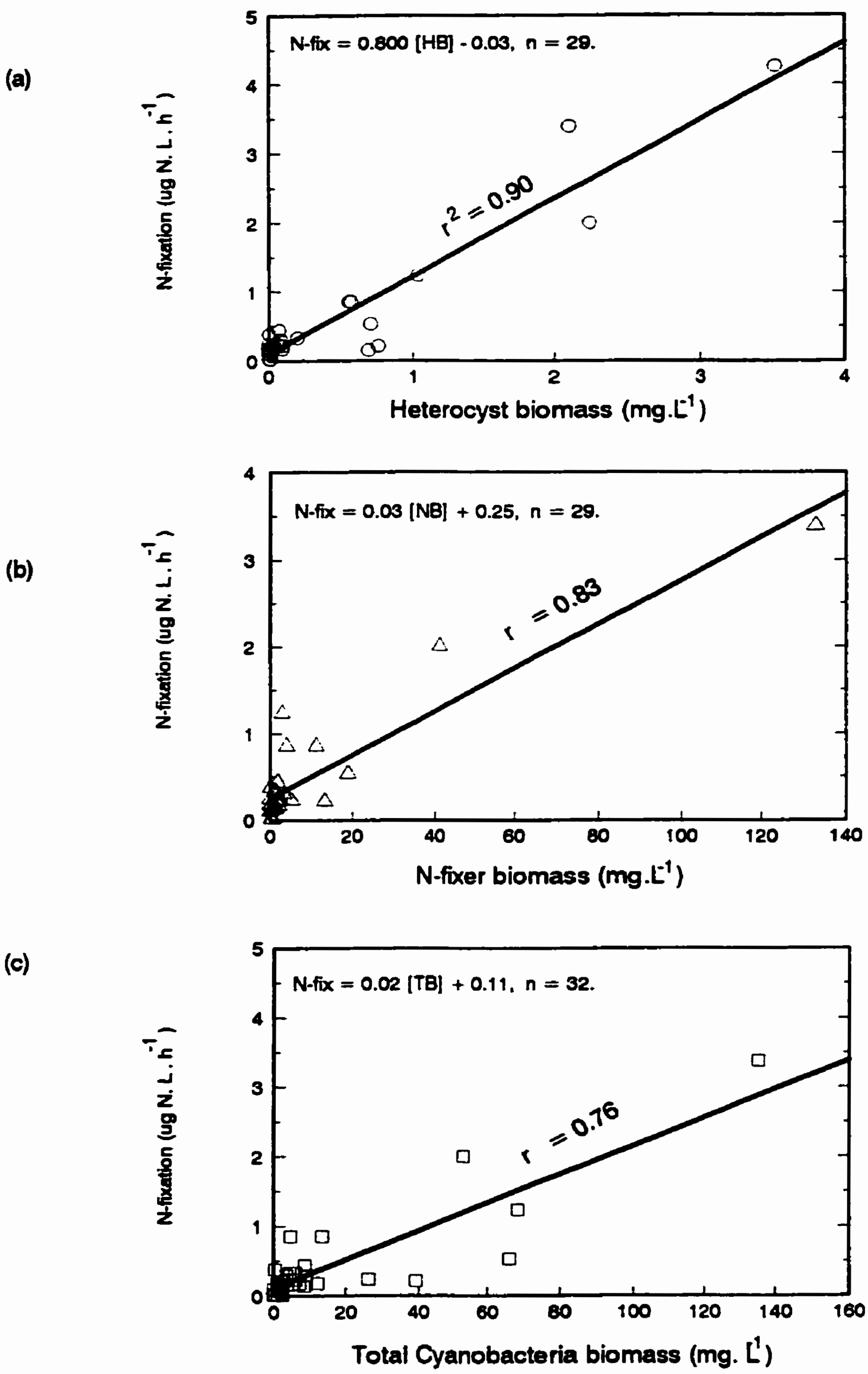


Figure. 5.6. Linear regression of the volumetric rates of N-fixation (N-fix) against (a) heterocysts biomass (HB), (b) N-fixer biomas(NB) and (c) total cyanobacteria biomass (TC) of Lake Victoria.

Calculated and predicted N-fixation

The measured daily rates of N-fixation were highly correlated with predicted rates of N-fixation based on heterocyst biomass (Figure 5.7 a). Daily rates of N-fixation predicted using heterocysts derived N-fixation rates and either specific I_k (NP1) or average I_k (NP2) for Lake Victoria had similar slopes (Figure 5.7 a) and were not significantly different ($P< 0.01$) from calculated N-fixation values using measured N-fixation (NC) and α values (Table 5.3). Comparison of calculated rates of areal daily and annual N-fixation to corresponding values predicted from heterocyst biomass show similar spatio-temporal trends in both inshore and offshore (Figure 5.7 a, b, c). Similarly, the annual calculated N-fixation of 14.4 g N m^{-2} y^{-1} for Napoleon Gulf and 10.4 g N m^{-2} y^{-1} for Bugaia were of the same order of magnitude as respective predicted values of 15.5 g N m^{-2} y^{-1} and 9.5 g N m^{-2} y^{-1}. Annual N-fixation predicted using an average I_k for Napoleon Gulf (13.7 g N m^{-2} y^{-1}) and Bugaia (8.4 g N m^{-2} y^{-1}) was slightly lower but not significantly different from their respective calculated values.

Table 5.3. Average daily calculated rates of N-fixation normalized to chlorophyll-a (NC) and predicted daily rates of N-fixation based on heterocysts and specific I_k (NP1) and on average I_k (NP2) during 1998.

	NC	NP1	NP2
Average	37.4	39.5	35.1
Std	46.3	42.2	34.8
C.v.	124	107	99
N	23	23	23

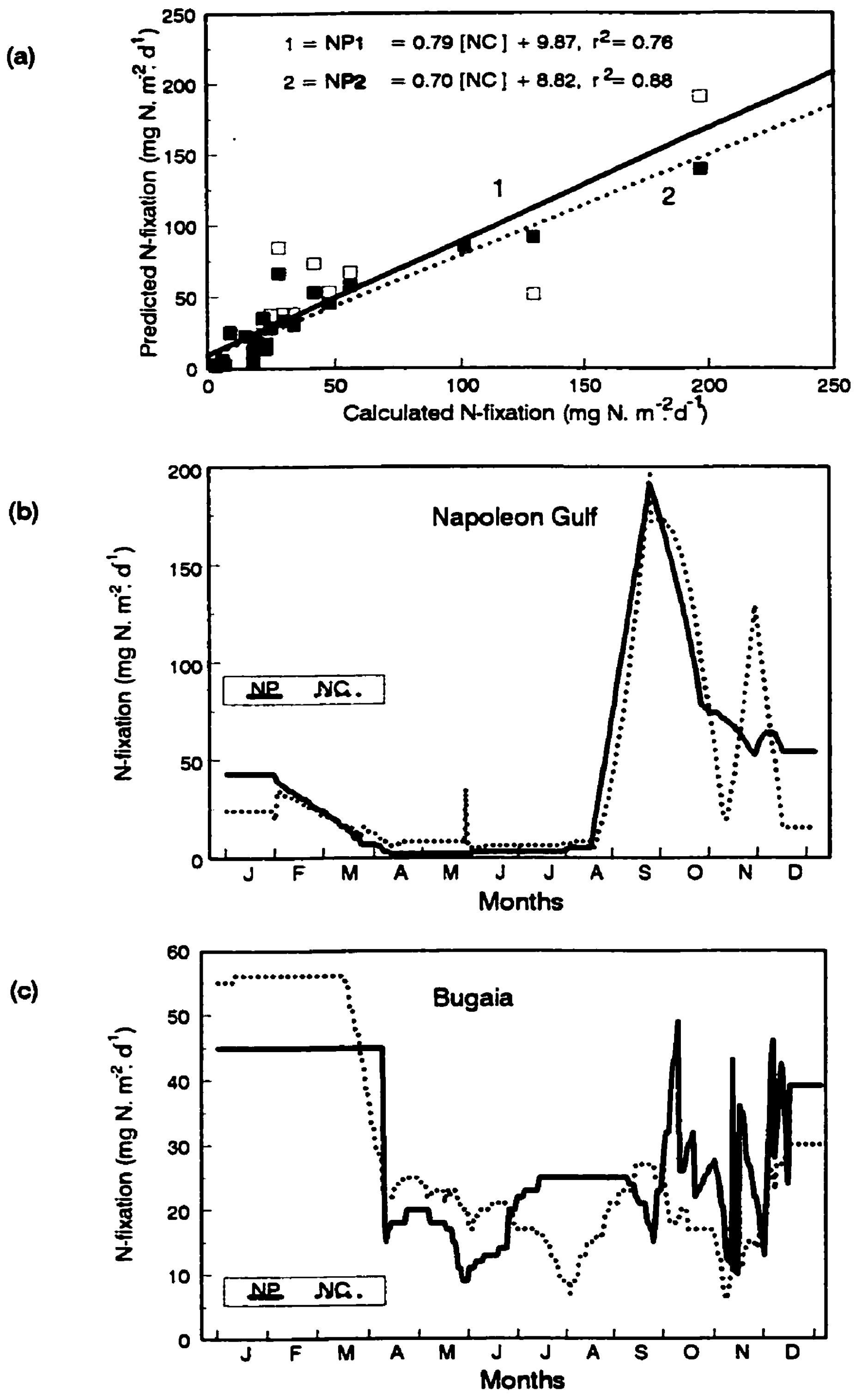


Figure. 5.7. (a) Linear regression of predicted N-fixation (NP) aganist calculated N-fixation (NC), (b) temporal variation of NP and NC of (a) Napoleon Gulf, (c) Bugaia. NP1 was predicted using individual I_K and NP2 with average I_K.

Discussion

Algal biomass as chlorophyll-a and total cyanophyte biomass were much higher inshore than offshore because mean light conditions were better and the light dependent carbon and nitrogen fixation reactions less light limited (Chapter 3, 4). Inshore, reduced mixing depth allows relatively high mean water column irradiances (I_{24}, $\geq$ 11.0 mE $^{-2}$ min^{-1}) which permit growth of higher algal biomass before self-shading. In contrast, algal biomass was low offshore because the deeper mixed layer leads to light deficiency, as indicated by $I_K/I_{24} < 1$, most of the year. In the modern Lake Victoria, the euphotic depth is often $\leq$ 10 m offshore and is half as shallow inshore (Chapter 4), and stratification is necessary to create a good light environment for planktonic algae. But mixing depths are always $\geq$ 20 m at Bugaia and compatible with only low algal biomasses as light limits photosynthesis over most of mixing layer.

Total cyanobacteria, N-fixer and heterocyst biomass as well as chlorophyll-a varied seasonally, but similar temporal trends occurred at inshore and offshore sites. Variation in algal biomass was likely a result of combined effects of the mixing and thermal stratification regime which cause changes in nutrient concentrations (Hecky 1993, Hecky et al. 1996) and underwater light conditions (Chapter 4). In Lake Victoria, light-limited algal crops generally coincide with minor and deeper mixing periods. As mixed layer depths increase, for example on de-stratification in April-May and during strong mixing in June-July (Chapter 1, 3), the mean water column irradiances become very low (2-5 mE m^{-2} min^{-1}) leading to diminished total cyanophyte and chlorophyll-a concentrations. Guildford and Hecky reported (1984) reported light limitation of phytoplankton growth at similar I_{24}.

Light deficiency with possibly enhanced N availability during destratification and deep mixing may be largely responsible for the decline of the heterocyst and N-fixation processes that require energy. N-fixation requires both ATP and a source of reducing power (reductant) such as NADH and NADPH. Photosynthesis provides much of this energy and reductant from new organic matter production when carbon and N-fixation occurs contemporaneously (Turpin 1991). Lack of sufficient recent photosynthate or stored carbon due to severe light limitation may lead to a reduction of diazotrophic activity and subsequent reductions in total cyanophyte biomass as observed in Lake Victoria. A decline in N-fixer and heterocyst biomasses due to inadequate light energy seems likely given that light can be the overwhelming constraint to phytoplankton production in Lake Victoria (Mugidde 1992, 1993). Lehman et al. (1998) inferred from modeling and experimental approaches that when mixing depth equals or greatly exceeds the critical depth, 5-18 m, defined as depth where net primary production above that point is balanced by respiration, algal growth ceases and biomass levels decline in Lake Victoria. The critical depth of 5-18 m at Bugaia far exceeds the Z_{mix}/Z_{eu} values of 4-5 that result in light limitation (Talling et al. 1971). These results are consistent with observations from other Great Lakes of the world, such as Lakes Superior, Ontario, Erie and Michigan, where inadequate light due to deep mixing constrains phytoplankton growth and influences algal species during winter mixing (Fahnenstiel et al. 2000, Reynolds et al. 2000, Guildford et al. 2000).

The low cyanobacteria and chlorophyll-a abundances in June-July were not a result of nutrient deficiency as both N and P deficiency were alleviated inshore and offshore. Nutrient limitation was absent because deeper mixing causes low light availability at this time and entrains higher nutrient concentrations (Talling 1986). It also re-oxygenates deeper waters (Hecky et al. 1994) eliminating the anoxic-oxic interface that prevents ammonium diffusion from the hypolimnion (Hecky et al. 1996). Reduced N loss via denitrification and increased N fluxes delivered into the euphotic zone during destratification result in no N-deficiency in June-July as indicated by the low C: N ratios (< 8.3) in both inshore and offshore surface waters. Consequently, the diazotrophic activity may also be less because other N sources, such as ammonium and nitrate, are adequate at this time of the year. The preferential uptake of dissolved inorganic N, if present in abundance, inhibits N-fixation and is an adaptation resulting in energetic savings due to the higher energy requirements for N-fixation (Reuter 1988, Turpin 1991, and De Nobel et al. 1998).

Elevated algal biomass during the early to mid-stratification period were likely a result of increased water thermal stability (Wedderburn number > 1.0). Stratification improves light conditions between September and December and induces nutrient deficiency, especially inshore, which favors N-fixing species and cyanobacteria to grow and accumulate. Diffusion of DIN from the hypolimnion is prevented by denitrification at the anoxic-oxic interface in the water column (Hecky et al. 1994, 1996). Consequently, N-deficiency becomes frequent and leads to the maintenance of N-fixing cyanobacteria. Better light environment inshore because of shallow mixing depths may compensate for P-deficiency, while maintaining the N-deficit and allowing higher N-fixers and heterocysts biomasses than offshore. Healey (1975) found from culture experiments that algae reduce their need for P as light becomes more available. At this time of the year, excess P at Bugaia can readily be assimilated into new algal biomass as

N-fixation provides the required N. Only further inshore does soluble reactive P fall to low values suggesting P-deficiency.

The lower N-fixer and heterocyst biomasses between January and April, given the simultaneous increase in the light resource and increased N demand, suggests that light and macronutrients interactions may not be the only factors influencing algal biomass production in Lake Victoria. It is possible that algal biomass production can be constrained by availability of micronutrients, especially Fe that plays a crucial role in nitrogen and carbon metabolism of cyanobacteria (Reuter 1988, 1991, Kudo et al. 2000, Guildford et al. 2001). Iron has been found to influence phytoplankton photosynthesis, growth and biomass in freshwater lakes (Twiss et al. 2000) and marine environments (Kudo et al. 2000, Fitzwater et al. 2000, Watson et al. 2000). In oceanic environments, deficiency of bio-available iron leads to low chlorophyll-a concentrations despite high nutrient concentration (Pichford and Brindley 1999). Because of iron's low solubility in oxic conditions (Stal et al. 1999), it may limit N-fixation and algal growth in the oxygen-saturated surface waters of Lake Victoria, with its long water residence time in excess of a century. Anoxic deep water can lead to removal of Fe to the sediments as iron sulfide.

Iron is biochemically involved in nitrogen metabolism as it forms part of the nitrogenase complex and is necessary for N-fixation even when anoxic conditions and appropriate energy resources are established (De Nobel et al. 1998, Howarth and Marion 1999). In Lake Victoria, prolonged thermal stratification may raise the opportunity for epilimnetic trace metal depletion as iron and molybdenum are often depleted from stratified epilimnia of lakes (Coale at al. 1996). Guildford et al. (2001) were able to demonstrate iron stimulation of algal growth and N-fixation in lakes Victoria and

Malawi. The role of trace metals in phytoplankton dynamics of the African Great Lakes, in particular Lake Victoria, needs further investigation as factors that affect micronutrients supply rate, chemical speciation or recycling can alter algal biomass production as well as species composition.

In addition to other factors, nutrients and light availability drive the phytoplankton species composition of the modern Lake Victoria. The higher P loads relative to N from the catchment (Hecky 1993, Lipiatou et al. 1996) and resultant high concentrations of total P (> 2.0 μM) has doubtlessly contributed to the dominance of cyanobacteria in Lake Victoria (Kling et al. 2001). As well, light and nutrient availability also determine temporal variation of individual species. When thermal stratification raises light availability and N-demand, the heterocystous N-fixing cyanobacteria, *Cylindrospermopsis* and *Anabaena* dominate other cyanobacteria. Dominance by the heterocystic N-fixing cyanobacteria is maintained until N-deficiency is ameliorated by N-fixation and remineralization, the introduction of N from other sources, or until light becomes limiting because of shading by algae or deep mixing. The high abundance of the *Anabaena* inshore and during periods of thermal stability may be related to the simultaneous effects of N-deficiency and high light. *Anabaena* is a "sun" species with high light requirements and has been shown to competitively displace other species under saturating irradiances in N-limited culture experiments (Nobel et al. 1998). *Cylindrospermopsis* is a low light species that will be abundant with the small and fast growing non-nitrogen fixing species that tend to dominate offshore where deeper mixing and light limitation can slow the grow rate of the large heterocystous N-fixers.

The finding that pronounced and prolonged blooms of cyanobacteria, including the toxic species *Cylindrospermopsis, Anabaena* and *Microcystis,* were associated with lake characteristics of thermal stratification, high light and increasing total N, can be useful in predicting the occurrence of nuisance and toxic bloom events in Lake Victoria. It is important that environment factors associated with the continued presence of toxic cyanobacteria be investigated further as phycotoxin production has been confirmed in Lake Victoria (H. Kling, FWI, Winnipeg). Phycotoxin effects may already be having adverse consequences on the productivity of the fishery and may be responsible for some of the massive fish kills that frequently occur in Lake Victoria. Elsewhere, cyanobacterial microcystin toxins have been demonstrated to alter the hatching time of rainbow trout and adversely affect the survival, growth and morphology of zebrafish (Oberemm et al. 1999). Microcystin toxins have been shown to slow down zooplankton growth, and Daphnia can potentially transfer toxins to higher trophic levels in the aquatic food (Thostrup et al. 1999). The continued presence of toxic cyanobacteria and toxin production are a serious concern for water and fisheries managers as well to the lakeside communities who heavily depend on lake for fish food and drinking water. Airborne microcystin can directly affect people, especially when showering and also when on the water during algal blooms (Kotak et al. 1994, Dunn, 1996,).

The strong and significant relationship between heterocysts and volumetric N-fixation permitted prediction of daily and annual integral rates that were consistent with measured rates of N-fixation. N-fixation predicted from heterocysts abundance and light extinction, can be used to estimate lakewide N-fixation given that predicted daily rates of N-fixation had similar spatio-temporal patterns as measured rates and were of similar magnitude. Acquisition of data on heterocyst abundance and light attenuation with limited seasonal measurements of N-fixation provide an alternative and less expensive alternative for estimation of lakewide N-fixation. This model can also be used to predict the timing of heterocystic cyanobacterial blooms that may allow water treatment plants to alter their intake locations or strategically add additional water treatment such as ozonation.

In summary, results from this study show that Lake Victoria supports a large cyanobacteria crop dominated by heterocystous N-fixers through much of the annual cycle. Its eutrophic character due to high P loading (Hecky 1993), and being a high N sink (Hecky et al 1996), are largely responsible for the dominance of cyanobacteria today (Kling et al. 2001). Circumstantial evidence indicates that light (Mugidde 1992, chapter 4) and nutrient availability (chapters 3, 4, 5) were two important factors influencing total cyanophyte biomass as well as N-fixer and heterocysts biomass production in Lake Victoria. Biomass of heterocystous and non-heterocystous cyanobacteria were higher during the stratified phase when light was adequate, but were limited under conditions of light-deficiency caused by deep water-column mixing offshore or self shading inshore. As heterocyst biomass increased, rates of N-fixation increased proportionally and so did concentrations of total N. This allowed algal biomass increases and blooms to proliferate in the surface waters. N-fixation was successfully predicted when calculated N-fixation parameters were substituted with values predicted from heterocyst biomass because of the strong relationship between heterocysts and N-fixation. Heterocyst biomass can be used to infer N-fixation and N-availability in Lake Victoria and as guide to water resource management in the lake.

Chapter 6: General summary and conclusion

Summary

1. During the period of study, 1994-1998, the persistent eutrophic condition of Lake Victoria was indicated by water column characteristics of high concentrations of P and N, elevated total phytoplankton biomass (as chlorophyll-a) and total cyanobacteria biomass (as biovolume), reduced water transparency, hypolimnetic anoxia and frequent cyanobacterial blooms.
2. Total P concentrations were of the same order of magnitude (1.5-12 μM), average 2.6-3.1 μM, in both inshore and offshore surface waters. Increased P was released into the water column at Bugaia when the lake was deeply and strongly mixing (July-August), and concentrations remained high until periods of re-stratification in September. However, average total N concentrations in the range 37 μM to 106 μM were three times higher inshore than offshore. Maximum total N concentrations occurred during periods of shallower mixing and coincided with elevated rates of planktonic N-fixation in September-December.
3. Deoxygenation of bottom waters of Lake Victoria has become extensive and now occurs in the shallow inshore bays, such as Napoleon Gulf, for most the year. Extensive anoxic conditions were associated with high water column stability (Wedderburn number >1.0), that restricted dissolved oxygen exchange between surface and bottom waters leading to hypolimnetic anoxia. Once Lake Victoria becomes thermally stable, its bottom water is depleted of dissolved oxygen.
4. Surface inshore waters had higher phytoplankton biomasses and rates of N-fixation than offshore. Chlorophyll-a concentrations and total cyanobacteria, N-fixer and

heterocyst biomass were, respectively, 5x, 6x, 8x and 5x higher inshore than offshore because light was often inadequate for algal growth offshore. Inshore regions are the shallower parts of the lake that are compatible with potentially higher mean water column irradiances and will have denser algal populations before and when self shading occurs. Inshore waters also have faster nutrient regeneration from sunken particulate organic matter as a larger proportion of the epilimnetic waters are in contact with the bottom sediments. Therefore, nutrient regeneration to the euphotic zone is more effective inshore than offshore. However, P regeneration may be more efficient than N due to denitrification under low oxygen conditions.

5 Relatively low chlorophyll-a concentrations and cyanobacteria biomasses in June-July are due to low light as indicated by $I_{24}/I_K < 1.0$, accompanying full water column mixing, rather than nutrient supply or heavy grazing. De-stratification in April-May, and complete circulation brought about by surface cooling around July, lowers the mean water column irradiances (2-5 mE m^{-2} min^{-1}) to less than the threshold I_k that indicates light saturation. Previous studies document grazing pressure by the zooplankton as insufficient to control algal biomass and this may partly be responsible for accumulation of particulate nutrients. At all sites investigated, particulate organic P and N were the most abundant form of P and N most of the year, suggesting loss terms must be low. The dominant cyanobacterial species have low sinking rates and can modify their buoyancy through gas vacuolation which further allows accumulation of biomass in the upper water column.

6 Changes in nutrient availability, as indicated by particulate nutrient ratios and dissolved inorganic nutrients concentrations, were related to the mixing and thermal

conditions in the lake. Increased P and N-deficiency occurred during periods of stable thermal stratification. There are three reasons why P and N availability were lower during the stratified period. First, thermal stratification restricts nutrient supply from the hypolimnion to the epilimnion. Second, the oxic-anoxic interface in the water column promotes N loss via denitrification (Hecky et al. 1996) further reducing regeneration of DIN and raises the potential for N-deficiency. Third, improved light conditions as indicated by $I_K/I_{24} > 1.0$ allow accumulation of elevated algal biomasses before self-shading. High consumption of dissolved inorganic nutrients by elevated algal biomasses results in increased P and N-deficiency, especially inshore where highest algal biomasses occur.

7 Offshore, TN:TP deviations from balanced N and P concentrations tended to be small based on the average molar ratio of 16. Offshore, approximately 33% of the particulate N:P ratios and 29% of the C:N ratios were in excess of Healey and Hendzel (1980) cutoff values indicative of severe P and N-deficiency. Inshore, 58% of the observations of particulate ratios indicated severe P-limitation and 21% N-limitation. The higher maximum particulate N:P ratios of 80 and 32 at inshore and offshore, respectively indicate that P-deficiency can be more severe inshore than offshore. In contrast, C:N ratios were as high as 18 and 12 at offshore and inshore, respectively, indicating that N-deficiency can be more severe offshore than inshore.

8 P and N deficiency were relaxed in June-July partly because of reduced demand from algal growth because of increased light limitation and because of entrainment of nutrient-rich hypolimnetic waters due to stronger mixing. Although stronger and deeper mixing relaxes nutrient deficiency, it results in severe light deficiency that

constrains algal biomass production. These low algal biomasses leave most of the new dissolved inorganic nutrients unutilized.

9. Offshore, algal biomass production was often suppressed by light limitation as P and N-deficiency were less frequent and SRP was often in excess of 1.0 μM. High P concentrations created an N-demand that was often met through internal cycling within the mixed water column if biomass was low. The higher $\delta\ ^{15}N$ of particulate organic matter (POM) offshore (average = 8.9) results from recycling of N which was adequate to meet the low N demand. The high delta $\delta\ ^{15}N$ of POM implies that internal cycling processes, rather that N-fixation, contributed the larger fraction of N-demand offshore.

10. The low N availability relative to P in surface waters was partly a result of P return from the low-oxygen hypolimnetic waters, especially offshore. Enhanced N loss relative to P due to differential recycling efficiencies can also be an explanation for the recurrent low N:P ratios in surface waters during mixing. These low N:P ratios select for dominance by cyanobacteria during stratification and are dictating the dominance of N-fixers and heterocyst biomass production in Lake Victoria. Nevertheless, high N input by the N-fixing cyanobacteria often redressed the low N availability, as indicated by the high N:P ratios and low C:N ratios, especially in inshore surface waters.

11. Two prominent ecological groups of cyanobacteria were recognized: (i) the large heterocystous N-fixing cyanobacteria, *Anabaena* and *Cylindrospermopsis*, known for their high light requirements, and, therefore, achieving their maximum abundances during improved light conditions when the lake was stratified. N-fixing

cyanobacteria were most abundant and contributed the greatest proportion ($\geq$ 80%) to the total cyanophyte biomass maxima in October in Napoleon Gulf. Offshore at Bugaia, N-fixing cyanobacteria comprised a smaller proportion ($\leq$ 40 %) of the total cyanophyte biomass most of the year, except in October-November and in May. (ii) Small-celled coccoid species dominated other cyanobacteria most of the year and contributed significantly (>60 %) to the total cyanobacteria biomass maxima offshore.

12. N-fixation was carried out by the autotrophic heterocystous N-fixing cyanobacteria, as rates of N-fixation were highly correlated with biomass of heterocystous N-fixing cyanobacteria. Heterocysts were the best prediction of N-fixation and their strong and significant relationship allowed development of a simple and sensitive N-fixation model that correctly predicted the magnitude and spatio-temporal patterns of rates of N-fixation. This model provides a useful tool for estimating lakewide N-fixation and is also a promising tool for predicting the timing of potentially toxic cyanobacteria blooms.
13. Higher diazotrophic activity inshore than offshore was indicated by three pieces of evidence. First, volumetric and areal rates of N-fixation were respectively 8 and 2 times higher inshore than offshore. Second, the higher N-fixer and heterocyst biomass indicated higher diazotrophic activity inshore than offshore. Third, the 3- to 6-fold lower $\delta\,^{15}N$ of POM inshore than offshore provided further evidence of reduced diazotrophic activity offshore. Low $\delta\,^{15}N$ was consistent with enhanced N-fixation inshore, because N-fixation of atmospheric N_2 with $\delta\,^{15}N$ of zero dilutes the $\delta\,^{15}N$ of POM .

14. The simultaneous effects of nutrient and light availability affected N-fixing cyanobacteria and heterocyst biomass as well as rates of N-fixation. Biomass of N-fixing cyanobacteria were elevated when Wedderburn numbers were increasing or near maximum and the lake was stably stratified. Thermal stratification permitted better light conditions through reduced depth of the mixing layer, and increased N deficiency and diazotrophic activity. With falling Wedderburn numbers, nutrient deficiency and light sufficiency decreased and diazotrophic activity decreased in concert.
15. Later in the stratified period (January-April), N-fixation as well as N-fixer and heterocyst biomass were lower than expected from considerations of the N-demand by the algae. Low N-fixation and biomass may, in part, be a consequence of low light availability due to the progressive deepening of the thermocline from January until complete mixing in June-July. With lower, light-limited N-demand for phytoplankton growth recycling of previously fixed N can satisfy the N-demand during this period. Trace metal limitation, in particular Fe, has been hypothesized as a possible factor that could limit diazotrophic activity at this time of the year.
16. Rates of N-fixation in Lake Victoria were among the highest when compared to literature values from tropical and temperate freshwater lakes. Although biological N-fixation contributed a small fraction (1-20 %) of the daily N-demand because recycled N met most of the N-demand, it constituted approximately 80% of the total annual N input into Lake Victoria. However, this high N income may almost be balanced by high annual N-loss via denitrification due to persistent hypolimnetic anoxia. Denitrification and stratification synergistically contribute to the maintenance

of N-limitation in Lake Victoria.

Conclusions

A combination of light and nutrient limitation regulates phytoplankton biomass, species composition and rates of N-fixation in Lake Victoria. Emerging evidence from particulate nutrient ratios shows that both P and N were only temporarily limiting, but light limitation ultimately controls phytoplankton biomass production and rates of N-fixation, especially in offshore areas and when the lake was mixing. These finding are not surprising, as historic studies have suggested N limitation, and various modern studies have inferred or indicated that N and P were potentially limiting in Lake Victoria. The current study shows how patterns of nutrient and light availability are related to water column stability, and how they may influence biological variables. This also adds more to our knowledge of phytoplankton biomass and species composition. It provides the most detailed data available on nutrient and light status, and new information on spatio-temporal variability of N-fixation in Lake Victoria.

Circumstantial evidence allows the general conclusion that thermal stratification and destratification exert considerable influence on light availability, which in turn controls phytoplankton biomass, and biomass, in turn, controls nutrient availability in Lake Victoria. Phosphorus limitation was stronger inshore where maximum algal biomasses occur than offshore as indicated by the high elemental particulate N:P ratios. The TN:TP ratio, used as indicator of P-status, indicated that P was potentially a system limiting factor, especially in the shallow inshore regions of the lake. This observation is not in conflict with findings that anthropogenic nutrient supply is enriched with P relative to N (Hecky 1993, Lehman et al. 1998), and therefore low N:P ratios are expected in Lake Victoria. The low N:P loading ratios are counteracted by biological buffers and mechanisms that include changes in algal species composition and N-fixation. High N input via fixation modifies N:P ratios and frequently drives the phytoplankton community to conditions of P-deficiency, as indicated by high N:P ratios, especially inshore. N-deficiency fuels proliferation of nuisance N-fixing cyanobacteria blooms that reach their maximum abundances during the stratified period. High N income via N-fixation often alleviates N limitation, but high organic loading to the hypolimnion enhances denitrification (Hecky et al. 1996) along the persistent mid water column oxic-anoxic interface and serves as an important N sink that is equilibrium with N-fixation in the lake today (Chapter 4). N and P deficiency are infrequent and rarely extreme because of self shading. Shading most often determines upper level of biomass concentrations. Further P and N loading will only aggravate algal blooms by promoting higher concentrations in the shallower areas of the lake. Nutrient reductions will not reduce productivity but would reduce incidences of algal blooms and might cause shifts to less obnoxious algal species.

Nutrient enrichment has had both detrimental and beneficial effects in Lake Victoria. Increased nutrients stimulate high algal N-and C-fixation which provide the required new production that maintains the current high fish production in Lake Victoria. Increased algal primary productivity has likely contributed to increased fish production, although we cannot attribute the higher fish yields only to higher production since fishing effort has also expanded. Increased fish production is beneficial to the people in the region as a source of affordable animal protein, and the fish industry provides job opportunities to all gender groups. Fish yields that are 5 times higher than in the 1960s and that exceed 500,000 tonnes (Ogutu-Ohwayo et al. 1996) provide a major export that is economically important to the three riparian states. Despite that there is no direct evidence that eutrophication may be damaging the fisheries, there is great concern that fish production may not be sustainable because of the already poor water quality of Lake Victoria. Already, fish are restricted to the shrunken aerobic surface waters and more productive inshore waters where they are heavily over-exploited. This along with other effects of eutrophication, in particular the proliferation of cyanobacteria known to be poor quality food, threaten sustainable fish production in Lake Victoria. Of great concern are the increased frequency of harmful algal species that form conspicuous blooms which become positively buoyant and aggregate into large visible patches in surface waters. Blooms of cyanobacteria have received much attention due to their interference with abstraction and treatment of drinking waters, and their possible toxicity that may be responsible for some of the fish kills that occur in Lake Victoria today.

Application of results

It has been recognized that remedial action to mitigate eutrophication of Lake Victoria requires concerted regional and international effort. Regional management and research efforts are being provided by the Lake Victoria Fisheries Organization (LVFO) and Lake Victoria Environmental Management Project (LVEMP). Progress so far is in the right direction as tripartite environmental management agreements have been signed and relevant watershed and in-lake studies are ongoing. This study contributes to common strategies of eutrophication control measures based on reduction of nutrients that limit algal biomass production as the most efficient option. Current studies confirm that both P and N are limiting in particular places and particular times and contribute to the eutrophication of Lake Victoria. Consequently, reductions of both P and N are essential in the control of nuisance cyanobacteria blooms and ultimate reversal of eutrophication that threatens the ecosystem health of Lake Victoria. Even though N is the limiting element, it can enter from the atmosphere through biological N-fixation (Chapter 4) as long as P and light allow. Therefore, direct N reduction is practically difficult and ineffective, and its reduction may result in even increased frequency of potentially toxic species such as *Cylindrospermopsis*, *Anabaena* and *Microcystis*.

Reduction of P load is the most efficient and feasible option for reducing eutrophication effects and ultimately, restoring Lake Victoria. P reduction is practical, as P is not maintained by equilibrium with an infinite atmospheric reservoir as N is. P reduction will lead to reductions in algal biomass and will also lessen the N demand that favors growth of the harmful toxic cyanobacteria in the modern Lake Victoria. Reductions in algal biomass will improve the water quality and possibly increase algal productivity. This is possible as reductions in algal biomasses will result in improved light conditions and primary productivity, that would be maintained over a greater depth range and, capable of maintaining the high fish yields or even supporting increased fish production in Lake Victoria. The fact that anthropogenic nutrient supply to Lake Victoria has increased (Hecky 1993, Lipiatou et al. 1996) and atmospheric nutrient chemistry has changed over the African Great Lakes including Lake Victoria (Bootsma 1993, Bootsma and Hecky 1998) is useful information for management of Lake Victoria today. Recent studies indicate that rainfall contributes approximately 5 kt per year of TP into Lake

Victoria (Chapter 4) and rivers almost twice as much. Total N income through rainfall was approximately 83 kt year^{-1} and half as high entered through rivers. Atmospheric deposition is recognized as a potentially large source of inorganic P and N to Lake Victoria (R. Tamahtamah, U of Waterloo, personnel communication). These nutrients can stimulate productivity of bacteria and phytoplankton production in Lake Victoria. The nutrient load via precipitation is magnified as rainfall accounts for >90% of water budget of Lake Victoria.

These high nutrient loads are characteristic of disturbed watershed where extensive agriculture and land clearing are common (Bootsma and Hecky 1999, Carignan et al 2000). Based on the above information, nutrient reduction into Lake Victoria requires reduction of direct and indirect anthropogenic loads that contribute to enrichment of rivers and to modification of the precipitation chemistry of Lake Victoria. Reduction of nutrient loads requires watershed management and good soil conservation practices aimed at reducing extensive vegetation clearing, soil erosion and vegetation burning. In addition, municipal and industrial effluents should reduced to acceptable nutrient concentrations and ratios so to reduce local proliferation algal biomass and weeds, such as water hyacinth.

Management strategies to protect water quality of Lake Victoria should give high priority to actions that control nutrient loads into the lake. Management strategies should also give consideration to other stressors that include exotic species and habitat loss. Effective watershed management should involve educational programs aimed at sensitizing the local people as to how their activities including intense subsistence crop farming, animal husbandry, mining and releasing of waste products, change the atmospheric and river chemistry, which in turn impact water quality and aquatic biota. Unless local people recognize the adverse impacts of their uncontrolled soil erosion and generation of waste products and take action to reduce the nutrient emissions, eutrophication reversal will be difficult to achieve. Recognition by the riparian governments and water resources managers that safe fish production and clean water for humans and animals requires a Lake Victoria that is free of pollutants and toxins is already progress in the right direction. As the catchment of Lake Victoria is beyond the three riparian countries, countries beyond the lake borders should be encouraged to participate in remedial actions. Management effects are expected to be rather slow given the large catchment and the great diversity in the degree of economic development of the lake-basin countries, with corresponding differences in according priority to environmental protection.

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Appendices

Appendix 1. Minimum, average and maximum Wedderburn numbers (W) for offshore (Bugaia) Lake Victoria, during 1994-998.

Date	Wedderburn number (W)
30-May-94	1.6
10-Jun-94	0.3
29-Jun-94	0.9
26-Jul-94	0.9
27-Jul-94	0.8
01-Sep-94	1.0
28-Sep-94	0.7
29-Sep-94	0.8
29-Oct-94	0.8
30-Oct-94	0.7
23-Nov-94	1.4
24-Nov-94	0.2
01-Feb-95	0.5
02-Feb-95	1.2
03-Mar-95	2.3
05-Mar-95	3.6
05-May-95	2.9
21-May-95	1.9
12-Jul-95	1.3
13-Jul-95	1.0
31-Aug-95	0.5
01-Sep-95	0.8
20-Oct-95	0.6
21-Oct-95	0.6

Appendix 1 (continued)

Date	Wedderburn number
20-Dec-95	3.6
21-Dec-95	2.5
26-Jan-96	2.1
27-Jan-96	2.7
06-Apr-96	1.1
21-Jun-96	0.2
22-Jun-96	0.1
27-Oct-96	2.6
23-Mar-98	1.0
10-Apr-98	0.2
31-Jul-98	0.7
30-Sep-98	3.1
03-Nov-98	1.7
26-Nov-98	1.8
11-Dec-98	1.2
Overall minimum	0.1
Overall average	1.3
Overall maximum	3.6
Std	1.0
N	39

Appendix 2. The daily N-demand of inshore stations (Napoleon Gulf (NPL), Buvuma Channel (BUV), Pilkington Bay (PLK), Itome Bay and offshore at Bugaia (BUG) during 1998. The daily N-demand was calculated from the reciprocal of the C:N molar ratios and average phytoplankton carbon fixation (0.57 moles C.d^{-1}) for Lake Victoria. The percentage daily N-fixation contribution to the daily N-demand = (N-fixation per day/Daily N-demand) x 100.

Date	Station	C:N ratio (molar)	Daily N-demand (in moles)	Daily N-demand (mg N m^{-2} d^{-1})	Daily N-fix (mg N m^{-2} d^{-1})	N-fix/N-demand (%)
29-Jan-98	NPL	6.9	0.08	1151	24	2.1
10-Feb-98	NPL	6.4	0.09	1248	30	2.4
26-Mar-98	NPL	7.8	0.07	1027	16	1.6
10-Apr-98	NPL	6.9	0.08	1151	12	1.0
27-May-98	NPL	6.9	0.08	1164	35	3.0
26-Jun-98	NPL	6.8	0.08	1177	12	1.0
23-Jul-98	NPL	6.8	0.08	1177	12	1.0
24-Aug-98	NPL	9.0	0.06	888	27	3.0
22-Sep-98	NPL	6.0	0.09	1326	172	13.0
22-Oct-98	NPL	12.0	0.05	501	101	20.2
04-Nov-98	NPL	7.0	0.08	1142	115	10.1
13-Dec-98	NPL	5.6	0.10	1422	15	1.1
02-Feb-98	BUV	7.7	0.07	1042	47	4.5
26-Mar-98	BUV	6.1	0.09	1318	20	1.5
09-Apr-98	BUV	8.0	0.07	1000	36	3.6
30-May-98	BUV	8.7	0.07	919	13	1.4
27-Jun-98	BUV	8.0	0.07	999	13	1.3
25-Aug-98	BUV	6.5	0.09	1235	16	1.3
09-Sep-98	BUV	6.8	0.08	1180	195	16.5
22-Oct-98	BUV	7.2	0.08	1110	169	15.2
24-Nov-98	BUV	6.8	0.08	1177	37	3.1

Appendix 2 (continued)

Date	Station	C:N ratio (molar)	Daily N-demand (in moles)	Daily N-demand (mg N m^{-2} d^{-1})	Daily N-fix (mg N m^{-2} d^{-1})	N-fix/N-demand (%)
11-Dec-98	BUV	6.8	0.08	1176	19	1.6
02-Feb-98	PLK	6.3	0.09	1259	16	1.3
27-Mar-98	PLK	6.9	0.08	1162	29	2.5
10-Apr-98	PLK	7.1	0.08	1119	15	1.3
27-May-98	PLK	9.3	0.06	859	8	0.9
23-Jun-98	PLK	6.7	0.09	1195	14	1.2
24-Aug-98	PLK	6.6	0.09	1204	12	1.0
22-Sep-98	PLK	7.3	0.08	1100	142	12.9
24-Nov-98	PLK	7.2	0.08	1115	53	4.8
13-Dec-98	PLK	5.3	0.11	1501	18	1.2
16-Mar-98	Itome	8.5	0.07	940	28	3.0
31-Jul-98	Itome	6.9	0.08	1156	8	0.7
10-Sep-98	Itome	7.5	0.08	1062	103	9.7
30-Sep-98	Itome	6.8	0.08	1175	124	10.6
27-Oct-98	Itome	6.6	0.09	1214	27	2.2
26-Nov-98	Itome	7.0	0.08	1143	50	4.4
11-Dec-98	Itome	7.0	0.08	1141	22	1.9
16-Mar-98	BUG	9	0.04	609	9	1.5
11/26/98	BUG	7	0.05	732	18	2.5
16-Feb-98	BUG	8.0	0.05	665	56	8.4
16-Mar-98	BUG	8.2	0.05	647	56	8.7
08-Apr-98	BUG	6.3	0.06	851	24	2.8
29-May-98	BUG	7.3	0.05	732	19	2.6
07/31/98	BUG	6.0	0.06	885	12	1.4
08/31/98	BUG	8.2	0.05	651	23	3.5

Appendix 2 (continued)

Date	Station	C:N ratio (molar)	Daily N-demand (in moles)	Daily N-demand (mg N m^{-2} d^{-1})	Daily N-fix (mg N m^{-2} d^{-1})	N-fix/N-demand (%)
09/30/98	BUG	9.1	0.04	582	26	4.5
10/27/98	BUG	5.9	0.06	909	15	1.7
11/26/98	BUG	11	0.03	484	18	3.7
12/11/98	BUG	6.4	0.06	825	27	3.3
01-Sep-94	BUG	8.9	0.04	598	15	2.5
29-Sep-94	BUG	8.0	0.05	662	15	2.3
30-Oct-94	BUG	7.9	0.05	676	15	2.2
25-Nov-94	BUG	7.6	0.05	697	18	2.6
06-May-95	BUG	9.1	0.04	585	9	1.5
21-May-95	BUG	7.9	0.05	672	9	1.3
13-Jul-95	BUG	6.9	0.06	774	8	1.0
21-Oct-95	BUG	7.9	0.05	672	15	2.2
01-Sep-95	BUG	8.4	0.05	635	26	4.1
01-Nov-95	BUG	17.2	0.02	309	18	5.8
28-Jan-96	BUG	7.5	0.05	705	20	2.8
06-Apr-96	BUG	8.0	0.05	667	20	3.0
08-Oct-97	BUG	7.8	0.05	682	15	2.2
Overall average						3.9
Overall minimum						0.7
Overall maximum						20.2
N						63